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Cultural Practices for Prevention and Mitigation of Mountain Pine Beetle Infestations

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In recent years, the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, has impacted >8.9 million hectares of forests in the western United States. During endemic populations, trees weakened by other agents are often colonized by *D. ponderosae* but may be difficult to detect due to their scarcity. Once populations reach incipient levels, tree defenses are often insufficient in deterring mass attacks, and populations rapidly increase causing substantial levels of tree mortality under certain circumstances. There are two general approaches for reducing the negative impacts of *D. ponderosae* on forests. Direct control involves short-term tactics designed to address current infestations by manipulating beetle populations and includes the use of fire, insecticides, semiochemicals, sanitation harvests, or combinations of these treatments. Indirect control is preventive and designed to reduce the probability and severity of future infestations by manipulating stand, forest and/or landscape conditions by reducing the number of susceptible host trees through thinning, prescribed burning, and/or alterations of age classes and species composition. We review tree, stand, and landscape factors associated with *D. ponderosae* infestations and analyze the effectiveness of treatments for preventing and mitigating undesirable levels of tree mortality. We describe the current state of our knowledge and identify gaps for making informed management decisions.

Keywords: *Dendroctonus ponderosae*, direct control, indirect control, *Pinus contorta, Pinus ponderosa.*

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a major disturbance in conifer forests of western North America where it colonizes several tree species, most notably, lodgepole pine, *Pinus contorta* Dougl. ex Loud., ponderosa pine, *P. ponderosa* Dougl. ex Laws., sugar pine, *P. lambertiana* Dougl., limber pine, *P. flexilis* E. James, western white pine, *P. monticola* Dougl. ex D. Don, and whitebark pine, *P. albicaulis* Engelm. (Gibson et al. 2009). Recent outbreaks have been severe, long lasting, and well documented (Bentz et al. 2009). Historically, the occurrence of episodic outbreaks of *D. ponderosae* was not usual, but the magnitude and extent of recent outbreaks may have exceeded the range of historic variability in some cases and have occurred in areas where outbreaks were less common (e.g., *P. albicaulis* forests, Logan et al. 2010). While *D. ponderosae* is an important part of the ecology of these forests, extensive levels of tree mortality resulting from outbreaks may have undesirable impacts, e.g., negatively affecting esthetics, recreation, fire risk and severity, human safety, timber production, and real estate values, among many other factors. The nature and extent of these impacts depends primarily on the resources affected and how they are valued by society, and by the extent and severity of the outbreak. Traditionally, impacts were defined based on the value of forest products (timber) lost. Today, forest uses and the diversity of stakeholders involved are much more diverse, and society's perceptions of the impacts of *D. ponderosae* outbreaks have changed as has the acceptability of some management techniques (Orcherton 2008). Our objective is to review factors associated with *D. ponderosae* infestations and to analyze the effectiveness of cultural practices for preventing and mitigating undesirable levels of tree mortality attributed to *D. ponderosae*. While our synthesis concentrates on the western United States, specifically the Intermountain West, we draw heavily from research conducted and practical experience gained throughout western North America.

Interactions between *Dendroctonus ponderosae* and Host Trees

When actively searching for host trees, adult bark beetles maintain limited energy reserves (Atkins 1966) and are highly susceptible to predation, starvation, and adverse weather conditions. Therefore, it is important that susceptible hosts be located with efficiency, a process primarily mediated by semiochemicals in many bark beetle

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species. Progar et al. (2014) synthesize information related to the chemical ecology of *D. ponderosae* relevant to host finding, host selection, host colonization, and mating behaviors. A thorough comprehension of these and related topics is important to understanding how *D. ponderosae* coordinates attacks within forests at various spatial scales and how this influences forest susceptibility and levels of tree mortality, but is beyond the scope of our synthesis. Accordingly, we encourage the reader to review Progar et al. (2014) and other works relevant to these topics (e.g., Logan et al. 1998).

Once a tree is attacked, successful colonization requires overcoming tree defenses that consist of anatomical and chemical components that are both constitutive and inducible (Franceschi et al. 2005). This can only be accomplished by recruitment of a critical minimum number of beetles to "mass attack" the tree and overwhelm host defenses (Raffa et al. 1993). This number varies with changes in host tree vigor (Keen 1936, Larsson et al. 1983) as more vigorous hosts required higher densities of beetles to overcome host defenses. Most hosts of *D. ponderosae* have well-defined resin duct systems, which are capable of mobilizing large amounts of oleoresin following wounding (Christiansen et al. 1987, Huber et al. 2004). This is considered the primary defense of conifers against bark beetle attack (Vité 1961, Reid et al. 1967). Beetles that initiate host selection are often killed by drowning or immobilization in resin (termed "pitch-out") especially when adequate moisture, flow, and oleoresin exudation pressure exist (Raffa and Berryman 1983). Based on research conducted in British Columbia, Canada, Boone et al. (2011) reported *P. contorta* trees that exuded more resin and accumulated higher monoterpene concentrations in response to simulated attacks [a 1.0-cm diameter hole bored into the tree and inoculated with *Grosmannia clavigera* (Robinson-Jeffrey & R.W. Davidson)] largely escaped successful attacks by *D. ponderosae* when populations were low. However, when populations reached incipient levels, tree defenses were insufficient in deterring mass attacks. Variability in resin chemistry and toxicity to *D. ponderosae* also influence colonization success (Smith 1966, 1975, Reid et al. 1967). For example, Reid and Purcell (2011) investigated the effect of body condition (size) on the survivorship of *D. ponderosae* collected in Banff National Park, Alberta, Canada that were later exposed to host monoterpenes (α-pinene, myrcene, terpinolene, and limonene) by fumigation in the laboratory. They reported that limonene was most toxic to *D. ponderosae*, and that larger beetles survived higher concentrations of all monoterpenes. At the same time, the presence of some monoterpenes, including α-pinene (Pitman et al. 1968), myrcene, and terpinolene (Borden et al. 1987, Seybold 2002, Borden et al. 2008), enhance attraction of *D. ponderosae* to the host tree.

During endemic populations, trees weakened by other agents are often colonized by *D. ponderosae* (Boone et al. 2011) but may be difficult to detect on the landscape due to their scarcity or patterns of *D. ponderosae* attack (termed "strip attack") insufficient to cause tree mortality and associated crown fade (yellow, red, or brown needles). As an infestation develops it is well established that *D. ponderosae* initially colonizes the largest trees within *P. contorta* forests (Shepherd 1966, Rasmussen 1972), with progressively smaller trees being attacked over time (Klein et al. 1978, Cole and Amman 1980, Amman and Cole 1983) as the proportion of uninfested, larger trees declines. Based on research conducted in Oregon, Mitchell and Preisler (1991) reported that small *P. contorta* were not colonized unless they were near currently infested larger trees and that larger trees ($\geq$23 cm dbh, diameter at 1.37 m in height) were colonized with greater frequency than could be accounted for by a random attack model. This is despite larger-diameter trees having more pronounced defenses (Shrimpton 1973, Boone et al. 2011) but provide for a higher reproductive potential and probability of survival (Amman 1969, 1975, Reid and Purcell 2011, Graf et al. 2012) because of the greater quantity of food (phloem) available on which larvae feed. Safranyik et al. (1974) reported that *P. contorta* $\leq$25 cm dbh serve as *D. ponderosae* sinks, whereas trees $>$25 cm dbh serve as sources producing more *D. ponderosae* than required to overcome host defenses. This is why the development of outbreaks is consistently associated with mature and overmature forests (Gibson et al. 2009), specifically when abiotic conditions are favorable to beetle development (Bentz et al. 2010). Hicke and Jenkins (2008) estimated the susceptibility of *P. contorta* forests to *D. ponderosae*-caused tree mortality in the western United States and reported that many forests (46% of all *P. contorta*) exhibited conditions that are highly susceptible to infestation. Susceptibility was highest in the southern Rocky Mountains and lowest in the coastal states (Hicke and Jenkins 2008).

In *P. ponderosa*, attacks are often concentrated in the small- to mid-diameter classes (Geiszler et al. 1980a, Olsen et al. 1996) perhaps due to the larger range in tree sizes encountered in these forests as compared to *P. contorta*. Although *P. ponderosa* as small as 2.54 cm dbh may be colonized during outbreaks most are $>$12.7 cm dbh, but no clear preference for larger trees is evident (McCambridge et al. 1982). However, most large trees ($>$30.4 cm dbh) will have been killed by the end of an outbreak (Negrón and Popp 2004). In some locations where they coexist (Miller and Keen 1960), the role of *D. ponderosae* in *P. ponderosa* is secondary to that of western pine beetle, *D. brevicomis* LeConte, particularly in larger-diameter trees. For example, Fettig et al. (2010a) reported that *D. ponderosae* attacks were often confined to small-diameter ($<$31.8 cm dbh) *P. ponderosa* in California with single trees or small groups of trees being killed.

Stand Density—Effects on Microclimate, Tree Spacing, and Growing Space

In recent years, significant attention has been given to the effects of reductions in stand density associated with thinning on microclimate, tree spacing, and changes in host vigor and how these factors influence the development of *D. ponderosae* infestations (Logan and Amman 1998). Amman et al. (1988) and Bartos and Amman (1989) suggested that changes in microclimate were the principle factor associated with reductions in stand susceptibility to *D. ponderosae* (*see* Risk and Hazard Rating) following thinning in *P. contorta*. Since then, it has been well established that 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 (Fettig et al. 2007) and 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 successes (Progar et al. 2014). Geiszler and Gara (1978) discussed the role of tree spacing in the switching behavior of *D. ponderosae* from a tree currently under attack to an adjacent tree. The killing of groups of trees is fundamental to expansion of infestations (Geiszler et al. 1980b), particularly in *P. contorta*. Whitehead et al. (2004) and Whitehead and Russo (2005) used this and related information to develop thinning guidelines based on residual spacing of leave trees that was effective for reducing the susceptibility of *P. contorta* stands to *D. ponderosae* during outbreaks in British Columbia (*see* Thinning). In studies

conducted in *P. contorta* the importance of increases in host tree vigor and its effect on stand susceptibility has been emphasized less than in *P. ponderosa* (Eaton 1941).

High stand densities increase competition among trees for growing space (Reineke 1933). Fettig et al. (2007) used the concept of growing space as a mechanism to illustrate how changes in host tree vigor influence susceptibility of individual trees and stands to bark beetle attack. Trees use growth factors, such as sunlight, water, nutrients, temperature, oxygen, and carbon dioxide, until one or more factors becomes limiting (Oliver and Larson 1996). Disturbances can make growing space available to some trees at the expense of others (e.g., herbivory) or alter the amount of growing space available to all trees (e.g., prolonged drought). For example, when soil moisture is limited trees close their stomata to avoid excessive water loss, which inherently leads to reduced productivity as stomatal closure also prohibits uptake of carbon dioxide and, therefore, photosynthesis. A tree's photosynthates are allocated to different uses in an order of priorities (Oliver and Larson 1996): (1) maintenance respiration, (2) production of fine roots, (3) reproduction, (4) primary (height) growth, (5) xylem (diameter) growth, and (6) insect and disease resistance mechanisms. While somewhat conceptual, this hierarchy illustrates how production of insect resistance mechanisms are compromised first when growing space becomes limited by one or more factors. Conversely, it demonstrates how cultural practices that release growing space through reductions in tree density influence the susceptibility of individual trees, stands, and forests to *D. ponderosae* by strengthening insect resistance mechanisms (Fettig et al. 2007).

