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Review

The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States

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Abstract

Insects are major components of forest ecosystems, representing most of the biological diversity and affecting virtually all processes and uses. In the USA, bark beetles (Coleoptera: Curculionidae, Scolytinae) heavily influence the structure and function of these ecosystems by regulating certain aspects of primary production, nutrient cycling, ecological succession and the size, distribution and abundance of forest trees. The purpose of this report is to review tree and stand factors associated with bark beetle infestations and analyze the effectiveness of vegetation management practices for mitigating the negative impacts of bark beetles on forest ecosystems. We describe the current state of our knowledge and identify gaps for making informed decisions on proposed silvicultural treatments. This review draws from examination of 498 scientific publications (many of which are cited herein) on this and related topics.

Keywords: Stand density; Thinning; Prescribed fire; Slash management; Scolytinae; *Dendroctonus*; *Ips*; *Scolytus*

Contents

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1. Introduction

Bark beetles (Coleoptera: Curculionidae, Scolyinae), a large and diverse group of insects consisting of approximately 550 species in North America (Wood, 1982), are commonly recognized as the most important mortality agent in coniferous forests (Furniss and Carolin, 1977; Dale et al., 2001; Logan and Powell, in press; Fig. 1). The last decade has seen unprecedented levels of tree mortality in spruce forests of south-central Alaska and the Rocky Mountains (Wittwer, 2000), lodgepole pine, *Pinus contorta* Dougl. ex Loud., forests of western Canada and the Rocky Mountains (Wilent, 2005; Struck, 2006), southern pine forests in Florida, Kentucky, North Carolina, South Carolina and Tennessee (Coulson et al., 2003; Nowak, 2004), pinyon-juniper woodlands of the southwestern USA (Shaw et al., 2005) and ponderosa pine, *P. ponderosa* Dougl. ex Laws., forests of Arizona (USDA Forest Service, 2004) and California (USDA Forest Service, 2002). In all cases, bark beetle epidemics were a significant factor contributing to tree mortality.

Most bark beetles feed on the phloem tissue of woody plants and often directly kill the host. These insects influence forest ecosystem structure and function by regulating certain aspects of primary production, nutrient cycling, ecological succession and the size, distribution and abundance of forest trees (Mattson and Addy, 1975; Mattson, 1977; Schowalter, 1981, 1994; Mattson et al., 1996; Coulson and Wunneburger, 2000). Attacks reduce tree growth and hasten decline, mortality and subsequent replacement by other tree species. Bark beetles impact timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, real estate values, biodiversity, endangered species and cultural resources (Coulson and Schneider, 1992; Coulson and Stephen, 2006). In short, impacts affect ecological, economic, social and political concerns (Smardon and Karp, 1993) and are influenced by past forest management practices (Coulson and Stephen, 2006). Managing and predicting the impacts of bark beetles on forests requires an understanding of the normal (nominal) conditional states of the forest and of individual stands that comprise the forest. These include natality, growth, mortality and renewal (Coulson and Stephen, 2006).

Fig. 1. *Dendroctonus ponderosae*-caused tree mortality (red-topped and fading trees) in *P. contorta* forests, British Columbia, Canada, 2005. Photo: C.J. Fettig, USDA Forest Service, Pacific Southwest Research Station.

In this paper, we review tree and stand factors associated with bark beetle infestations and analyze the effectiveness of vegetation management practices for mitigating the negative impacts of bark beetles on forest ecosystems. We describe the current state of our knowledge and identify gaps for making informed decisions on proposed treatments. Specifically, we concentrate on coniferous forests of the western and southern USA, but occasionally draw on literature from other regions, primarily western Canada.

2. Bark beetle–tree interactions and forest health

Individual trees utilize growth factors, such as sunlight, water, nutrients, temperature, oxygen and carbon dioxide, until one or more factors become limiting (Oliver and Larson, 1996). Therefore, a forest contains a certain amount of intangible growing space, which varies spatially and temporally. The concept of growing space provides an excellent mechanism to illustrate how changes in host vigor influence susceptibility of individual trees to bark beetle attack. Disturbances can make growing space available to some tree species at the expense of others (e.g., herbivory), or alter the amount of growing space available to all trees (e.g., prolonged drought). As growing space diminishes, a tree's photosynthates are allocated to different uses in an order of priorities (Oliver and Larson, 1996): (1) maintenance respiration (Kramer and Kozlowski, 1979), (2) production of fine roots (Fogel and Hunt, 1979), (3) reproduction (Eis et al., 1965), (4) primary (height) growth (Oliver and Larson, 1996), (5) xylem (diameter) growth (Waring and Schlesinger, 1985), and (6) insect and disease resistance mechanisms (Mitchell et al., 1983; Oliver and Larson, 1996). This hierarchy is not absolute, but illustrates how production of insect resistance mechanisms may be compromised when growing space becomes limited by one or more factors.

In order to reproduce, bark beetles must successfully locate and colonize suitable hosts. Once a host has been identified, using a variety of behavioral modalities (Strom et al., 1999; Bishir et al., 2004), colonization begins with the biting process (Nebeker et al., 1993). Given the cues received during this process and other factors, such as the beetle's internal physiology (Wallin and Raffa, 2000), the host is either rejected or accepted. If the host is rejected, the beetle takes flight presumably in search of another host. If the host is accepted, colonization in the case of living hosts requires overcoming tree defenses that consist of anatomical and chemical components that are both constitutive and inducible (Wood, 1972; Hodges et al., 1979, 1985; Raffa et al., 1993; Franceschi et al., 2005). This can only be accomplished by recruitment of a critical minimum number of beetles (Wood, 1972; Hodges et al., 1979, 1985; Raffa et al., 1993), which varies with changes in host vigor. Several bark beetle species (e.g., *Ips* spp.) preferentially attack logs, slash, or dead and dying trees. In these cases, little or no host resistance is encountered.