Risk and Hazard Rating

A number of risk and hazard rating systems have been developed to describe the susceptibility of a stand to *D. ponderosae* (Bentz et al. 1993). However, use of the terms "risk" and "hazard" have varied by author causing confusion in interpretation. In this section we refer to whether a rating system addresses the probability of stand infestation (defined as "risk" by some authors) although not necessarily with a statistical probability or the extent of tree mortality after an infestation has begun (defined as "hazard" by some authors). We save the term "risk" solely for rating systems in which measures of insect population pressure are included (Waters 1985), which is rare for *D. ponderosae*. Rating systems are tools for land managers to identify stands that can foster initiation and/or expansion of *D. ponderosae* infestations that may be suitable for management. They represent a critical step in long-term forest planning. *Dendroctonus* spp. capable of causing extensive tree mortality most often exhibit preference for larger-diameter trees growing in high-density stands with a high percentage of host type (Fettig et al. 2007). Different species will more likely respond to one or more of these conditions. Below, we concentrate on rating systems relevant to *D. ponderosae* in *P. contorta* and *P. ponderosa*. Although some models have been developed for other host systems (e.g., *P. albicaulis*), these have not been extensively studied.

Pinus contorta

Amman et al. (1977) developed one of the first rating systems for use in *P. contorta* forests to determine the extent of expected tree mortality attributed to *D. ponderosae* based on elevation and latitude, average stand age, and average stand diameter of trees ≥12.7 cm dbh. Each variable was ranked 1–3 based on categories defined for low, moderate, and high susceptibility. Individual values were then multiplied to provide an overall stand rating. Stands growing at lower elevations and latitudes with an average stand age of >80 years and an average diameter of all trees ≥12.7 cm dbh of ≥20.3 cm were classified as high susceptibility. Another method proposed by Mahoney (1978) used the radial increment ratio of the last 5 years to the previous 10 years, referred to as periodic growth ratio (PGR). A stand where trees exhibited a mean PGR of ≥0.9 was considered to be vigorous and likely to exhibit lower levels of tree mortality compared to ratios of <0.9. Schenk et al. (1980) developed a stand hazard rating (SHR) index based on a crown competition factor and the percentage of basal area of the stand represented by *P. contorta*, which were surrogate measures of stand vigor and food availability, respectively. The rating estimated the percentage of *P. contorta* basal area expected to be killed by *D. ponderosae*. From a study conducted in Oregon, Stuart (1984) developed a discriminant function that included quadratic mean diameter and the number of tree rings in the last centimeter of radial growth. The function identified whether a stand would be attacked or not by a *D. ponderosae* population representing a measure of the probability of stand infestation.

Anhold et al. (1996) described three relative density zones corresponding to different levels of *D. ponderosae* susceptibility (extent of tree mortality) in young *P. contorta* based on nonlinear tree mortality/stand density relationships. The first density management regime involved carrying a low density [i.e., stand density index (SDI) <140] throughout the rotation. Since SDI is an indicator of the amount of growing space available (Reineke 1933), and thus well correlated with tree growth, it is not surprising that SDI would be useful in predicting levels of tree mortality attributed to *D. ponderosae*. The second density management regime was designed to maintain relative density above a threshold level (i.e., SDI >245). Although this threshold represents >35% maximum SDI and suggests increases in susceptibility are likely due to decreases in host vigor and host defenses, the authors indicated that under these stand conditions the phloem is so thin as a result of tree competition that beetle development is poor (Anhold et al. 1996). Stands with density indices between these thresholds (140–245 SDI) were found to be very susceptible to *D. ponderosae* attack and subsequent tree mortality.

Probably the most common and effective rating system for use in *P. contorta* is that of Shore and Safranyik (1992). This is the only true risk rating system (sensu Waters 1985) that incorporates a stand susceptibility index (meaning likelihood of stand infestation and extent of tree mortality) with the potential challenge of an active *D. ponderosae* infestation in proximity to the stand. Susceptibility is calculated based on four factors: (1) percentage of susceptible basal area (trees ≥15 cm dbh), (2) average stand age of dominant and codominant trees, (3) stand density of all trees ≥7.5 cm dbh, and (4) the geographic location of the stand in terms of latitude, longitude, and elevation. Insect population data, referred to as a "beetle pressure index," incorporates the proximity and size of the *D. ponderosae* population. The stand susceptibility index and the beetle pressure index are then used to compute an overall stand risk index (Shore and Safranyik 1992, Shore et al. 2000).

Pinus ponderosa

P. ponderosa is an integral component of three cover types and a major component of >65% of all forests in the western United States (Burns and Honkala 1990). Although *D. ponderosae* outbreaks commonly occur in *P. ponderosa* they are sometimes viewed

Table 1. Rating system for the probability of *Pinus ponderosa* stands becoming infested by *Dendroctonus ponderosae* in the Black Hills of South Dakota and Wyoming. A number of rating systems utilize this approach of assigning values to model variables that are then multiplied (or added) to obtain an overall rating (modified from Stevens et al. 1980).

	Probability on infestation classes		
Variables	Low = 1	Moderate = 2	High = 3
Stand structure		Two-storied	Single-storied
Mean dbh[1] (cm)	<15.2	15.2–25.4	>25.4
Basal area (m^2/ha)	<18.4	18.4–34.4	>34.4
Stand value	**Overall rating**		
2–6	Low		
8–12	Moderate		
18–27	High		

[1]Diameter at breast height, 1.37 m.

as less substantial than in *P. contorta* likely because, in general, *P. ponderosa* stands are less dense, less continuous, and exhibit a higher diversity of stand ages and tree sizes (*see* Type Conversion and Mixed-Species Stands and Landscapes). Sartwell and Stevens (1975) described conditions under which *D. ponderosae* outbreaks were likely to occur in *P. ponderosa* forests in Oregon and the Black Hills of South Dakota and Wyoming. The authors defined suitable conditions as pure to nearly pure even-aged *P. ponderosa*, 50–100 years of age, with tree sizes 20–30 cm dbh and basal areas >34 m^2/ha. Stevens et al. (1980) captured these conditions and formalized a rating system for the Black Hills utilizing stand structure, mean stand diameter, and basal area. Each variable is assigned a rating value and all values are multiplied to obtain a stand rating, which then classifies the stand as low, moderate, or high "risk," referring to the probability of stand infestation (Table 1). Munson and Anhold (1995) developed a similar rating system based on their experiences in the Colorado Plateau, particularly in southern Utah, to classify stands as low, moderate, or high probability of infestation using measures of basal area, average *P. ponderosa* dbh, proportion of *P. ponderosa*, and number of currently infested trees.

Working with even-aged stands in the Black Hills, Schmid and Mata (1992) conducted long-term monitoring in thinned plots and used the metric of growing stock level (GSL) to characterize susceptibility (probability of stand infestation) to *D. ponderosae*. GSL is a function of mean stand diameter and tree spacing and is equal to basal area (ft^2/ac) when mean dbh is 25.4 cm (Schmid and Mata 1992, Schmid et al. 1994). The authors indicated that in their study area GSL was mostly equivalent to basal area and suggested that the "threshold" for susceptibility of *P. ponderosa* stands to *D. ponderosae* was 120 (~27.5 m^2/ha) GSL. Stands of 80 (~18.4 m^2/ha) to 120 GSL were considered of moderate susceptibility. These values apply to homogenously spaced trees in even-aged stands. However, a way to accurately calculate GSL or its relationship to basal area is not readily available making these data difficult to interpret and compare to other literature and stand conditions, or to implement in a formal rating system.

Many authors discuss tree vigor as an important factor in tree and stand susceptibility to bark beetle attack yet the term is often not appropriately defined. Some of the early work utilizing the concept of tree vigor (based on crown condition and amount of foliage) to estimate susceptibility of individual trees was conducted by Keen (1936) in California and Oregon. Waring and Pitman (1980) and Larsson et al. (1983) used grams of wood produced per square meter of leaf area as a measure of tree vigor and related it to the number of trees/ha killed by *D. ponderosae* in stands thinned to various levels. They proposed a threshold of 100 g of wood/m^2 leaf area below which individual trees were more likely to be attacked. This threshold translated to a basal area level of ~21 m^2/ha. Dolph (1982) adapted the work of Waring and Pitman (1980) and Larsson et al. (1983) and proposed that vigor of <50 g of wood/m^2 leaf area represented high susceptibility; 50–100 g of wood/m^2 leaf area represented moderate susceptibility; and >100 g of wood/m^2 leaf area represented low susceptibility.

Uneven-aged management of *P. ponderosa* is becoming more common in the United States yet little work has been conducted evaluating susceptibility of these stands to *D. ponderosae*. Negrón and Popp (2004) sampled unmanaged, infested and uninfested uneven-aged *P. ponderosa* stands and used classification trees to model the probability of infestation and the extent of tree mortality expected. Their study showed that in the Colorado Front Range, characterized by poor growing sites, the probability of stand infestation is 0.71 when *P. ponderosa* basal area is >17.1 m^2/ha and decreases to 0.21 when *P. ponderosa* basal area is ≤17.1 m^2/ha. Interestingly, these values are similar to those reported by Larsson et al. (1983) in Oregon. Working in the Black Hills where uneven-aged management is increasingly emphasized, Negrón et al. (2008) used similar methods to develop a classification tree model to determine the probability of stand infestation by *D. ponderosae*. Stands with basal area <6.0 m^2/ha, comprised of trees >25.4 cm, had a probability of infestation of 0.06 while stands with basal area ≥6.0 m^2/ha, comprised of trees >25.4 cm, had a probability of 0.55. The extent of tree mortality was also modeled with regression trees and linear regression using initial *P. ponderosa* basal area or *P. ponderosa* SDI.

Limitations

Bentz et al. (1993) evaluated several *D. ponderosae* rating systems in *P. contorta* forests in Montana and reported that none provided adequate predictions. Alternatively, Shore et al. (2000) evaluated the Shore and Safranyik (1992) rating system in *P. contorta* forests in British Columbia and reported most stands fell within the 95% prediction interval of the original model data. In *P. ponderosa*, Chojnacky et al. (2000) evaluated the Stevens et al. (1980) and Munson and Anhold (1995) systems based on data collected at 45 sites across Arizona, Colorado, and Utah. The Munson and Anhold (1995) system was viewed as reasonably effective for use in this region but that of Stevens et al. (1980), developed for the Black Hills, was less effective. However, the Munson and Anhold (1995) system rated all 45 study sites as either moderately or highly susceptible to bark beetle attack, which raises concerns about its lack of sensitivity (Chojnacky et al. 2000).

Rating systems should be used for identifying areas most susceptible to *D. ponderosae*, but actual predictions should not be taken at face value. These systems are influenced by, among other factors, geographic location, site quality, and tree-diameter distributions. Boone et al. (2011) showed that as *D. ponderosae* populations increase they undergo a density-dependent shift in host preference from vigor-impaired *P. contorta* to the most vigorous trees within a stand, which may also affect the accuracy of rating predictions. Furthermore, measures of density and SDI used in these systems are usually stand-level means, while differences in microtopography may create localized differences in productivity important to determining susceptibility (Fettig 2012), specifically in reference to the

probability of stand infestation. Furthermore, we do not know how climate change will affect the predictive capacities of rating systems as it is likely relationships will change due to the effects of projected changes on host-tree vigor and distributions (Fettig et al. 2013), and on the temperature-dependent life history traits of *D. ponderosae* (Bentz et al. 2010). Despite this, we expect *D. ponderosae* will play a significant role in colonizing and killing trees stressed by projected changes in climate but that threshold values identified in many rating systems will require revision (e.g., reductions in existing tree density thresholds associated with highly susceptible stands).

Treatment Options

There are two general approaches for reducing the negative impacts of bark beetles on forests referred to as "direct control" and "indirect control." Direct control involves short-term tactics designed to address current infestations by manipulating beetle populations and includes the use of fire, insecticides, semiochemicals, sanitation harvests, or combinations of these treatments (Carroll et al. 2006). There is no effective biological control agent available for *D. ponderosae*, but research is ongoing concerning development of pathogenic fungi (C.J.F. et al., unpublished data). Indirect control is preventive and designed to reduce the probability and severity (extent of tree mortality) of future infestations by manipulating stand, forest, and/or landscape conditions by reducing the number of susceptible host trees through thinning, prescribed burning, and/or alterations of age classes and species composition (Shore et al. 2006, Whitehead et al. 2006). In this context, the focus is on the residual structure and composition of forests following treatment and not on impacts to *D. ponderosae* populations. Whether employing direct and indirect control, all tactics should emphasize ecologically sound strategies that also address other resource objectives (*see* Designing Direct and Indirect Control Strategies That Meet Other Resource Objectives).

Direct Control

The first documented use of direct control against *D. ponderosae* occurred in the early 1900s in the Black Hills (Hopkins 1905). It was quickly acknowledged that a successful direct control program required prompt and thorough applications of the most appropriate tactics at a magnitude dictated by the *D. ponderosae* population and predicted rates of increase in the near term. It is important to emphasize that direct control only treats the symptom. Effects are transient, but when treatments are properly applied may provide short-term reductions in levels of tree mortality within affected areas (Carroll et al. 2006) sufficient until the outbreak subsides or until long-term susceptibility can be addressed through indirect control (Whitehead et al. 2006). Direct control strategies often target reducing localized populations of the insect, slowing the rate of spread, and providing protection of individual trees or stands.

Craighead et al. (1931) summarized direct control treatments implemented in the 1920s in the western United States and identified their limitations, several of which are relevant today. Direct control is an expensive endeavor, and therefore, decisions regarding its use and implementation are often dictated by more practical concerns such as resource availability (e.g., budget, time, personnel, and equipment), market conditions, logistical constraints (e.g., accessibility and ownership patterns), and environmental concerns. On federal lands in the western United States, appeals and litigation often limit or delay implementation of direct control affecting the success of proposed treatments. Furthermore, treatments applied to areas adjacent to untreated areas (e.g., wilderness) where elevated populations occur are likely to be less successful due to immigration of *D. ponderosae* from untreated to treated areas. In general, efficacy varies with *D. ponderosae* population density, rate of growth, and the spatial extent of the infested area. Coggins et al. (2011) found that mitigation rates of >50% (sanitation harvests) coupled with ongoing detection and monitoring of infested trees within treated sites in British Columbia was sufficient to control *D. ponderosae* infestations, especially with persistent implementation. Alternatively, others have stressed that many large-scale, well-funded, and well-coordinated direct control efforts (sanitation harvests) were largely ineffective (*see* Wickman 1987 regarding programs conducted at Crater Lake National Park, Oregon in 1925–1934) and that resources would be better allocated to indirect control. While we emphasize the value and importance of indirect control (*see* Indirect Control), sanitation is likely to be effective if the following criteria are followed (Carroll et al. 2006, Coggins et al. 2008): (1) early detection, (2) rapid response, (3) continued monitoring to identify current attacks, and (4) persistent application of treatments until *D. ponderosae* populations return to endemic levels. Endemic populations are most amenable to direct control as *D. ponderosae* populations grow relatively slowly initially, and removal of any individuals may suppress the population and perhaps even cause local extinction (Carroll et al. 2006).

Sanitation

Sanitation involves the identification of currently infested trees and subsequent felling and removal or treatment (e.g., burning or debarking) to destroy *D. ponderosae* adults and brood beneath the bark. In some cases, an emphasis is placed on removal of newly infested trees during early stages of colonization to reduce the quantity of attractive semiochemicals (i.e., aggregation pheromones and host volatiles) released into the stand (Progar et al. 2014), but this is rare due to complications regarding the identification of newly attacked trees and the level of responsiveness required in their removal. Rarely is sanitation fully effective as infested trees are sometimes difficult to detect requiring regular inspection with ground-based surveys, aerial surveys, and/or satellite detection, and ongoing annual tracking (Wulder et al. 2006, Coops et al. 2008). Typically, trees that have been dead for one or more years and which the beetles have vacated are detected based on patterns of crown fade (from yellow to red, Klutsch et al. 2009), and currently infested trees, which usually exhibit little or no crown fade, are then detected by their proximity to faded trees (Wulder et al. 2006, 2009) and confirmed by the presence of pitch tubes and/or boring dust (Gibson et al. 2009). If a low proportion of currently infested trees are felled (<50%) populations generally continue to increase causing additional tree mortality. For example, if 90% of infested trees were treated each year, it would require ~6 years of continuous sanitation to suppress a population that doubles annually (i.e., a rate commonly observed during epidemics) and initially infesting 10,000 trees (Carroll et al. 2006). Carroll et al. (2006) provide a graphical representation of the proportion of a *D. ponderosae* population (P) that must be removed in relation to the yearly rate of increase (R) to suppress population growth ($P = 1–1/R$) that may be useful. Where it is economically feasible, infested trees may be harvested and transported to mills where broods will be killed during processing. Where suitable markets do not exist, felled trees may be burned (Wickman 1987), chipped (Fettig et al. 2006), peeled (Craighead et al. 1931),

or treated by solarization (i.e., placement of infested material in the direct sun, which is often sufficient to kill brood beneath the bark in warmer climates) (Patterson 1930, Negrón et al. 2001). Solarization treatments are generally confined to small-scale infestations since turning of the infested material is often required to ensure adequate treatment of the infested bole. Peeling has also been successfully implemented in standing trees (Evenden 1927) but is rarely used today.

Wulder et al. (2011) monitored the success of sanitation for reducing levels of tree mortality attributed to *D. ponderosae* at two sites in western Canada using high-resolution aerial imagery and field measurements. They indicated that sanitation slowed the rate of population growth, with G:R ratios (number of currently infested green trees/red-faded trees; values >1 indicate that populations are increasing) found to be decreasing or stable while sanitation was ongoing. When sanitation was discontinued at one site, G:R increased markedly (1.94:1), while continued sanitation at the second site further reduced the G:R (0.22:1) (Wulder et al. 2011). These data provide a detailed account of the effectiveness of sanitation in *P. contorta* if conducted at appropriate temporal and spatial scales. However, sanitation is very labor intensive often requiring multiple-year treatments and, therefore, may be cost prohibitive depending on market conditions (e.g., for felled material and labor), accessibility, and the infrastructure required to maintain sanitation throughout an epidemic. Identifying susceptible sites (*see* Risk and Hazard Rating), coupled with the ability to address the infestation and resource values adversely affected by an outbreak, will determine where this strategy is most cost-effective.

Sanitation and Attractants

Synthetic attractants (baits) combined with sanitation have been used successfully to suppress existing infestations of *D. ponderosae* (Gibson et al. 2009). Strategies vary depending on population density, size of the infested area, stand susceptibility, and infestation status of surrounding untreated sites. As with any technique involving the use of attractants, there is a risk of causing undesirable levels of tree mortality. "Spot baiting" was developed to eliminate small ("spot") infestations of ≤50 trees (Schmid et al. 1989). Typically, two to three uninfested trees are baited in the center of the "spot" at least 10 m apart prior to beetle flight to concentrate existing infestations within a small group of trees that will be harvested. This approach is successfully used to control small, isolated infestations; however, it is not effective if surrounding areas contain epidemic populations. A similar tactic, "mop-up baiting," is occasionally used in areas where sanitation harvests have occurred (Borden et al. 1983). Baits are applied to residual trees in the vicinity of the area where sanitation harvests were implemented in hopes of concentrating beetles within areas where additional sanitation will be applied. "Grid baiting" has been used to address infestations of >50 infested trees (Gray and Borden 1989, Amman and Lindgren 1995, Trzcinski and Reid 2008). Infested areas are inundated with baits, allowing the infestation to increase within baited areas reducing the chance of population expansion into adjacent, unbaited areas. Susceptible trees are often baited on a 50-m grid, and a 50-m buffer is implemented between the area treated and the block boundary in which baits are not used in hopes of reducing the dispersal of semiochemicals into adjacent areas. Baits are deployed before *D. ponderosae* flight with all infested host trees removed, peeled or burned following flight. During the following year, sanitation harvests are used to treat any newly infested trees (Borden et al. 1983). Vandygriff et al. (2000) successfully used attractants to focus *D. ponderosae* infestations in areas designated for future fuelwood harvests in Idaho, thereby addressing multiple resource objectives.

Sanitation and Inhibitors

Verbenone is regarded as the principle antiaggregation pheromone of *D. ponderosae* and has been shown to reduce the incidence of successful attacks in *P. contorta* but rarely in *P. ponderosa* (Progar et al. 2014). Formulations registered and commercially available in the western United States include pouches (several registrants) and the Disrupt Micro-Flake VBN and Disrupt Bio-Flake VBN formulations (Hercon Environmental, Emigsville, PA). Removal of competing attractants by sanitation of trees containing live brood or beetles in addition to treatment with verbenone is the current integrated pest management practice recommended for *D. ponderosae* in the western United States. In recent years, significant advances have occurred in the development of semiochemical-based tools to protect trees from bark beetle attack. For a complete review on the use of verbenone and other inhibitors (e.g., nonhost volatiles) relevant to *D. ponderosae* we refer the reader to Progar et al. (2014).

Sanitation and Push-Pull

"Push-pull" combines the use of inhibitors (the "push") and baited traps and/or baited trees (the "pull") to divert beetles from high-value stands. Lindgren and Borden (1993) examined push-pull for *D. ponderosae* in British Columbia and reported that the addition of a "pull" component marginally improved efficacy. More recently, Gillette et al. (2012) added a perimeter of baited traps to verbenone-treated stands and reported adding a pull component provided no additional tree protection in California and Washington. Push-pull should be used in *P. contorta* stands with densities >400 stems/ha, mean dbh >25 cm, and with current infestation rates of <15% of available trees, and should be combined with sanitation of currently infested trees to achieve maximum efficacy (Lindgren and Borden 1993, Borden et al. 2006).

Insecticides

The use of insecticides typically involves topical sprays to the tree bole or systemic insecticides injected directly into the tree. In an operational context, only high-value, individual trees growing in unique environments (e.g., developed campgrounds and wildland-urban environments) are treated. During large-scale outbreaks, thousands of trees may be treated annually in the western United States. Fettig et al. (2013) discuss the efficacy, residual activity, and environmental safety of insecticides commonly used to protect trees from bark beetle attack in the western United States. Remedial applications to kill adults and brood within currently infested hosts by penetrating the bark are no longer used. Despite significant reductions in brood survival being demonstrated in early studies (Klein 1978), there was limited evidence of any impact to adjacent levels of tree mortality. Furthermore, there were concerns about the effects of remedial treatments on nontarget invertebrates, specifically natural enemy communities.

Fire

Early attempts to burn standing infested trees were largely ineffective (Evenden 1927, 1929). Later developments resulted in

higher heat intensities that penetrated bark deep enough to cause substantial mortality of brood (Klein 1978) but are seldom used today due to logistical constraints and wildfire risks. The application of prescribed fire and/or broadcast burns to suppress *D. ponderosae* populations is ineffective (Carroll et al. 2006).

Salvage

We mention salvage because the term is often inappropriately used in bark beetle literature. Technically, salvage is not a direct control method as its implementation has no immediate effect on *D. ponderosae* populations (i.e., beetles have already vacated the trees). Salvage involves the felling and removal of trees killed by *D. ponderosae* (or other agents) before they lose their economic value and may occur for several years in *P. ponderosa* (Schmid et al. 2009) up to a decade or more in *P. contorta* (Lewis and Hartley 2006) after a *D. ponderosae* outbreak has subsided. Once a tree falls to the forest floor, decay rates increase and logistical concerns generally preempt use of these trees for lumber.

Indirect Control

Two requirements must be met for a *D. ponderosae* outbreak to develop: (1) there must be several years of favorable weather (Safranyik 1978), including summer heat accumulations and winter temperatures conducive to beetle survival (Safranyik et al. 1975, Carroll et al. 2004) and adaptive seasonality (Bentz et al. 2010); and (2) there must be an abundance of susceptible host trees (*see* Risk and Hazard Rating). In many areas, age-class structure and forest species composition will be the dominant factor influencing outbreak intensity and severity (Taylor and Carroll 2004). Cultural practices that address these factors will influence the susceptibility of forests to *D. ponderosae* infestations.