Most coniferous species, particularly pines, have a well-defined resin duct system, which is capable of mobilizing large amounts of oleoresin following wounding (Christiansen et al., 1987). This has traditionally been considered the primary defense of conifers against bark beetle attack (Vité, 1961; Rudinsky, 1966; Reid et al., 1967; Smith, 1975; Hodges et al., 1979). Beetles that initiate host selection are often killed by drowning or immobilization in resin especially when adequate moisture, flow and oleoresin exudation pressure exist (Vité and Wood, 1961; Lorio and Hodges, 1968; Raffa and Berryman, 1983). Resin chemistry also plays an important role in the ability of a tree to resist bark beetle attack (Reid et al., 1967; Smith, 1975; Hodges et al., 1979) and is known to influence bark beetle physiology and behavior (Seybold et al., 2000). In many cases, monoterpene volatiles released from oleoresin function as host attractants (kairomones) for bark beetles and their associates. Ironically, some monoterpenes are physiologically toxic to bark beetles when present in high concentrations, such as those occurring in fresh resin (Smith, 1966; Cook and Hain, 1988).

One of the best-recognized inciting factors in tree and forest health decline is deficiency in moisture availability (Craighead, 1925a; St. George, 1930; Manion, 1981; Mattson and Haack, 1987; Guarin and Taylor, 2005), which directly affects the fitness and survivorship of insect herbivores (Price, 1997) as well as host tree resistance mechanisms (Lorio and Hodges, 1968, 1977). Short-term deficiencies may result in recurrent bark beetle outbreaks of limited scale and extent (Struble, 1966). Long-term deficiencies are often correlated with large-scale outbreaks (Furniss and Carolin, 1977; Drooz, 1985; USDA Forest Service, 2004; Shaw et al., 2005). For example, in southern California the amount of ponderosa pine mortality associated with western pine beetle, *D. brevicomis* LeConte, infestations reached unprecedented levels after years of extended drought (USDA Forest Service, 2002). The availability of moisture to trees is not solely regulated by the amount of precipitation, but also by its distribution and storage, climatic and edaphic factors, tree physiology, forest structure and other factors (Pritchett and Fisher, 1987).

3. Western coniferous forests

3.1. Tree and stand factors associated with bark beetle infestations

Factors such as stand density, basal area or stand density index, tree diameter and host density are consistently identified as primary attributes associated with bark beetle infestations. Craighead (1925b) and Miller (1926) were among the first to demonstrate that slower growing trees were more susceptible to western pine beetle attack. Further investigations (Person, 1928, 1931) led to development of a classification system for rating ponderosa pine susceptibility to western pine beetle (Keen, 1936). Since that time, a considerable amount of effort has been devoted to the identification of tree and stand conditions associated with bark beetle attack in western coniferous forests. However, it is important to note that despite the existence of conducive stand conditions certain abiotic factors must also be met before large-scale infestations occur (Carroll et al., 2004).

3.1.1. Ponderosa pine forests

Sartwell (1971) presented data on radial growth and its relationship to mountain pine beetle, *D. ponderosae* Hopkins, attack and suggested that slow growth was indicative of nearly all trees killed by mountain pine beetle in the Pacific Northwest. From a sample of 666 attacked trees, 99.5% had a periodic annual increment of <0.24 cm for decades prior to attack. He also indicated that of nearly 4000 trees killed by mountain pine beetle, 91% had crown ratios $\leq 30\%$, suggesting that tree competition, primarily for soil moisture, fosters an increased likelihood of mountain pine beetle attack. Poorer sites experienced higher levels of mountain pine beetle-caused tree mortality than did high quality sites of similar initial stocking. The author concluded that thinning to reduce tree competition and increase individual tree growth may be critical for long-term prevention of mountain pine beetle outbreaks in ponderosa pine (Sartwell, 1971). Similarly, Larsson et al. (1983) observed that ponderosa pine vigor decreased as stand density increased.

McCambridge et al. (1982) examined the characteristics of ponderosa pine stands infested by mountain pine beetle in north-central Colorado. Initial (i.e., prior to infestation) basal area was significantly higher in areas that experienced large amounts of tree mortality compared to areas of moderate mortality, 28 and 22.3 m^2/ha, respectively. Initial numbers of trees and initial basal area were positively correlated with numbers of trees and basal area killed. The results suggest a higher probability of mountain pine beetle-caused tree mortality in dense ponderosa pine forests. Stand density has also been positively correlated with roundheaded pine beetle, *D. adjunctus* Blandford, infestation levels in the southwestern USA (Negrón, 1997; Negrón et al., 2000). Similarly, Olsen et al. (1996) examined spatial variation in ponderosa pine stands and concluded that stocking was higher in areas prone to mountain pine beetle infestation. The authors suggested that variation in stand conditions resulted in clusters of trees with different probabilities of infestation. They concluded that active management through thinning is critical to maintaining healthy trees that are less susceptible to mountain pine beetle attack (Olsen et al., 1996). Negrón and Popp (2004) reported that plots infested by mountain pine beetle had significantly higher total basal area, ponderosa pine basal area, stem density and stand density index.

Feeney et al. (1998) assessed the effects of thinning from below (alone and in combination with prescribed burning) on tree growth, leaf physiology and several environmental factors in ponderosa pine on the Gus Pearson Natural Area in Arizona. Soil water content was greater in thinned treatments than in the untreated control. Similar findings have been reported in northern Arizona (Kolb et al., 1998; Skov et al., 2005; Zausen et al., 2005) and western Montana (Sala et al., 2005), and can be attributed to increased water availability resulting from decreased tree competition. Trees in thinned treatments had greater foliar nitrogen content, needle toughness and basal area increment. Resin flow was also greater in the thinned and prescribed burned treatment than in the thinned treatment and control. The results suggest that restoration treatments improved tree vigor, growth and decreased the likelihood of bark beetle attacks on individual trees (Feeney et al., 1998). Similarly, Kolb et al. (1998) compared measures of tree susceptibility to bark beetle attack in thinned ponderosa pine plots in northern Arizona. Phloem thickness significantly increased with decreasing stand density. Duration of resin flow and 24 h resin flow were significantly higher in thinned plots of 6.9, 18.4 and 27.5 m^2/ha compared to the untreated control. Increases in these variables suggest improved host vigor and reduced likelihood of bark beetle attack (Kolb et al., 1998).