Clearcutting

In *P. contorta*, clearcutting small- to moderate-sized blocks will create age and size mosaics within landscapes of pure even-aged forests that ultimately reduce impacts caused by *D. ponderosae* (Amman 1976). Stand attributes such as species composition, growth and yield, site quality, phloem thickness, stand density, average age, and elevation-latitude are factors used by resource managers to develop prescriptions that minimize stand and/or landscape levels of tree mortality where this silvicultural practice is employed. Although clearcutting is often viewed as having negative impacts on esthetics, this can be minimized by careful location of boundaries, use of irregularly shaped boundaries, prompt establishment of regeneration, and by minimizing the size of patches. Clearcutting should be coordinated with other resource disciplines to develop strategies that meet multiple objectives (*see* Designing Direct and Indirect Control Strategies That Meet Other Resource Objectives).

Thinning

Thinning has long been advocated as a preventive measure to alleviate or reduce the amount of bark-beetle-caused tree mortality in western forests (Whitehead et al. 2004, 2006, Fettig et al. 2007). Among other factors, thinning reduces host availability that supports beetle populations; reduces competition among trees for nutrients, water, and other resources thereby increasing vigor (Eaton 1941); and affects microclimate decreasing the effectiveness of chemical cues used in host finding, selection and colonization (Thistle et al. 2004) and influencing beetle survival (Amman et al. 1988). However, thinning conducted in a careless manner may result in increases in other subcortical insects and root pathogens (Harrington et al. 1985). With a thorough understanding of potential risks, prudent treatments can be implemented to minimize unwanted consequences.

Table 2. Favorable conditions for reducing the probability of *Dendroctonus ponderosae* infestation and extent of tree mortality by thinning in *Pinus contorta* forests in the western United States (adapted from Bollenbacher and Gibson 1986 and Whitehead and Russo 2005).

Parameter	Value
Stand composition	>80% *Pinus contorta*
Stand age	60–110 yr
Basal area	>29.8 m^2/ha
Stand density	750–1,500 trees/ha (>7.5 cm dbh[1])
Average diameter	>20 cm dbh
Elevation	<1,800 m
Percentage of trees currently-infested	<10%

[1]Diameter at breast height, 1.37 m.

Pinus contorta

Thinning implemented for *D. ponderosae* in *P. contorta* include thinning from above or diameter-limit thinning and thinning from below (Cole and Cahill 1976, McGregor et al. 1987) applied to reduce basal area (Amman et al. 1977, Cahill 1978, Bennett and McGregor 1980), remove trees with thick phloem (Hamel 1978), and/or increase residual tree spacing (Whitehead and Russo 2005) (Table 2). Schmidt and Alexander (1985) found that thinning from above often reduced stand susceptibility to *D. ponderosae* until residual trees grew to susceptible sizes; however, it left stands with reduced silvicultural value that were often vulnerable to windthrow or snow damage. Thinning from below may optimize the effects of microclimate, intertree spacing, and tree vigor (Whitehead and Russo 2005, Coops et al. 2008) even though residual trees are of diameter classes considered more susceptible to attack (Waring and Pitman 1980, Mitchell et al. 1983). However, this practice may not be economically viable since only smaller-diameter trees are removed. Recommended residual conditions include intertree spacings of at least 4 m (Whitehead et al. 2004, Whitehead and Russo 2005) or 400–625 trees/ha (Whitehead and Russo 2005).

Whitehead et al. (2004) and Whitehead and Russo (2005) investigated the effectiveness of thinning for reducing the amount of *D. ponderosae*-caused tree mortality in British Columbia. Treatments were installed to determine if changes in intertree spacing, microclimate, and tree vigor translated to a lower frequency of *D. ponderosae* attacks. G:R ratios, total number and density of trees attacked, and mortality due to attack were lower in thinned stands than in corresponding untreated areas at every site (Table 3). At one site, >80% of all trees >20 cm dbh were attacked in the untreated control. The data strongly suggest that thinning mature *P. contorta* stands from below to a uniform residual intertree spacing of at least 4 m is effective for mitigating levels of tree mortality attributed to *D. ponderosae* (Table 3). However, Whitehead and Russo (2005) cautioned that during large-scale outbreaks thinning will not be effective when affected stands suffer a large influx of immigrant *D. ponderosae*.

Coops et al. (2008) reviewed nine studies conducted in the United States and Canada (seven exclusive to *D. ponderosae*) that examined the effects of thinning implemented for bark beetle management. Across all studies, lower levels of *D. ponderosae* attack and

Table 3. Cumulative number of *Pinus contorta* killed by *Dendroctonus ponderosae* 9–12 yr after thinnings were conducted, British Columbia, Canada (adapted from Whitehead et al. 2004, modified from Fettig et al. 2007).

Location and year of treatment	Treatment	No. trees attacked/ha	Green: red attack ratio[1]
Cranbook (1992)	Untreated	22	1.8
	Spaced to 4 m	2	0.3
	Spaced to 5 m	7	0.5
Parson (1993)	Untreated	56	2.9
	Untreated	15	0.3
	Spaced to 4 m	0	–
	Spaced to 5 m	0	–
Hall Lake (1994)	Untreated	158	1.8
	Thinned to 500 trees/ha	37	1.4
Quesnel (1991)	Untreated	452	3.3
	Spaced to 4 m	167	1.2

[1]Ratios >1.0 indicate that infestations are building.

Table 4. Cumulative number of trees killed by bark beetles over a 10-year period following thinning (18.4 m^2/ha, 27.6 m^2/ha, 41.3 m^2/ha) to reduce stand susceptibility to bark beetles in *Pinus ponderosa*–*Pinus jeffreyi* forests, Tahoe National Forest, California, 1999–2009 (modified from Fettig et al. 2012).

	Total number of trees killed by bark beetles (all bark beetle species)			
	A. concolor	*P. ponderosa*	*P. jeffreyi*	All tree species
Low density	10	0	0	10
Medium density	20	5	0	25
High density	28	2	2	32
Untreated control	17	16	7	40
Total	75	23[2]	9	107
Mean dbh[1]	31.1 (15–61)	28.4 (18–51)	26.0 (18–32)	30.1 (15–61)

[1]Diameter at breast height (cm, 1.37 m in height), range in parentheses.
[2]Majority (22) attributed to *D. ponderosae*.

associated levels of tree mortality occurred in thinned and spaced treatments than in untreated stands. However, the authors cautioned that thinning is only effective in the transition between endemic and incipient phases of attack and not during epidemics (Coops et al. 2008). While thinning during endemic or during the transition between endemic and incipient populations is most effective (McGregor et al. 1987, Whitehead et al. 2004, 2007, Whitehead and Russo 2005), thinning may also be useful during an outbreak, specifically if combined with sanitation harvests and/or other direct control tactics (Waring and Pitman 1985).

Coops et al. (2009) investigated the merits of thinning in four stands of *P. contorta* in British Columbia using Landsat TM imagery, two of which were thinned (spaced to 4–5 m) in 1993. Two years after thinning stand vigor in the unthinned stands had not changed, however, in the thinned stands a substantial increase in tree vigor was observed (to 100–160 g wood/m^2 leaf area based on Waring and Pitman 1985; *see* Risk and Hazard Rating). Subsequent assessments in 2001 indicated that stand vigor remained higher in the thinned stands compared to unthinned stands, which corresponded to differences in the levels of tree mortality attributed to *D. ponderosae* following an infestation in 2002.

Bollenbacher and Gibson (1986) described a management strategy to limit the adverse effects of *D. ponderosae* in *P. contorta* forests of Montana that many still consider a useful decisionmaking tool today. The authors reported a list of attributes used to assess the potential effectiveness of thinning for reducing the probability of *D. ponderosae* infestation and extent of tree mortality, including site productivity, slope, average diameter, age, density, elevation, wind firmness, current *D. ponderosae* activity levels, tree vigor, and resource objectives (Table 2). They stated that stands of high productivity, 60–125 years old, at <1,829 m elevation and with basal areas >29.8 m^2/ha are considered high priority for treatment. Stands with current beetle infestation rates of >10% could result in excessive tree mortality if thinning is not completed prior to the next *D. ponderosae* flight period (Bollenbacher and Gibson 1986).

Pinus ponderosa

Thinning reduces levels of *P. ponderosa* mortality attributed to *D. ponderosae*, and where various prescriptions have been evaluated, areas of lowest tree density had less tree mortality often on both a numerical and proportional basis (e.g., Cole and McGregor 1988, Fiddler et al. 1989, Egan et al. 2010, Fettig et al. 2012). This relationship is consistent among the wide diversity of stand conditions encountered in forests containing *P. ponderosa*. McCambridge and Stevens (1982) conducted an evaluation of thinning treatments in *P. ponderosa* in the Black Hills and reported reductions in the amount of *D. ponderosae*-caused tree mortality immediately after thinning in two of three stands (the date of thinning of the third stand was not reported). Basal areas in the unthinned stands were 46.1, 41.8, and 44.8 m^2/ha compared to 19.5, 17.2, and 10.3 m^2/ha in thinned stands (McCambridge and Stevens 1982). In northeastern California, Egan et al. (2010) reported that higher levels of tree mortality occurred in unthinned *P. ponderosa* plantations (16.1 trees killed/ha) compared to precommercially thinned stands (1.2 trees killed/ha). Similarly, Fiddler et al. (1989) showed that thinning significantly reduced the amount of *P. ponderosa* mortality caused by *D. ponderosae* in California. No tree mortality occurred in stands of <9 m^2/ha of basal area, which agrees with the optimal stocking level of 11m^2/ha described by Oliver (1979, 1995). Mortality was reduced in thinned plots regardless of the level of thinning.

Fettig et al. (2012) evaluated the effectiveness of thinning to reduce stand susceptibility to bark beetles (several species) over a 10-year period in *P. ponderosa* and Jeffrey pine, *P. jeffreyi* Grev. & Balf., forests on the Tahoe National Forest, California. Treatments included thinning from below to a residual basal area of: (1) 18.4 m^2/ha (low density thin), (2) 27.6 m^2/ha (medium density thin), (3) 41.3 m^2/ha (high density thin), and (4) an untreated control. Throughout the study, only 107 trees died due to bark beetle attack, of which ~21% were *P. ponderosa* killed by *D. ponderosae*. In the low density thin, no pines were killed by bark beetles during the 10-year period (Table 4). Significantly fewer trees (/ha/yr) were killed in the low density thin than the high density thin or untreated control; however, no significant effect was observed for the percentage of trees (/yr) killed by bark beetles.

Schmid and Mata (2005) monitored levels of tree mortality attributed to *D. ponderosae* in 1-ha plots over a 17-year period in the Black Hills. The authors concluded that the effectiveness of thinning *P. ponderosa* forests to residual densities between 18.4 m^2/ha and 27.6 m^2/ha for reducing susceptibility to *D. ponderosae* was questionable. However, they suggested that their results were confounded by small study plots being surrounded by extensive areas of unmanaged forest where *D. ponderosae* populations were epidemic. Schmid and Mata (2005) concluded that reduced long-term tree

mortality will be accomplished when an area of sufficient size is managed so that thinned stands are separated from unmanaged stands by natural buffers or areas of lower tree density. Their data indicate that *P. ponderosa* stands of ≤16.1 m^2/ha were less frequently attacked by *D. ponderosae* but reinforce the importance of managing forests at appropriate spatial scales. Later, Schmid et al. (2007) reported thinning to 18.4 m^2/ha in susceptible stands may not be sufficient to yield long-term reductions in susceptibility if not followed with subsequent thinnings over time to maintain lower tree densities.