In Arizona, Stone et al. (1999) examined the effect of thinning on ponderosa pine trees the first year following such treatments. They reported, among other factors, an increase in volumetric soil water content, predawn xylem water potential, net photosynthetic rate, foliar nitrogen concentration and bud and needle size. The results suggest an increase in tree and stand health as a result of thinning by increasing foliar growth and uptake of water and nutrients, which agrees with data reported by others for similar stands (Wallin et al., 2004). Zausen et al. (2005) investigated the effects of thinning, and thinning and prescribed fire, on ponderosa pine water stress, oleoresin exudation pressure, phloem thickness, and radial growth. Phloem thickness and basal area increment were lower in unmanaged than in managed stands. In addition, tree competition (i.e., density) and water stress were positively correlated. Contrary to expectations, oleoresin exudation flow was greater in unmanaged (and thinned and burned) stands than in thinned only stands, which differs from Kolb et al. (1998). This may be due to standardization of tree dbh (diameter at 1.37 m in height) to 27–33 cm across all treatments and the shorter duration and lower intensity of thinning in Zausen et al. (2005) as compared to Kolb et al. (1998). In Kolb et al. (1998), an initial thinning in 1962 was followed by additional thinnings every decade to maintain a relatively constant stand density. In contrast, in Zausen et al. (2005) treatments created stands with a lower range of basal areas and thinnings were conducted only once in each stand 8–16 years prior to field measurements.

3.1.2. Lodgepole pine forests

Amman et al. (1977) summarized factors influencing the susceptibility of lodgepole pine forests to mountain pine beetle attack. Tree diameter and stand age, among other factors, were positively correlated with likelihood of mountain pine beetle attack. As a result, Cahill (1978) suggested the use of clearcutting and partial cuts to manage mountain pine beetle infestations with the primary objective of removing larger diameter trees (Cole and Amman, 1969; Roe and Amman, 1970; Safranyik et al., 1974; Mitchell and Preisler, 1991), which contain resources for significant brood production (Amman, 1972) and reduced intraspecific competition (Shrimpton and Thomson, 1985). Other authors have suggested that shorter rotations and maintenance (or promotion) of multiple tree species and age classes minimize the amount of mountain pine beetle-caused tree mortality (Roe and Amman, 1970; Safranyik et al., 1974; Taylor and Carroll, 2004; Whitehead et al., 2004). A heterogeneous landscape is thought to be more resistant and resilient to insect-caused disturbances (Price, 1997). Waring and Pitman (1985) observed that trees with low vigor were more heavily attacked by mountain pine beetle and some produced no resin (Waring and Pitman, 1983, 1985), the primary defense mechanism of conifers against bark beetle attack (Vité, 1961; Rudinsky, 1966; Reid et al., 1967; Smith, 1975; Hodges et al., 1979). Berryman (1978) proposed that phloem thickness, climatic suitability and host resistance were key variables necessary to predict the amount of mountain pine beetle-caused tree mortality in lodgepole pine forests and incorporated these factors into models (Amman, 1985).

3.1.3. *Douglas-fir forests*

Douglas-fir beetle, *D. pseudotsugae* Hopkins, infestations have been associated with mature stands of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and certain geological formations (Garrison-Johnston et al., 2003). This is consistent with the beetle's preference for larger diameter trees (Furniss et al., 1979, 1981; Shore et al., 1999). Negrón (1998) examined the probability of infestation and extent of tree mortality caused by Douglas-fir beetle in the Colorado Front Range. Several characteristics, such as poor growth, stand density and the amount of Douglas-fir, were positively correlated with infestation levels. Shore et al. (1999) reported that infested groups of trees were positively correlated with mean dbh, tree height, age, bark and phloem thickness and poor growth. All of these factors are consistent with our understanding of Douglas-fir beetle ecology (Schmitz and Gibson, 1996).

3.1.4. *Spruce forests*

Massey and Wygant (1954) reported the mean diameter of attacked Engelmann spruce, *Picea engelmannii* Parry ex Engelm., decreased during a spruce beetle, *D. rufipennis* (Kirby), outbreak on White River National Forest in Colorado thereby suggesting a preference by spruce beetle for larger diameter trees. Dymerski et al. (2001) reported similar results in spruce beetle-affected Engelmann spruce stands in central Utah. In Alaska, Hard et al. (1983) and Hard (1985) examined conditions during the beginning of a spruce beetle outbreak in white spruce, *P. glauca* (Moench) Voss. Attacked trees were characterized by low radial growth, which was inversely related to tree density. Holsten (1984) established a transect across mixed spruce forests and reported higher levels of tree mortality on north-facing slopes and a preference by spruce beetle for larger diameter trees. Periodic annual increment (last 5 years) was 0.25 cm for infested and 0.51 cm for uninfested trees. These data agree with those of Hard et al. (1983) who indicated that spruce beetle exhibited a preference for slow growing trees. Holsten et al. (1995) reported that, following a spruce beetle epidemic, increased radial growth in surviving trees, primarily as a result of reductions in tree density and competition, reduced stand susceptibility to future infestations in the short-term.

3.1.5. *True fir forests*

Few data are available on true fir forests. McMillin et al. (2003) related the extent of subalpine fir, *Abies lasiocarpa* (Hook.) Nutt., mortality caused by western balsam bark beetle, *Dryocoetes confusus* Swaine, to forest conditions in north-central Wyoming. Significant positive linear relationships were found between amount of fir mortality and percentage of subalpine fir trees, subalpine fir basal area, and subalpine fir stand density index. In addition, a significant positive linear relationship was found between percentage of wind-thrown fir and percentage of logs utilized by western balsam bark beetle. Additional studies are required to more fully understand factors associated with bark beetle infestations in true fir forests.

3.1.6. *Pinyon-juniper forests*

Few data are available on pinyon-juniper forests. Negrón and Wilson (2003) examined attributes of pinyon pine, *P. edulis* Engelm., forests associated with the probability of infestation by pinyon ips, *I. confusus* (LeConte), on the Coconino National Forest in Arizona. Results suggested that infestations were related to stand density and dwarf mistletoe, *Arceuthobium divaricatum* Engelmann, infection, among other factors. Within infested plots, ips-killed trees were significantly larger in diameter, had higher mistletoe infection levels and smaller crown ratios. Pinyon pine stand density index was a good predictor of the likelihood of infestation at the plot level as 82% of cases were correctly classified.

To our knowledge, published data are not available for other cover types, such as Sierra Nevada mixed conifer, and bark beetle species, such as fir engraver, *Scolytus ventralis* LeConte. Studies are required to identify stand characteristics associated with bark beetle infestations in these and other conifer systems.

3.2. *Risk and hazard rating models*

Rating systems are intended to serve as general guides that aid in the identification of susceptible stands. These models use factors that have been correlated with bark beetle infestations (see Section 3.1) to predict probability of infestation or extent of tree mortality (Negrón, 1997, 1998). Many of these factors are consistent among cover types, which is interesting considering the many sampling methods, statistical analyses and modeling efforts used in their development. Our use of the terms *hazard* and *risk* follow the definitions of Waters (1985) based on Paine et al. (1984). For forested stands, hazard relates to factors, such as tree species composition, age-size structure, stand density and precipitation, which affect the likelihood of bark beetle occurrence. We also use the term *probability of infestation* to describe the likelihood of attack and *extent of mortality* to describe potential levels or amount of tree mortality when bark beetle epidemics occur (Negrón, 1997, 1998). Risk is a function of insect presence, abundance and distribution as it relates to stand hazard or potential for tree mortality. Hedden (1981) provides a useful review of risk and hazard rating systems.

Different types of rating systems are available. Some consist of numerical values assigned to tree or stand characteristics that result in a classification of hazard (e.g., Schmid and Frye, 1976). Others use quantitative techniques, such as discriminant analysis, which generate equations that use tree or stand characteristics to classify the likelihood of attack (e.g., Shore et al., 1999). Classification models have also been used to develop rating systems. Reynolds and Holsten (1994, 1996) used this technique for estimating the extent of tree mortality caused by spruce beetle in Alaska. Negrón et al. (1999) used regression analyses to develop models that estimate the amount of Douglas-fir beetle-caused tree mortality. Incorporation of insect population data into risk rating systems is a challenging task particularly in reference to bark beetles. Such data are not readily available, and spatial and temporal patterns of bark beetle populations are not well understood. Temporal fluctuations in host vigor, as influenced by climatic and other factors, further complicate the relationship.

3.2.1. *Ponderosa pine forests*

Negrón and Popp (2004) established 35 clusters of mountain pine beetle-infested and uninfested plots in ponderosa pine forests of north-central Colorado. Based on data collected from the plots, the authors developed several classification models for estimating the probability of infestation by mountain pine beetle. The simplest model indicated a 50% greater probability of infestation when ponderosa pine basal area was $>17.1\ \text{m}^2/\text{ha}$ than when ponderosa pine basal area was $\leq 17.1\ \text{m}^2/\text{ha}$ (Negrón and Popp, 2004).

In the Sacramento Mountains of New Mexico, Negrón (1997) developed probability of infestation and extent of tree mortality models for the roundheaded pine beetle in ponderosa pine. Periodic annual increment (last 5 years) was significantly lower in infested than in uninfested plots. A classification model to estimate the probability of infestation indicated that 5-year growth rates of ≤ 0.66 cm resulted in a 95% probability of infestation.

In the Pinaleño Mountains of Arizona, plots infested with roundheaded pine beetle had significantly higher stand densities compared to uninfested plots (Negrón et al., 2000). A classification model indicated a 60% probability of infestation when periodic growth ratio (ratio of most recent 5-year growth to that of the previous 5 years) was ≤ 1.14. A periodic growth ratio >1.14 resulted in a 20% probability of infestation. A second classification model found a 72% probability of infestation when ponderosa pine basal area was $>24.1\ \text{m}^2/\text{ha}$. In the Pine Valley Mountains of Utah, stand density index was significantly greater in infested plots than in uninfested plots (Negrón et al., 2000). Classification models indicated a probability of infestation of 93% with a growth rate ≤ 0.66 cm and 23% with >0.66 cm. A second classification model indicated a 91% probability of infestation with ponderosa pine basal area $>57.4\ \text{m}^2/\text{ha}$ compared to 32% with a ponderosa pine basal area $\leq 57.4\ \text{m}^2/\text{ha}$. For both locations, tree mortality models were developed using ponderosa pine basal area and growth rate 5 years prior to insect outbreak. One example is a regression tree for the Pinaleño Mountains that indicated an expected mortality of $16.3\ \text{m}^2/\text{ha}$ when ponderosa pine basal area was $\leq 35.6\ \text{m}^2/\text{ha}$, an expected mortality of $32.3\ \text{m}^2/\text{ha}$ when ponderosa pine basal area was $>35.6\ \text{m}^2/\text{ha}$ but $\leq 73.5\ \text{m}^2/\text{ha}$, and an expected mortality of $75.8\ \text{m}^2/\text{ha}$ when ponderosa pine basal area was $>73.5\ \text{m}^2/\text{ha}$ (Negrón et al., 2000).

3.2.2. *Lodgepole pine forests*

Bollenbacher and Gibson (1986) described a management strategy to limit the adverse effects of mountain pine beetle outbreaks in lodgepole pine forests of Montana. The authors reported a list of attributes that were used to evaluate stands for favorable thinning responses. These included site productivity, slope, average diameter, age, density, elevation, wind firmness, current mountain pine beetle activity levels, tree vigor and other resource objectives. The authors stated that stands of high productivity, 60–125 years old, at <1829 m elevation and with basal areas $>29.8\ \text{m}^2/\text{ha}$, should receive priority consideration. Stands with current beetle infestation rates of $>10\%$ could result in excessive mortality in residual trees if thinning is not completed prior to the next mountain pine beetle flight period (Bollenbacher and Gibson, 1986).