Cochran and Barrett (1985) studied the effects of thinning on the growth and mortality of *P. ponderosa* in eastern Oregon over 24 years. Plots were thinned at the beginning of the study to various densities and again at the end of the 10th and 19th growing seasons. After the first year, nearly all of the tree mortality that occurred during the next 23 years was attributed to *D. ponderosae*. High levels of tree mortality occurred on plots where SDI values were >140. No mortality occurred in the least dense plots (SDI = 55) or when average tree spacing was 7.62 m by 7.62 m or greater. The authors concluded *P. ponderosa* should be managed at low stand densities to avoid substantial mortality from *D. ponderosae* in eastern Oregon. In all cases, leaving susceptible hosts on site following a thinning treatment will require additional thinnings to maintain a stand structure that is less susceptible to infestation by *D. ponderosae*.

Pinus albicaulis

In the last decade, extensive levels of tree mortality have occurred across much of the range of *P. albicaulis* due to outbreaks of *D. ponderosae* and white pine blister rust, *Cronartium ribicola* J.C. Fitch (Jewett et al. 2011). The US Fish and Wildlife Service announced in 2011 that it determined *P. albicaulis* warranted protection under the Endangered Species Act but that adding the species to the Federal List of Endangered and Threatened Wildlife and Plants was precluded by the need to address other listing actions of higher priority (Federal Register 2011). Perkins and Roberts (2003) collected data from *P. albicaulis* stands in central Idaho to estimate the probability of attack by *D. ponderosae*. Stands with basal areas >10 m^2/ha or with an SDI >80 had a 100% probability of being attacked. However, thinning prescriptions to reduce the susceptibility of *P. albicaulis* to *D. ponderosae* are lacking (Gibson et al. 2009), but currently being developed (Keane et al. 2011). Any effective strategy will also have to address the effects of white pine blister rust on *P. albicaulis* regeneration.

Prescribed Fire

Jenkins et al. (2014) consider the effects of prescribed fire and other fuel reduction treatments on *D. ponderosae*. Based on research in northeastern California, Fettig et al. (2008) reported that applications of prescribed fire resulted in significant increases in *D. ponderosae*-caused tree mortality in *P. ponderosa* in all but the two largest dbh classes (>49.6 cm dbh). Alternatively, others have found no effect (Rasmussen et al. 1996, McHugh et al. 2003, Elkin and Reid 2004), particularly in *P. contorta*. Levels of tree mortality following prescribed fire depend on numerous factors including, but not limited to, beetle populations, tree species, tree size, phenology (season or life history stage), degree of fire-caused injuries, initial and postfire levels of tree vigor, the postfire environment, and the frequency and severity of other predisposing, inciting and contributing factors. Overall, managers should expect short-term increases in the amount of *D. ponderosae*-caused tree mortality following prescribed fire in *P. ponderosa* but concentrated in the smaller-diameter classes (Fettig and McKelvey 2010, Fettig et al. 2010a, 2010b). Most of the delayed mortality attributed to *D. ponderosae* occurs during the first few years following prescribed fire (Fettig et al. 2010a), but in the longer-term burned areas benefit from the positive impacts of prescribed fire on growing space and other factors (*see* Effects on Microclimate, Tree Spacing, and Growing Space) that reduce forest susceptibility to *D. ponderosae* (Fettig et al. 2007, Fettig and McKelvey 2010).

Rotation Lengths

Several authors have suggested that shorter rotations and promotion of multiple-age classes will minimize the amount of *D. ponderosae*-caused tree mortality (Roe and Amman 1970, Safranyik et al. 1974, Taylor and Carroll 2004, Whitehead et al. 2004). Depending on site quality, *P. contorta* stands tend to be least susceptible to *D. ponderosae* when <60 years of age (Safranyik et al. 1974).

Type Conversion and Mixed-Species Stands and Landscapes

Fettig et al. (2007) concluded that efforts to prevent undesirable levels of *D. ponderosae*-caused tree mortality must also account for the spatial distribution of cover types. In many areas, treatments should be implemented to increase heterogeneity (e.g., of age, size, and species compositions) as homogeneous forested landscapes promote creation of large contiguous areas susceptible to similar disturbances, such as *D. ponderosae* outbreaks. Studies have shown that insects tend to focus host searching in patches of high host concentrations (Root 1973), which increases the probability of encounters with suitable hosts. In mixed-species stands or landscapes this occurs with less efficiency (Cole and Amman 1980, McGregor and Cole 1985).

Designing Direct and Indirect Control Strategies That Meet Other Resource Objectives

When designing direct and indirect control strategies, there are opportunities for collaboration with other resource disciplines allowing additional objectives to be met with little or no additional cost. For example, while prescriptions differ between thinning treatments implemented for fuels reduction (i.e., reducing surface fuels, increasing the height to live crown, decreasing crown density, and retaining large trees of fire-resistant species; Agee and Skinner 2005) and prevention of bark beetle infestations (*see* Thinning), there is considerable opportunity to alter fuel treatments without reducing their efficacy while increasing the effectiveness of these same treatments for reducing the susceptibility of forests to *D. ponderosae*. However, this can only be accomplished by increasing levels of communication and coordination between the forest health/entomology and fire ecology/management communities (Jenkins et al. 2009). Whitehead et al. (2007) examined 10 sites in British Columbia 5–14 years after thinning was implemented to reduce susceptibility to *D. ponderosae* while maintaining other resources objectives (e.g., esthetics, recreation, and timber) and determined current stand composition and structure from direct sampling and pre- and posttreatment stand characteristics from stand reconstruction. In all cases, the potential for active crown fire was reduced as well as susceptibility to *D. ponderosae*, but the magnitude of the effects varied with prescription, intensity of removal, and treatment scale.

In other cases, some resource objectives (e.g., wildlife) may be

negatively impacted by implementation of certain direct or indirect control tactics, and it is prudent to identify as many of these impacts as possible and to adjust strategies accordingly (e.g., reducing the scale, frequency, and/or intensity of treatment). While *D. ponderosae* infestations affect timber and fiber production, and indirectly a range of ecosystem services, it is important to note that numerous organisms benefit from their activity. For example, snags created by *D. ponderosae* create structure and food sources that have significant values to wildlife, specifically cavity-nesting birds (Saab et al. 2014). Furthermore, mortality of individual or small groups of trees affects fine-scale spatial heterogeneity that influences the frequency and severity of other disturbances (e.g., wildfire) (Fettig 2012).

Even-Aged Versus Uneven-Aged Management

P. contorta and *P. ponderosa* forests are exposed to disturbances that cause substantial levels of tree mortality over relatively large areas, most notably wildfires and *D. ponderosae* outbreaks. Although even-aged silviculture is ecologically appropriate in many cases due to the lack of shade tolerance in these species (Burns and Honkala 1990), uneven-aged management may be more desirable to meet other resource objectives. As a result, single tree and group tree selection have become more common and popular in the western United States for protecting esthetics, providing habitat for wildlife, and managing recreation sites. "Free selection," a combination of single tree and group tree selection with reserve trees left in all structural stages, is recommended for creating irregular structures that are preferred habitats for species such as the northern goshawk, *Accipiter gentiles* (L.) (Graham and Jain 2005). Uneven-aged management produces stand conditions that are less susceptible to *D. ponderosae* because they provide for a diversity of age classes and irregular structure. Openings of sufficient size will permit regeneration of *P. contorta* when seed and seedbed conditions are sufficient for germination and survival (Alexander 1975, Stuart et al. 1989). The more intermediate shade tolerance of *P. ponderosa* allows for regeneration under partial shade (Shepperd and Battaglia 2002), particularly on good sites with adequate moisture.

Acceptability

Few contemporary studies have evaluated the social acceptance of direct and indirect control tactics. McFarlane et al. (2006) examined public attitudes relevant to management preferences for *D. ponderosae* in Banff and Kootenay National Parks, Canada. Data were collected by mail survey from 1,385 residents living in or near the parks. All groups agreed that "allowing the outbreak to follow its course without intervention" was not an acceptable option. Preferred options included "sanitation cutting to remove infested trees from small areas" (*see* Sanitation) and the "use of pheromones to attract beetles to one area" (*see* Sanitation and Attractants). Other acceptable options included the use of prescribed burning, sanitation of large areas, and "thinning the forest to remove some of the uninfested but susceptible trees" (*see* Thinning). In the United States, active management other than prescribed fire within our National Park system and wilderness areas is rare and often contentious, so it is difficult to gauge the relevance of these data to our society and the management of our national forest (USDA Forest Service), state or private lands. However, the level of support for implementing these strategies within Banff and Kootenay National Parks is interesting. We refer the reader to Gillette et al. (2014) who describe the range of potential outcomes expected from implementation of the direct and indirect control tactics discussed here.

Conclusions

Widespread outbreaks of *D. ponderosae* have now impacted >8.9 million ha in the western United States but appear to have peaked in 2009 (USDA Forest Service 2012). These mortality events are part of the ecology of western forests and influence many ecological processes, but the economic and social implications are significant. Outbreaks will continue to occur as long as susceptible forests and favorable climatic conditions coincide. The only long-term solution is to change forest structure and composition to increase resiliency. In many ways, the current outbreak provides both a lesson and opportunity for land managers to learn from and to re-engage the issue of resiliency as they develop prescriptions for future forests. As demonstrated here, there are a wide variety of tactics available to reduce the severity and extent of *D. ponderosae* infestations when properly applied at appropriate spatial and temporal scales. Experience has shown that even a course of no action is not without consequence, although the no action alternative may be an appropriate response under some circumstances. In areas where active management is appropriate, we should avoid the situation where *D. ponderosae* dictates priorities and management options. Several assessments have concluded forests are increasingly vulnerable to tree mortality as a result of the direct and indirect effects of climate change (Fettig et al. 2013) and that the use of sound, ecologically appropriate management strategies and prioritizing of their application to enhance resiliency is critical. This will be challenging given, among other factors, the uncertainty of the effects of climate change on the distribution, physiology, and life history of *D. ponderosae* and its many host tree species.

Literature Cited

AGEE, J.K., AND C.N. SKINNER. 2005. Basic principles of forest fuel reduction treatments. *For. Ecol. Manage.* 211:83–96.

ALEXANDER, R.A. 1975. Partial cutting in old-growth lodgepole pine. USDA For. Serv., Res. Pap. RM-RP-136, Fort Collins, CO. 17 p.

AMMAN, G.D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. USDA For. Serv., Res. Note INT-RN-96, Ogden, UT. 8 p.

AMMAN, G.D. 1975. Insects affecting lodgepole pine productivity. P. 310–341 in *Management of lodgepole pine ecosystems: Symposium and proceedings*, Baumgartner, D.M. (ed.). Washington State University, Cooperative Extension Service, Pullman, WA.

AMMAN, G.D. 1976. Integrated control of the mountain pine beetle in lodgepole pine forests. P. 439–446 in *XVI IUFRO World congress proceedings*. IUFRO, Div. II, Oslo, Norway.

AMMAN, G.D., AND W.E. COLE. 1983. Mountain pine beetle dynamics in lodgepole pine forests. USDA For. Serv., Gen. Tech. Rep. INT-GTR-145, Part 2, Ogden, UT. 59 p.

AMMAN, G.D., AND B.S. LINDGREN. 1995. Semiochemicals for management of mountain pine beetle: Status of research and application. USDA For. Serv., Gen. Tech. Rep. INT-GTR-318, Ogden, UT. 22 p.

AMMAN, G.D., AND J.A. LOGAN. 1998. Silvicultural control of the mountain pine beetle: Prescriptions and the influence of microclimate. *Am. Entomol.* 44:166–177.

AMMAN, G.D., M.D. MCGREGOR, D.B. CAHILL, AND W.H. KLEIN. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA For. Serv., Gen. Tech. Rep. INT-GTR-36, Ogden, UT. 19 p.