Shore and Safranyik (1992) developed a risk rating system for mountain pine beetle that included stand susceptibility and beetle pressure indices. Factors included in this model are percentage of susceptible pine basal area, which incorporates factors such as tree diameter and stand composition, age, tree density, and location, which captures latitude, longitude, and elevation. The beetle pressure index is a combination of the size and proximity of an infestation to the modeled stand. Risk is calculated using a weighted equation (Shore and Safranyik, 1992).

3.2.3. *Whitebark pine forests*

Perkins and Roberts (2003) collected data from whitebark pine, *Pinus albicaulis* Engelm., stands in central Idaho to estimate the probability of attack by mountain pine beetle. Logistic regression models were calibrated from reconstructed pre-epidemic stand conditions and post-epidemic tree mortality levels resulting from a widespread outbreak that occurred from 1909 to 1940. Basal area and stand density index (SDI) were key factors differentiating attacked and unattacked stands. Whitebark pine stands with basal areas $>10\ \text{m}^2/\text{ha}$ or with an $\text{SDI} > 80$ had a 100% probability of being attacked.

3.2.4. *Douglas-fir forests*

Weatherby and Thier (1993) developed a rating model for Douglas-fir beetle based on stand basal area, proportion of stand basal area represented by Douglas-fir, average stand age, and average dbh of all Douglas-firs >22.9 cm. Basal areas of $>27.5\ \text{m}^2/\text{ha}$, proportion of stand basal area in Douglas-fir $>50\%$, average stand age >120, and average dbh of Douglas-fir sawtimber >35.6 cm were characteristic of stands with a high likelihood of Douglas-fir beetle infestation.

Negrón et al. (1999) presented models developed from empirical data to estimate the extent of tree mortality once a Douglas-fir beetle infestation occurs. As an example, if stand basal area of Douglas-fir is $\leq 36\ \text{m}^2/\text{ha}$, expected mortality averages $14\ \text{m}^2/\text{ha}$; if Douglas-fir basal area is $>36\ \text{m}^2/\text{ha}$ but $\leq 69\ \text{m}^2/\text{ha}$, expected mortality averages $29\ \text{m}^2/\text{ha}$; and if Douglas-fir basal area is $>69\ \text{m}^2/\text{ha}$, expected mortality averages $62\ \text{m}^2/\text{ha}$. Shore et al. (1999) evaluated factors that influence the probability of Douglas-fir beetle infestation based on 19 infested and uninfested tree groups in British Columbia. An initial model used mean diameter, phloem thickness and aspect while a second model included mean tree height, phloem thickness, aspect and a standardized variable (tree dbh/previous 10 years growth).

3.2.5. *Spruce forests*

The most commonly used hazard rating system in spruce forests is that of Schmid and Frye (1976). The system uses the following variables: physiographic location (Knight et al., 1956), mean dbh of live spruce >25.4 cm (Massey and Wygant, 1954), basal area (Schmid and Hinds, 1974) and proportion of spruce in the canopy (Knight et al., 1956). Stands growing on well-drained sites and with mean dbh of live spruce >25.4 cm being >40.6 cm (i.e., large-diameter trees), basal areas >34.3 m^2/ha and proportions of spruce >65% are more susceptible to spruce beetle attack (Schmid and Frye, 1976). Reynolds and Holsten (1994, 1996) used data from 374 plots to predict spruce mortality on the Kenai Peninsula of Alaska, expert knowledge from various scientists, and an analytic hierarchy process method to develop a risk model. The process identified stand hazard (the presence of factors conducive to spruce beetle infestation) and the occurrence of windthrow as the two most important factors in stand risk.

3.2.6. *Usefulness of rating models*

Some authors have questioned the accuracy of risk and hazard rating systems. Bentz et al. (1993) evaluated four mountain pine beetle rating systems, those of Amman et al. (1977), Berryman (1978), Mahoney (1978) and Schenk et al. (1980), using data from 105 lodgepole pine stands in Montana. They reported that none was found to provide adequate predictions and identified several important factors that should be considered while developing rating systems. Their results suggest that these systems may be site (or region) specific and that caution should be taken when using models in areas other than where they were developed.

3.3. *Effectiveness of thinning for preventing bark beetle infestations*

Thinning is defined as a cultural treatment made to reduce stand density primarily to improve growth or enhance forest health (Helms, 1998). Specifically, thinning is commonly used to redistribute growing space to desirable trees, utilize anticipated mortality resulting from stem exclusion, create early cash flows, set back succession and reduce risks associated with fire, insects and diseases (Smith, 1986a). The tools and methods by which thinning is implemented are quite diverse, and their application can result in significantly different stand structures. In general, low thinning removes trees from smaller diameter classes (over-topped trees), crown thinning focuses on mid-canopy trees, and selection thinning focuses on the largest trees in the stand. Depending on the insect species of concern, each of these methods would have a functionally different response on the abundance and distribution of preferred hosts as well as that of the insect herbivore.

In western North America, thinning has long been advocated as a preventive measure to alleviate or reduce the amount of bark beetle-caused tree mortality (Furniss and Carolin, 1977; McGregor and Cole, 1985; Wood et al., 1985; Whitehead et al., 2004) (Fig. 2A and B). However, thinnings conducted in a careless manner may also result in physical damage to residual trees, soil compaction and increased rates of windthrow (Blanche et al., 1985a; Wood et al., 1985). While thinning may reduce tree and stand susceptibility to bark beetle attack, there may be elevated potentials for increases in subcortical insects and root pathogens (Harrington et al., 1985; Wood et al., 1985; Witcosky et al., 1986). In some cases, root diseases have been shown to increase the susceptibility of trees to bark beetle attack (Goheen and Cobb, 1980). However, with knowledge of these potential risks, prudent silvicultural treatments can be implemented to minimize potential unwanted consequences.