AMMAN, G.D., M.D. MCGREGOR, R.F. SCHMITZ, AND R.D. OAKES. 1988. Susceptibility of lodgepole pine to infestation by mountain pine beetles following partial cutting of stands. *Can. J. For. Res.* 18:688–695.

ANHOLD, J.A., M.J. JENKINS, AND J.N. LONG. 1996. Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. *West. J. Appl. For.* 11:50–53.

ATKINS, M.D. 1966. Behavioral variation among scolytids in relation to their habitat. *Can. Entomol.* 98:285–288.

BARTOS, D.L., AND G.D. AMMAN. 1989. Microclimate: An alternative to tree vigor as a basis for mountain pine beetle infestations. USDA For. Serv., Res. Paper INT-RP-400, Ogden, UT. 10 p.

BENNETT, D.D., AND M.D. MCGREGOR. 1980. A demonstration of basal area cutting to manage mountain pine beetle in second growth ponderosa pine. USDA For. Serv., FPM Rep. 88–16, Missoula, MT. 5 p.

BENTZ, B.J., C.D. ALLEN, M. AYRES, E. BERG, A. CARROLL, M. HANSEN, ET AL. 2009. *Bark beetle outbreaks in western North America: Causes and consequences.* University of Utah Press, Salt Lake City, UT. 65 p.

BENTZ, B.J., G.D. AMMAN, AND J.A. LOGAN. 1993. A critical assessment of risk classification systems for the mountain pine beetle. *For. Ecol. Manage.* 61:349–366.

BENTZ, B.J., J. RÉGNIÈRE, C.J. FETTIG, E.M. HANSEN, J.L. HAYES, J.A. HICKE, ET AL. 2010. Climate change and bark beetles of the western United States and Canada: Direct and indirect effects. *Bioscience* 60:602–613.

BOLLENBACHER, B., AND K.E. GIBSON. 1986. *Mountain pine beetle: A land manager's perspective.* USDA For. Serv., FPM Report 86–15, Missoula, MT. 5 p.

BOONE, C.K., B.H. AUKEMA, J. BOHLMANN, A.L. CARROLL, AND K.P. RAFFA. 2011. Efficacy of tree defense physiology varies with bark beetle population density: A basis for positive feedback in eruptive species. *Can. J. For. Res.* 41:1174–1188.

BORDEN, J.H., A.L. BIRMINGHAM, AND J.S. BURLEIGH. 2006. Evaluation of the push–pull tactic against the mountain pine beetle using verbenone and non-host volatiles in combination with pheromone-baited trees. *For. Chron.* 82:579–590.

BORDEN, J.H., J.E. CONN, L.M. FRISKIE, B.E. SCOTT, L.J. CHONG, H.D. PIERCE, ET AL. 1983. Semiochemicals for the mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in British Columbia: Baited-tree studies. *Can. J. For. Res.* 13:325–333.

BORDEN, J.H., D.S. PURESWARAN, AND J.P. LAFONTAINE. 2008. Synergistic blends of monoterpenes for aggregation pheromones of the mountain pine beetle (Coleoptera: Curculionidae). *J. Econ. Entomol.* 101:1266–1275.

BORDEN, J.H., L.C. RYKER, L. CHONG, H.D. PIERCE JR., B.D. JOHNSTON, AND A.C. OEHLSCHLAGER. 1987. Response of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests. *Can. J. For. Res.* 17:118–128.

BURNS, R.M., AND B.H. HONKALA. 1990. *Silvics of North America. Vol. I: Conifers.* USDA For. Serv., Agric. Handbk. 654, Washington, DC. 675 p.

CAHILL, D.B. 1978. Cutting strategies as control measures of the mountain pine beetle in lodgepole pine in Colorado. P. 188–191 in *Theory and practice of mountain pine beetle management in lodgepole pine forests: Symposium proceedings*, Berryman, A.A., G.D. Amman, and R.W. Stark (eds.). Washington State University, Pullman, WA.

CARROLL, A.L., T.L. SHORE, AND L. SAFRANYIK. 2006. Direct control: Theory and practice. P. 155–172 in *The mountain pine beetle - A synthesis of biology, management, and impacts on lodgepole pine*, Safranyik, L., and B. Wilson (eds.). Natural Resources Canada, Canadian Forest Service, Victoria, BC.

CARROLL, A., S. TAYLOR, J. RÉGNIÈRE, AND L. SAFRANYIK. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. P. 223–232 in *Mountain pine beetle symposium: Challenges and solutions*, Shore, T.L., J.E. Brooks, and J.E. Stone (eds.). Natural Resources Canada, Canadian Forest Service, Info. Rep. BC-X-399, Victoria, BC.

CHOJNACKY, D.C., B.J. BENTZ, AND J.A. LOGAN. 2000. Mountain pine beetle attack in ponderosa pine: Comparing methods for rating susceptibility. USDA For. Serv., Res. Pap. RMRS-RP-26, Fort Collins, CO. 10 p.

CHRISTIANSEN, E., R.H. WARING, AND A.A. BERRYMAN. 1987. Resistance of conifers to bark beetle attack: Searching for general relationships. *For. Ecol. Manage.* 22:89–106.

COCHRAN, P.H., AND J.W. BARRETT. 1985. Growth of ponderosa pine thinned to different stocking levels in central Oregon: 30-year results. USDA For. Serv., Res. Pap. PNW-RP-508, Portland, OR. 29 p.

COGGINS, S.B., N.C. COOPS, M.A. WULDER, C.W. BATER, AND S.M. ORTLEPP. 2011. Comparing the impacts of mitigation and non-mitigation on mountain pine beetle populations. *J. Environ. Manage.* 92:112–120.

COGGINS, S.B., M.A. WULDER, N.C. COOPS, AND J.C. WHITE. 2008. Linking survey detection accuracy with ability to mitigate populations of mountain pine beetle. *For. Chron.* 84:900–909.

COLE, D.M., AND M.D. MCGREGOR. 1988. Stand culture/bark beetle relationships of immature tree stands in the Inland Mountain West. USDA For. Serv., Gen. Tech. Rep. INT-GTR-243, Ogden, UT. 7 p.

COLE, W.E., AND G.D. AMMAN. 1980. Mountain pine beetle dynamics in lodgepole pine forests. Part 1: Course of an infestation. USDA For. Serv., Gen. Tech. Rep. INT-GTR-89, Ogden, UT. 56 p.

COLE, W.E., AND D.B. CAHILL. 1976. Cutting strategies can reduce probabilities of mountain pine beetle epidemics in lodgepole pine. *J. For.* 74:294–297.

COOPS, N.C., J.A. TIMKO, M.A. WULDER, J.C. WHITE, AND M.A. ORTLEPP. 2008. Investigating the effectiveness of mountain pine beetle mitigation strategies. *Int. J. Pest Manage.* 54:151–165.

COOPS, N.C., R.H. WARING, M.A. WULDER, AND J.C. WHITE. 2009. Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. *For. Ecol. Manage.* 113:1058–1066.

CRAIGHEAD, F.C., J.M. MILLER, J.C. EVENDEN, AND F.P. KEEN. 1931. Control work against bark beetles in western forests and an appraisal of its results. *J. For.* 29:1001–1018.

DOLPH, R.E. 1982. Identifying mature and overmature ponderosa pine most susceptible to mountain pine beetle attack in northeast Oregon. USDA For. Serv., FPM Rept, Portland, OR. 15 p.

EATON, C.B. 1941. Influence of the mountain pine beetle on the composition of mixed pole stands of ponderosa pine and white fir. *J. For.* 39:710–713.

EGAN, J.M., W.R. JACOBI, J.F. NEGRÓN, S.L. SMITH, AND D.R. CLUCK. 2010. Forest thinning and subsequent bark beetle-caused mortality in northeastern California. *For. Ecol. Manage.* 260:1832–1842.

ELKIN, C.M., AND M.L. REID. 2004. Attack and reproductive success of mountain pine beetles (Coleoptera: Scolytidae) in fire-damaged lodgepole pines. *Environ. Entomol.* 33:1070–1080.

EVENDEN, J.C. 1927. Big Hole Basin insect control project, Beaverhead National Forest. Progress report for the season of 1927. USDA Forest Insect Laboratory, Bureau of Entomology and Plant Quarantine, Coeur d'Alene, ID. 22 p.

EVENDEN, J.C. 1929. Plan of operation for control of the mountain pine beetle in lodgepole pine by burning standing trees. USDA Forest Insect Laboratory, Bureau of Entomology and Plant Quarantine, Coeur d'Alene, ID. 23 p.

FEDERAL REGISTER. 2011. Proposed rules, Tuesday, July 19, 2011. *Federal Register* 76:42631. Available online at www.federalregister.gov/articles/2011/07/19/2011-17943/endangered-andthreatened-wildlife-and-plants-12-month-finding-on-a-petition-to-listpinus; last accessed Jan. 31, 2013.

FETTIG, C.J. 2012. Forest health and bark beetles. P. 13–22 in *Managing Sierra Nevada forests.* USDA For. Serv., Gen. Tech. Rep. PSW-GTR-237, Albany, CA. 184 p.

FETTIG, C.J., R.R. BORYS, AND C.P. DABNEY. 2010a. Effects of fire and fire surrogate treatments on bark beetle-caused tree mortality in the Southern Cascades, California. *For. Sci.* 56:60–73.

FETTIG, C.J., R.R. BORYS, S.R. MCKELVEY, AND C.P. DABNEY. 2008.

Blacks Mountain Experimental Forest: Bark beetle responses to differences in forest structure and the application of prescribed fire in interior ponderosa pine. *Can. J. For. Res.* 38:924–935.

FETTIG, C.J., D.M. GROSMAN, AND A.S. MUNSON. 2013. Advances in insecticide tools and tactics for protecting conifers from bark beetle attack in the western United States. P. 472–492 in *Insecticides—Development of safer and more effective technologies*, Trdan, S. (ed.). InTech, Rijeka, Croatia.

FETTIG, C.J., C.J. HAYES, K.J. JONES, S.R. MCKELVEY, S.L. MORI, AND S.L. SMITH. 2012. Thinning Jeffrey pine stands to reduce susceptibility to bark beetle infestations in California, USA. *Agric. For. Entomol.* 14:111–117.

FETTIG, C.J., K.D. KLEPZIG, R.F. BILLINGS, A.S. MUNSON, T.E. NEBEKER, J.F. NEGRÓN, ET AL. 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. *For. Ecol. Manage.* 238:24–53.

FETTIG, C.J., AND S.R. MCKELVEY. 2010. Bark beetle responses to stand structure and prescribed fire at Blacks Mountain Experimental Forest, California, USA: 5-year data. *Fire Ecol.* 6:26–42.

FETTIG, C.J., S.R. MCKELVEY, D.L. CLUCK, S.L. SMITH, AND W.J. OTROSINA. 2010b. 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. *For. Ecol. Manage.* 260:207–218.

FETTIG, C.J., J.D. MCMILLIN, J.A. ANHOLD, S.M. HAMUD, R.R. BORYS, C.P. DABNEY, ET AL. 2006. The effects of mechanical fuel reduction treatments on the activity of bark beetles (*Coleoptera: Scolytidae*) infesting ponderosa pine. *For. Ecol. Manage.* 230:55–68.

FETTIG, C.J., M.L. REID, B.J. BENTZ, S. SEVANTO, D.L. SPITTLEHOUSE, AND T. WANG. 2013. Changing climates, changing forests: A western North American perspective. *J. For.* 111:214–228.

FIDDLER, G.O., D.R. HART, T.A. FIDDLER, AND P.M. MCDONALD. 1989. Thinning decreases mortality and increases growth of ponderosa pine in northeastern California. USDA For. Serv., Res. Pap. PSW-RP-194, Albany, CA. 11 p.

FRANCESCHI, V.R., P. KROKENE, E. CHRISTIANSEN, AND T. KREKLING. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytol.* 167:353–376.