Fig. 2. Thinning conducted in *P. ponderosa* stands to improve forest health conditions, Dixie National Forest, Utah, USA, 2004 (A: pretreatment, B: post-treatment). Photo: A.S. Munson, USDA Forest Service, Forest Health Protection.

3.3.1. Ponderosa pine forests

One of the first published accounts of thinning to reduce mountain pine beetle damage in ponderosa pine was based on the supposition that trees would be less likely to succumb to attack if their vigor was increased by removing competition (Eaton, 1941). Later, Sartwell and Stevens (1975) examined 44 groups of mountain pine beetle infestation in the Black Hills of South Dakota. From this survey, the authors proposed that stands containing >34.4 m^2/ha were more susceptible to mountain pine beetle infestation and therefore required thinning. As a result, Sartwell and Dolph (1976) conducted a thinning study in ponderosa pine in eastern Oregon. Although tree mortality in thinned areas was lower after 5 years, mountain pine beetle pressure was not extensive during this time. However, after Sartwell and Dolph (1976) published their results, the study area was subjected to one of the largest mountain pine beetle outbreaks on record. Two thinning treatments, 5.5 m × 5.5 m and 6.4 m × 6.4 m spacings, experienced little tree mortality (Dolph, 1982). These data, though not generated in a controlled experiment, provide strong evidence supporting the value of thinning for reducing mountain pine beetle impacts in ponderosa pine.

Similarly, McCambridge and Stevens (1982) conducted an evaluation of thinning treatments in ponderosa pine on the Black Hills National Forest in South Dakota. Reductions in the amount of mountain pine beetle-caused tree mortality were observed 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 as compared to 19.5, 17.2, and 10.3 m^2/ha in thinned stands (McCambridge and Stevens, 1982). Again these data, while not generated during a controlled experiment, provide strong evidence supporting the value of thinning in ponderosa pine.

In 1984, the USDA Forest Service began a study to determine the relationship between stand density and occurrence of mountain pine beetle-caused tree mortality in partially cut ponderosa pine stands on the Black Hills National Forest. Beetle activity was monitored in each 1 ha plot over a 17-year period (Schmid and Mata, 2005; Table 1). The authors concluded that the effectiveness of thinning unmanaged ponderosa pine forests to residual densities between 18.4 and 27.5 m^2/ha for reducing mountain pine beetle susceptibility seemed questionable (Schmid and Mata, 2005). However, they suggested that these results may be confounded by the fact that study plots were surrounded by extensive areas of unmanaged forest where mountain pine beetle populations were epidemic. Schmid and Mata (2005) stated 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 those of lower tree density. Their data indicate that ponderosa pine stands of ≤ 16.1 m^2/ha were less frequently attacked by mountain pine beetle (Table 1). These results stress the importance of managing forest stands at appropriate spatial scales.

Table 1
Mean percentage of *P. ponderosa* attacked by *D. ponderosae* 17 years after thinnings were conducted on the Black Hills National Forest, South Dakota, USA (adapted from Schmid and Mata, 2005)

Treatments[a]	Mean percentage of trees attacked (%)
GSL 13.8/16.1	9
GSL 18.4/20.7	53
GSL 23.0/25.3	48
Untreated control	77

[a] GSL = growing stock level (basal area (m^2/ha)).

Fiddler et al. (1989) showed that thinning significantly reduced the amount of ponderosa pine mortality caused by mountain pine beetle in northeastern California. No tree mortality occurred in stands of <9 m^2/ha of basal area, which agrees with the optimal stocking level of 11 m^2/ha described by Oliver (1979, 1995). Mortality was reduced in thinned plots regardless of the level of thinning.

Sánchez-Martínez and Wagner (2002) studied the relative abundance, based on trap catch, of bark beetles (several species) and bark beetle-attacked trees between managed and unmanaged stands in northern Arizona. Four stand conditions were assessed: (1) unmanaged stands with high tree density, (2) thinned stands, (3) thinned and burned (with prescribed fire) stands and (4) stands that had been burned within the last few years by high severity wildfires. Significantly more southern, *D. frontalis* Zimmermann, and western pine beetles (combined) were collected in baited multiple-funnel traps in thinned, and thinned and burned stands. The authors detected no significant difference in bark beetle infestation rates among treatments, but few trees were attacked by bark beetles overall (21 of 2136 trees sampled). The authors suggested that the relative population levels of bark beetles showed no significant sensitivity to changes is stand structure and fire occurrence or that changes were not apparent at the stand level. They concluded "...that high density conditions in unmanaged stands make them susceptible to other disturbances such as stand replacing wildfires, but their susceptibility to large bark beetle outbreaks could not be demonstrated on our study sites during this time period...".

3.3.2. Lodgepole pine forests

Thinning is recommended for maturing lodgepole pine stands based on data relating mountain pine beetle outbreaks to stand age, density and diameter distributions (see Sections 3.1 and 3.2). Variations on thinning treatments, including diameter-limit cutting (McGregor et al., 1987), thinning to reduce basal area (Amman et al., 1977; Cahill, 1978), and selective removal of trees with thick phloem (Hamel, 1978) have been examined. Today, spaced thinnings that optimize the effects of microclimate, inter-tree spacing and tree vigor, are proposed as a method to "beetle-proof" stands (Whitehead et al., 2004; Whitehead and Russo, 2005). The prescription requires thinning from below (low thinning) and wide residual inter-tree spacing to create stand conditions that are detrimental to beetle survival (Table 2).

Cole et al. (1983) conducted a diameter limit thinning study in lodgepole pine on the Shoshone National Forest in Wyoming. Four diameter limit treatments were included in the study, removing all trees >17.8 cm dbh, removing all trees >25.4 cm

Table 2
Favorable pre-treatment conditions for reducing *D. ponderosae*-caused tree mortality in *P. contorta* stands by thinning, British Columbia (adapted from Whitehead and Russo, 2005)

Parameter	Value
Stand composition	>80% lodgepole pine
Stand age	60–110 years at breast height
Stand density	750–1500 trees/ha (>7.5 cm dbh)
Average diameter	>20 cm dbh
Elevation	<1500 m

dbh, removing all trees >30.5 cm dbh, and a thinning treatment with a spacing objective of 247 trees/ha. The authors reported that 26.5% of trees were killed by mountain pine beetle in untreated control plots compared to <3% in all four of the thinning treatments.