GEISZLER, D.R., AND R.I. GARA. 1978. Mountain pine beetle attack dynamics in lodgepole pine. P. 182–187 in *Theory and practice of mountain pine beetle management in lodgepole pine forests: Symposium proceedings*, Berryman, A.A., G.D. Amman, and R.W. Stark (eds.). Washington State University, Pullman, WA.

GEISZLER, D.R., R.I. GARA, C.H. DRIVER, V.F. GALLUCCI, AND R.E. MARTIN. 1980a. Fire, fungi, beetles influences on a lodgepole pine ecosystem of south-central Oregon. *Oecologia* 46:239–243.

GEISZLER, D.R., R.I. GARA, AND V.F. GALLUCCI. 1980b. Modeling dynamics of mountain pine beetle aggregation in a lodgepole pine stand. *Oecologia* 46:244–253.

GIBSON, K., S. KEGLEY, AND B. BENTZ. 2009. Mountain pine beetle. USDA For. Serv., For. Insect Dis. Leafl. FIDL 2, Portland, OR. 12 p.

GILLETTE, N.E., C.J. MEHMEL, S.R. MORI, J.N. WEBSTER, D.L. WOOD, N. ERBILGIN ET AL. 2012. The push-pull tactic for mitigation of mountain pine beetle (Coleoptera: Curculionidae) damage in lodgepole and whitebark pines. *Environ. Entomol.* 41:1575–1586.

GILLETTE, N.E., D.L. WOOD, S. HINES, AND J. RUNYON. 2013. The once and future forest: Consequences of mountain pine beetle treatment decisions. *For. Sci.* 60(3):527–538.

GRAF, M., M.L. REID, B.H. AUKEMA, AND B.S. LINDGREN. 2012. Association of tree diameter with body size and lipid content of mountain pine beetles. *Can. Entomol.* 144:467–477.

GRAHAM, R.T., AND T.B. JAIN. 2005. Application of free selection in mixed forests of the inland northwestern United States. *For. Ecol. Manage.* 209:131–145.

GRAY, D.R., AND J.H. BORDEN. 1989. Containment and concentration of mountain pine beetle (Coleoptera: Scolytidae) infestations with semiochemicals: Validation by sampling of baited and surrounding zones. *J. Econ. Entomol.* 93:1399–1405.

HAMEL, D.R. 1978. Results of harvesting strategies for management of mountain pine beetle infestations in lodgepole pine on the Gallatin National Forest, Montana. P. 192–196 in *Theory and practice of mountain pine beetle management in lodgepole pine forests: Symposium proceedings*, Berryman, A.A., G.D. Amman, and R.W. Stark (eds.). Washington State University, Pullman, WA.

HARRINGTON, T.C., F.W. COBB JR., AND J.W. LOWNSBERRY. 1985. Activity of *Hylastes nigrinus*, a vector of *Verticicladiella wageneri*, in thinned stands of Douglas-fir. *Can. J. For. Res.* 15:579–593.

HICKE, J.A., AND J.C. JENKINS. 2008. Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. *For. Ecol. Manage.* 255:1536–1547.

HOPKINS, A.D. 1905. The Black Hills beetle. USDA Bureau of Entomology, Bull. 56, Washington, DC. 24 p.

HUBER, D.P.W., S. RALPH, AND J. BOHLMANN. 2004. Genomic hardwiring and phenotypic plasticity of terpenoid-based defenses in conifers. *J. Chem. Ecol.* 30:2399–2418.

JENKINS, M.J., C.J. FETTIG, AND E.G. HEBERTSON. 2009. Bark beetles, fuels and fire: A synthesis of our present understanding and implications for management. In *4th annual international congress on fire ecology and management: Fire as a global process*, Rideout-Hanzak, S., B.P. Oswald, and M. Beierle (compl.). Available online at http://fireecology.net/Congress09/Abstracts/FireEco2009/pdfs/80.pdf; last accessed Feb. 5, 2013.

JENKINS, M.J., J.B. RUNYON, C.J. FETTIG, W.G. PAGE, AND B.J. BENTZ. 2014. Interactions among the mountain pine beetle, fires, and fuels. *For. Sci.* 60(3):489–501.

JEWETT, J.T., R.L. LAWRENCE, L.A. MARSHALL, P.E. GESSLER, S.L. POWELL, AND S.L. SAVAGE. 2011. Spatiotemporal relationships between climate and whitebark pine mortality in the Greater Yellowstone Ecosystem. *For. Sci.* 57:320–335.

KEANE, R., B. ERICKSON, AND K. BUERMEYER. 2011. *Restoring whitebark pine ecosystems: Effects of daylighting, thinning, and prescribed burning treatments (The Daylite Study)*. Available online at www.firelab.org/ResearchProject_Files/daylite_studyplan.pdf; last accessed Feb. 26, 2013.

KEEN, F.P. 1936. Relative susceptibility of ponderosa pines to bark beetle attack. *J. For.* 34:919–927.

KLEIN, W.H. 1978. Strategies and tactics for reducing losses in lodgepole pine to the mountain pine beetle by chemical and mechanical means. P. 54–63 in *Theory and practice of mountain pine beetle management in lodgepole pine forests: Symposium proceedings*, Berryman, A.A., G.D. Amman, and R.W. Stark (eds.). Washington State University, Pullman, WA.

KLEIN, W.H., D.L. PARKER, AND C.E. JENSEN. 1978. Attack, emergence, and stand depletion trends of the mountain pine beetle in a lodgepole pine stand during an outbreak. *Environ. Entomol.* 112:185–191.

KLUTSCH, J.G., J.F. NEGRÓN, S.L. COSTELLO, C.C. RHOADES, D.R. WEST, J. POPP, ET AL. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *For. Ecol. Manage.* 258:641–649.

LARSSON, S., R. OREN, R.H. WARING, AND J.W. BARRETT. 1983. Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *For. Sci.* 29:395–402.

LEWIS, K.J., AND I.D. HARTLEY. 2006. Rate of deterioration, degrade, and fall of trees killed by mountain pine beetle. *BC J. Ecosystems Manage.* 7:11–19.

LINDGREN, B.S., AND J.H. BORDEN. 1993. Displacement and aggregation of mountain pine beetles, *Dendroctonus ponderosae* (Coleoptera: Scolytidae), in response to their antiaggregation and aggregation pheromones. *Can. J. For. Res.* 23:286–290.

LOGAN, J.A., W.W. MACFARLANE, AND L. WILLCOX. 2010. Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone ecosystem. *Ecol. Appls.* 20:895–902.

LOGAN, J.A., P. WHITE, B.J. BENTZ, AND J.A. POWELL. 1998. Model analysis of spatial patterns in mountain pine beetle outbreaks. *Theo. Pop. Bio.* 53:236–255.

MAHONEY, R.L. 1978. Lodgepole pine/mountain pine beetle risk classification methods and their application. P. 106–110 in *Theory and practice of mountain pine beetle management in lodgepole pine forests, symposium proceedings*, Berryman, A.A., G.D. Amman, and R.W. Stark (eds.), Univ. of Idaho, Moscow, ID.

MCCAMBRIDGE, W.F., F.G. HAWKSWORTH, C.B. EDMINSTER, AND J.G. LAUT. 1982a. *Ponderosa pine mortality resulting from a mountain pine beetle outbreak.* USDA For. Serv., Res. Pap. RM-RP-235, Fort Collins, CO. 7 p.

MCCAMBRIDGE, W.F., AND R.E. STEVENS. 1982b. Effectiveness of thinning ponderosa pine stands in reducing mountain pine beetle-caused tree losses in the Black Hills—Preliminary observations. USDA For. Serv., Res. Note RM-RN-414, Fort Collins, CO. 3 p.

MCFARLANE, B.L., R.C.G. STUMPF-ALLEN, AND D.O. WATSON. 2006. Public perceptions of natural disturbance in Canada's national parks: The case of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). *Bio. Con.* 130:340–348.

MCGREGOR, M.D., G.D. AMMAN., R.F. SCHMITZ, AND R.D. OAKES. 1987. Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. *Can. J. For. Res.* 17:1234–1239.

MCGREGOR, M.D., AND D.M. COLE (EDS.). 1985. Integrating management strategies for the mountain pine beetle with multiple-resource management of lodgepole pine forests. USDA For. Serv., Gen. Tech. Rep. INT-GTR-174, Ogden, UT. 68 p.

MCHUGH, C.W., T.E. KOLB, AND J.L. WILSON. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environ. Entomol.* 32:510–522.

MILLER, J.M., AND F.P. KEEN. 1960. Biology and control of the western pine beetle. USDA For. Serv., Misc. Publ. 800, Washington, DC. 381 p.

MITCHELL, R.G., AND H.K. PREISLER. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *For. Sci.* 37:1390–1408.

MITCHELL, R.G., R.H. WARING, AND G.B. PITMAN. 1983. Thinning lodgepole pine increases the vigor and resistance to mountain pine beetle. *For. Sci.* 2:204–211.

MUNSON, S., AND J. ANHOLD. 1995. Site risk rating for mountain pine beetle in ponderosa pine. USDA For. Serv., Unpublished Paper, For. Health Prot., Ogden, UT. 1 p.

NEGRÓN, J.F., K. ALLEN, B. COOK, AND J.R. WITHROW JR. 2008. Susceptibility of ponderosa pine, *Pinus ponderosa* (Dougl. ex Laws.), to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attack in uneven-aged stands in the Black Hills of South Dakota and Wyoming USA. *For. Ecol. Manage.* 254:327–334.

NEGRÓN, J.F., AND J.B. POPP. 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. *For. Ecol. Manage.* 191:17–27.

NEGRÓN, J.F., W.A. SHEPPERD, S.A. MATA, J.B. POPP, L.A. ASHERIN, A.W. SCHOETTLE ET AL. 2001. Solar treatments for reducing survival of mountain pine beetle in infested ponderosa and lodgepole pine logs. USDA For. Serv., Res. Pap. RMRS-RP-30, Fort Collins, CO. 11 p.

OLIVER, W.W. 1979. Fifteen-year growth patterns after thinning a ponderosa pine-Jeffrey pine plantation in northeastern California. USDA For. Serv., Res. Pap. PSW-RP-141, Albany, CA. 10 p.

OLIVER, W.W. 1995. Is self-thinning in ponderosa pine ruled by *Dendroctonus* bark beetles? P. 213–218 in *Forest health through silviculture: Proceedings of the 1995 national silviculture workshop*, Eskew, L.G. (compl.). USDA For. Serv., Gen. Tech. Rep. RM-GTR-267, Fort Collins, CO.

OLIVER, C.D., AND B.C. LARSON. 1996. *Forest stand dynamics.* John Wiley and Sons, Inc., New York. 520 p.

OLSEN, W.K., J.M. SCHMID, AND S.A. MATA. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *For. Sci.* 42:310–327.

ORCHERTON, D. 2008. Socio-economic impact of the mountain pine beetle. *BC J. Ecosystems Manage.* 9:51–59.

PATTERSON, J.E. 1930. Control of the mountain pine beetle in lodgepole pine by the use of solar heat. USDA For. Serv., Tech. Bull. 195, Washington, DC. 20 p.

PERKINS, D.L., AND D.W. ROBERTS. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *For. Ecol. Manage.* 174:495–510.

PITMAN, G.B., J.P. VITÉ, G.W. KINZER, AND A.F. FENTIMAN JR. 1968. Bark beetle attractants: *trans*-Verbenol isolated from *Dendroctonus. Nature* 218:168–169.

PROGAR, R.A., N.E. GILLETTE, C.J. FETTIG, AND K.H. HRINKEVICH. 2014. Applied chemical ecology of mountain pine beetle. *For. Sci.* 60(3): 414–433.

RAFFA, K.F., AND A.A. BERRYMAN. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecol. Monogr.* 53:27–49.

RAFFA, K.F., T.W. PHILLIPS, AND S.M. SALOM. 1993. Strategies and mechanisms of host colonization by bark beetles. P. 103–128 in *Beetle pathogen interactions in conifer forests*, Schowalter, T.D., and G.M. Filip (eds.). Academic Press, Inc., San Diego, CA.

RASMUSSEN, L.A. 1972. Attraction of mountain pine beetle to small diameter lodgepole pines baited with *trans*-verbenol and alpha-pinene. *J. Econ. Entomol.* 65:1396–1399.

RASMUSSEN, L.A., G.D. AMMAN, J.C. VANDYGRIFF, R.D. OAKES, A.S. MUNSON, AND K.E. GIBSON. 1996. Bark beetle and wood borer infestations in the Greater Yellowstone Area during four postfire years. USDA For. Serv., Res. Pap. INT-RP-487, Ogden, UT. 10 p.

REINEKE, L.H. 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46:627–638.

REID, M.L., AND J.R.C. PURCELL. 2011. Condition-dependent tolerance of monoterpenes in an insect herbivore. *Arthropod-Plant Interact.* 5:331–337.

REID, R.W., H.S. WHINEY, AND J.A. WATSON. 1967. Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue-stain fungi. *Can. J. Bot.* 45:1115–1126.

ROE, A.L., AND G.D. AMMAN. 1970. The mountain pine beetle in lodgepole pine forests. USDA For. Serv., Res. Pap. INT-RP-71, Ogden, UT. 23 p.

ROOT, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43:95–124.

SAAB, V., Q.S. LATIF, M.M. ROWLAND, T.N. JOHNSON, A.D. CHALFOUN, S.W. BUSKIRK, J.E. HEYWARD, AND M.A. DRESSER. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. *For. Sci.* 60(3):539–559.

SAFRANYIK, L. 1978. Effects of climate and weather on mountain pine beetle populations. P. 77–84 in *Theory and practice of mountain pine beetle management in lodgepole pine forests: Symposium proceedings*, Berryman, A.A., G.D. Amman, and R.W. Stark (eds.). Washington State University, Pullman, WA.

SAFRANYIK, L., D.M. SHRIMPTON, AND H.S. WHITNEY. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forestry Service, For. Tech. Rep. 1, Pacific Forest Research Centre, Victoria, BC. 24 p.

SAFRANYIK, L., D.M. SHRIMPTON, AND H.S. WHITNEY. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. P. 406–428 in *Management of lodgepole pine ecosystems: Symposium and proceedings*, Baumgartner, D.M. (ed.). Washington State University, Cooperative Extension Service, Pullman, WA.

SARTWELL, C., AND R.E. STEVENS. 1975. Mountain pine beetle in ponderosa pine, prospects for silvicultural control in second-growth stands. *J. For.* 73:136–140.

SCHENK, J.A., R.L. MAHONEY., J.A. MOORE, AND D.L. ADAMS. 1980. A model for hazard rating lodgepole pine stands for mortality by mountain pine beetle. *For. Ecol. Manage.* 3:57–68.

SCHMID, J.M., AND S.A. MATA. 1992. *Stand density and mountain pine beetle-caused tree mortality in ponderosa pine stands.* USDA For. Serv., Res. Note RM-RN-515, Fort Collins, CO. 4 p.

SCHMID, J.M., AND S.A. MATA. 2005. Mountain pine beetle-caused tree mortality in partially cut plots surrounded by unmanaged stands. USDA For. Serv., Res. Pap. RM-RP-54, Fort Collins, CO. 11 p.

SCHMID, J.M., S.A. MATA, AND R.D. AVERILL. 1989. Containment of small group infestations of the mountain pine beetle in ponderosa pine. USDA For. Serv., Res. Note RM-RN-493, Fort Collins, CO. 4 p.

SCHMID, J.M., S.A. MATA, R.R. KESSLER, AND J.B. POPP. 2007. The influence of partial cutting on mountain pine beetle-caused tree mortality in Black Hills ponderosa pine stands. USDA For. Serv., Res. Pap. RMRS-RP-68, Fort Collins, CO. 19 p.

SCHMID, J.M., S.A. MATA, AND R.A. OBEDZINSKI. 1994. Hazard rating ponderosa pine stands for mountain pine beetle in the Black Hills. USDA For. Serv., Res. Note RM-RN-529, Fort Collins, CO. 4 p.

SCHMID, J.M., S.A. MATA, AND W.C. SCHAUPP. 2009. Mountain pine beetle-killed trees as snags in Black Hills ponderosa pine stands. USDA For. Serv., Res. Note RMRS-RN-40, Fort Collins, CO. 6 p.

SCHMIDT, W.C., AND R.R. ALEXANDER. 1985. Strategies for managing lodgepole pine. P. 201–210 in *Lodgepole pine: The species and its management, Symposium proceedings*, Baumgartner, D.M., R.G. Krebill, J.T. Arnott, and G.F. Weetman (eds.). Washington State University, Spokane, WA.

SEYBOLD, S.J. 2002. Development of a monitoring and management tool for the central Rocky Mountain populations of the mountain pine beetle*, Dendroctonus ponderosae.* USDA For. Serv., Prog. Rep., Proj. No. R4–2001-01, Pacific Southwest Res. Stn., Davis, CA. 11 p.

SHEPHERD, R.F. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Can. Entomol.* 98:507–518.

SHEPPERD, W.D., AND M.A. BATTAGLIA. 2002. Ecology, silviculture, and management of Black Hills ponderosa pine. USDA For. Serv., Gen. Tech. Rep. RMRS-GTR-97, Fort Collins, CO. 112 p.

SHORE, J.L., AND L. SAFRANYIK. 1992. Susceptibility and risk rating stands for the mountain pine beetle in lodgepole pine stands. Forestry Canada, Info. Rep. BC-X-336, Victoria, BC. 12 p.

SHORE, T.L., L. SAFRANYIK, AND J.P. LEMIEUX. 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: Testing of a rating system. *Can. J. For. Res.* 30:44–49.

SHORE, T.L., L. SAFRANYIK, AND R.J. WHITEHEAD. 2006. Principles and concepts of management. P. 117–121 in *The mountain pine beetle—A synthesis of biology, management, and impacts on lodgepole pine*, Safranyik, L., and B. Wilson (eds.). Natural Resources Canada, Canadian Forest Service, Victoria, BC.

SHRIMPTON, D.M. 1973. Age- and size-related response of lodgepole pine to inoculation with *Europhium clavigerum. Can. J. Bot.* 51:1155–1160.

SMITH, R.H. 1966. Resin quality as a factor in the resistance of pines to bark beetles. P. 189–196 in *Breeding pest-resistant trees*, Gerhold, H.D., R.E. McDermott, E.J. Schreiner, and J.A. Winieski (eds.). Pergamon Press Inc., New York.

SMITH, R.H. 1975. Formula for describing effect of insect and host tree factors on resistance to western pine beetle attack. *J. Econ. Entomol.* 68:841–844.

STEVENS, R.E., W.F. MCCAMBRIDGE, AND C.B. EDMINSTER. 1980. Risk rating guide for mountain pine beetle in Black Hills ponderosa pine. USDA For. Serv., Res. Note RM-RN-385, Fort Collins, CO. 2 p.

STUART, J.D. 1984. Hazard rating of lodgepole pine stands to mountain pine beetle outbreaks in southcentral Oregon. *Can. J. For. Res.* 14:666–671.

STUART, J.D., J.K. AGEE, AND R.I. GARA. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. *Can. J. For. Res.* 19:1096–1104.

TAYLOR, S.W., AND A.L. CARROLL. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. P. 41–51 in *Mountain pine beetle symposium: Challenges and solutions.* Shore, T.L., J.E. Brooks, and J.E. Stone (eds.). Natural Resources Canada, Canadian Forest Service, Info. Rep. BC-X-399, Victoria, BC.

THISTLE, H.W., H. PETERSON, G. ALLWINE, B.K. LAMB, T. STRAND, E.H. HOLSTEN ET AL. 2004. Surrogate pheromone plumes in three forest trunk spaces: Composite statistics and case studies. *For. Sci.* 50:610–625.

TRZCINSKI, M.K., AND M.L. REID. 2008. Effect of management on the spatial spread of mountain pine beetle (*Dendroctonus ponderosae*) in Banff National Park. *For. Ecol. Manage.* 256:1418–1426.

USDA FOREST SERVICE. 2012. *Areas with tree mortality from bark beetles: Summary for 2000–2011, Western US.* 3 p.

VANDYGRIFF, J.C., L.A. RASMUSSEN, AND J.F. RINEHOLT. 2000. A novel approach to managing fuelwood harvest using bark beetle pheromones. *West. J. Appl. For.* 15:183–188.

VITÉ, J.P. 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa. Contr. Boyce Thompson Inst.* 21:37–66.

WARING, R.H., AND G.B. PITMAN. 1980. A simple model of host resistance to bark beetles. Oregon State Univ., Res. Note OSU-RN-65, School of Forestry, Corvallis, OR. 2 p.

WARING, R.H., AND G.B. PITMAN. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecol.* 66:889–897.

WATERS, W.E. 1985. Monitoring bark beetle populations and beetle-caused damage. P. 141–175 in *Integrated pest management in pine-bark beetle ecosystems*, Waters, W.E., R.W. Stark, and D.L. Wood (eds.). John Wiley and Sons, New York.

WHITEHEAD, R.J., AND G.L. RUSSO. 2005. "Beetle-proofed" lodgepole pine stands in interior British Columbia have less damage from mountain pine beetle. Canadian Forest Service, Natural Resources Canada, Info. Rep. BC-X-402, Victoria, BC. 17 p.

WHITEHEAD, R.J., G.L. RUSSO, B.C. HAWKES, AND O.B. ARMITAGE. 2007. A silvicultural assessment of 10 lodgepole pine stands after partial cutting to reduce susceptibility to mountain pine beetle. Canadian Forest Service, Natural Resources Canada, Info. Rep. FI-X-001, Victoria, BC. 48 p.

WHITEHEAD, R.J., L. SAFRANYIK, G. RUSSO, T.L. SHORE, AND A.L. CARROLL. 2004. Silviculture to reduce landscape and stand susceptibility to the mountain pine beetle. P. 233–244 *Mountain pine beetle symposium: Challenges and solutions*, Shore, T.L., J.E. Brooks, and J.E. Stone (eds.). Canadian Forest Service, Natural Resources Canada, Info. Rep. BC-X-399, Victoria, BC.

WHITEHEAD, R.J., L. SAFRANYIK, AND T.L. SHORE. 2006. Preventive management. P. 173–192 in *The mountain pine beetle—A synthesis of biology, management, and impacts on lodgepole pine*, Safranyik, L., and B. Wilson (eds.). Canadian Forest Service, Natural Resources Canada, Victoria, BC.

WICKMAN, B.E. 1987. The battle against bark beetles in Crater Lake National Park: 1925–34. USDA For. Serv., Gen. Tech. Rep. PNW-GTR-259, Portland, OR. 40 p.

WULDER, M.A., C.C. DYMOND, J.C. WHITE, AND B. ERICKSON. 2006. Detection, mapping, and monitoring of the mountain pine beetle. P. 123–154 in *The mountain pine beetle—A synthesis of biology, management, and impacts on lodgepole pine*, Safranyik, L., and B. Wilson (eds.). Canadian Forest Service, Natural Resources Canada, Victoria, BC.

WULDER, M.A., S.M. ORTLEPP, J.C. WHITE, N.C. COOPS, AND S.B. COGGINS. 2011. Monitoring the impacts of mountain pine beetle mitigation. *For. Ecol. Manage.* 258:1181–1187.

WULDER, M.A., J.C. WHITE., A.L. CARROLL, AND N.C. COOPS. 2009. Challenges for the operational detection of mountain pine beetle green attack with remote sensing. *For. Chron.* 85:32–38.