In a study conducted during increasing mountain pine beetle populations, McGregor et al. (1987) examined the effect of two diameter limit thinning treatments (all trees removed >25.4 cm and 30.5 cm dbh) and three thinning treatments to specified residual densities (18.4, 23.0 and 27.5 m^2/ha). In general, the amount of mountain pine beetle-caused tree mortality was significantly reduced by thinning, however, there was no significant difference among levels of thinning (Table 3).

Preisler and Mitchell (1993) used autologistic regression models to analyze mountain pine beetle colonization in thinned and unthinned lodgepole pine in Oregon. Results confirmed attacks in unmanaged forests were related to tree diameter, with preference exhibited for larger diameter trees (Cole and Amman, 1969; Roe and Amman, 1970; Safranyik et al., 1974; Amman et al., 1977). Thinned plots were initially reported to be unattractive to beetles, but when large numbers of attacks occurred, colonization rates were similar to those in unthinned plots (Preisler and Mitchell, 1993). Conditional probabilities of attack for trees near other attacked trees were actually greater in thinned plots, suggesting the wider spacings did not interfere with host finding when populations became epidemic. Similarly, Amman et al. (1988a,b) studied the effects of spacing and diameter distributions and concluded that tree mortality was reduced as basal area was lowered. However, if the stand was in the path of an ongoing mountain pine beetle epidemic, spacing and density had little effect. These data disagree with McCambridge and Stevens (1982) who reported decreases in the amount of mountain pine beetle-caused tree mortality in ponderosa pine in areas thinned during an active infestation.

Table 3
Mean percentage of *P. contorta* killed by *D. ponderosae* 5 years after thinnings were conducted on the Kootenai and Lolo National Forests, Montana, USA (adapted from McGregor et al., 1987)

Treatment[a]	Mean percentage of trees killed[b]	
	Kootenai	Lolo
25.4 cm dbh limit cut	6.0 ± 8.4 a	6.9 ± 2.5 a
30.5 cm dbh limit cut	8.6 ± 0.6 a	17.1 ± 6.5 a
18.4 m^2 residual BA	7.8 ± 6.7 a	6.7 ± 7.9 a
23.0 m^2 residual BA	4.0 a	6.0 ± 4.4 a
27.6 m^2 residual BA	38.6 ± 41.2 ab	13.1 ± 12.2 a
Untreated control	93.8 ± 10.8 b	73.1 ± 28.5 b

[a] dbh: diameter at breast height (1.37 m); BA: basal area (m^2/ha).

[b] Means ± S.D. followed by the same letter are not significantly different ($P > 0.05$; Tukey's).

Anhold et al. (1996) described three relative density zones corresponding to different levels of mountain pine beetle susceptibility in young lodgepole pine stands based on nonlinear tree mortality/stand density relationships (Anhold and Jenkins, 1987). The first density management regime involved carrying a low density (i.e., $\mathrm{SDI} < 140$) throughout the rotation. The second density management regime was designed to maintain relative density above a threshold level (i.e., $\mathrm{SDI} > 245$). Stands with density indices between these two thresholds were found to be very susceptible to mountain pine beetle attack and subsequent tree mortality. These authors describe a unique relationship that has not been reported elsewhere.

Mata et al. (2003) determined periodic diameter and basal area growth for lodgepole pine stands thinned to varying growing stock levels (GSL) at five locations in Colorado and Wyoming. In general, diameter growth in thinned plots was significantly greater than untreated controls. Data from these stands were entered into the susceptibility rating methods of Amman et al. (1977), Shore and Safranyik (1992) and Anhold et al. (1996) to determine stand susceptibility and results were discussed in terms of general applicability of these methods to thinned stands. Basal area growth was used to estimate the length of time required to reach specific susceptibility thresholds for mountain pine beetle infestation. For example, barring substantial tree mortality, GSL 80 (18.4 m^2/ha) stands were estimated to reach the susceptibility threshold of 27.5 m^2/ha in <25 years suggesting the need for a thinning interval of approximately 25 years.

Whitehead et al. (2004) and Whitehead and Russo (2005) examined side-by-side comparison trials to investigate the efficacy of thinning treatments for reducing the amount of mountain pine beetle-caused lodgepole pine mortality in British Columbia. These treatments were installed in 1991 to determine if changes in microclimate and tree vigor translated to a lower frequency of mountain pine beetle attacks. Green to red attack ratios (based on absence or presence of crown fade), total number and density of trees attacked (Table 4) and mortality due to beetle attack were lower in thinned stands than in corresponding untreated areas at every site. In untreated units, >80% of all trees >20 cm dbh were attacked (Table 4) and mortality average 135 trees/ha compared to 31 trees/ha in thinned stands. The data strongly suggest that thinning mature lodgepole pine stands from below to a uniform residual inter-tree spacing of at least 4 m is an effective tool for preventing mountain pine beetle infestations.

3.3.3. Spruce forests

Experiments have not been specifically conducted to determine the effects of thinning on spruce beetle activity. Single tree and group tree selection methods are often used to regenerate Engelmann spruce in the Rocky Mountains. The

Table 4
Cumulative number of *P. contorta* attacked by *D. ponderosae* 9–12 years after thinnings were conducted, British Columbia, Canada (adapted from Whitehead et al., 2004)

Location and treatment year	Treatment	No. of trees attacked/ha	Green:red attack ratio[a]
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

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

creation of gaps within these uneven-aged stands promotes spatial heterogeneity and species and age class diversities. Although residual stand structure may initially be composed of larger numbers of large diameter trees that are more susceptible to spruce beetle disturbance (Massey and Wygant, 1954), the gaps provide growing space for new age cohorts of younger trees that are much less susceptible to attack (Dymerski et al., 2001; Fig. 3). Some authors have speculated that the presence of nonhosts or unsusceptible hosts masks the apparency of susceptible hosts thus reducing overall stand susceptibility (Price, 1997). The relationship is not relevant to those forest types, such as ponderosa pine in the central Rockies, which are monotypic.

To our knowledge, published data are not available for other cover types. Additional studies are required to address these knowledge gaps.

3.3.4. *Effects of tree residues resulting from thinning operations on western bark beetle activity*

Several bark beetle species are attracted to slash created during thinning operations (Furniss and Carolin, 1977). Management guidelines are available (Craighead, 1927; Schmid, 1977; Fellin, 1980; Massey and Parker, 1981; Parker, 1991; Villa-Castillo and Wagner, 1996; Kegley et al., 1997). Engraver beetle, *Ips* spp., attacks on residual trees following thinning occur during the initial slash colonization period in some locations (Sartwell, 1970), but not others. In late summer, slash produced by lop-and-scattered treatments is suitable for colonization, but *Ips* flight activity is generally reduced (Fettig et al., 2004). Slash that is not colonized during early fall is usually unsuitable for colonization the following spring (Parker, 1991) or may be colonized by competitors (Craighead, 1927). Overwintering mortality, due to prolonged periods of low temperatures, may be significant in some bark beetle species (Amman, 1973), but not others (Safranyik and Linton, 1991).

Fig. 3. Thinning conducted in *P. engelmannii* stands to improve forest health conditions, Unita National Forest, Utah, USA, 2005. Photo: A.S. Munson, USDA Forest Service, Forest Health Protection.

Steed and Wagner (2004) reported that pine engraver, *I. pini* (Say), exhibits a preference for larger diameter logs. Total log length seems to have little effect on colonization, as the cutting of slash into short pieces (61 cm in length) was not effective in deterring colonization or minimizing reproductive success. The results support past recommendations that slash management efforts should concentrate on removing larger diameter material or rendering the phloem unsuitable for colonization through physical scarring or other techniques (Parker, 1991). Villa-Castillo and Wagner (1996) evaluated the effects of light intensity on the behavior and performance of pine engraver adults and brood in ponderosa pine. The authors reported that logs exposed to high natural light intensity (e.g., low density stands) were attacked less frequently and had lower brood production than logs exposed to low or moderate light densities.

Hindmarch and Reid (2001a) investigated how changes in forest structure due to thinning of mature lodgepole pine affected pine engraver reproduction in felled trees. Male beetles in thinned stands attracted more females than in unthinned stands. Also, females in thinned stands extended their egg galleries farther, laid more eggs and had higher egg densities than in unthinned stands (Hindmarch and Reid, 2001a). Hindmarch and Reid (2001b) found coarse woody debris was more abundant in thinned stands the first year following thinning, but then returned to background levels. Coarse woody debris serves as important habitat for several bark beetle species, including pine engravers (Kegley et al., 1997).

A relatively recent slash management treatment involves chipping of tree residues. Many land managers consider this to be an ideal treatment as woody biomass is retained on site for nutrient cycling; fire potential and soil impacts are reduced; and host material is eliminated in comparison to piled-and-burned and lopped-and-scattered treatments (Six et al., 2002; Fig. 4A–D). Fettig et al. (2006) reported a three-fold increase in the percentage of trees attacked by bark beetles (several species) in chipped versus lopped-and-scattered plots in Arizona and California. The authors suggested that extremely high levels of monoterpenes produced by chipping, and released into open airspace, may account for this effect observed for several bark beetle species. Higher levels of bark beetle colonization were associated with spring treatments, which corresponded with peak adult beetle flight periods as measured by baited multiple-funnel trap captures. Removal of chips from the base of residual trees resulted in a 20% reduction in bark beetle attacks, but was not statistically significant (Fettig et al., 2006). At the end of the 2-year study, there was no significant difference in the amount of bark beetle-caused tree mortality. However, the authors

Fig. 4. Hazardous fuel reduction treatments in *P. ponderosa* forests (A) chipped, (B) chipped-and-raked, (C) lop-and-scattered, and (D) untreated control, Tahoe and Kaibab National Forests, California and Arizona, USA, 2004. Photos: C.J. Fettig, USDA Forest Service, Pacific Southwest Research Station (A and D) and J.D. McMillin, USDA Forest Service, Forest Health Protection (B and C).

cautioned that the negative effects of prolonged and large numbers of bark beetle attacks (e.g., red turpentine beetle, *D. valens* LeConte, among others) may not be realized for some time (Fettig et al., 2006).

3.4. Effects of prescribed fire treatments on western bark beetle activity

Prescribed fire is often used to reduce the buildup of hazardous fuels, enhance wildlife habitat, improve grazing, thin overstocked stands, control some insects and diseases, prepare sites for regeneration and restore fire-adapted forest ecosystems. Forest managers must plan and execute prescribed burns carefully in order to minimize injury to desirable residual trees while still fulfilling management objectives. Bark beetles are often considered the most important mortality agent following fires in coniferous forests (Miller and Patterson, 1927; Fischer, 1980; Ryan and Reinhardt, 1988; McCullough et al., 1998; Bradley and Tueller, 2001; Fowler and Sieg, 2004; Parker et al., 2006; among others). Sublethal heating of critical plant tissue can stress trees, which then are more susceptibility to bark beetle attack (Elkin and Reid, 2004). Research efforts have focused on documenting the effects of mixed-severity wildfire and prescribed fire on subsequent amounts of bark beetle-caused tree mortality (Geiszler et al., 1984; McIver, 2001). In reference to prescribed fire, perhaps most significant is the National Fire and Fire Surrogate Study, a large-scale interdisciplinary study examining the ecological consequences of reintroducing fire and fire surrogate treatments (e.g., thinning) back into fire-adapted forest ecosystems (McIver, 2001; http://www.fs.fed.us/ffs). Some investigators, acknowledging a direct relationship between fire injury and bark beetle attacks, have focused on manipulation of prescribed burn treatments to reduce subsequent tree mortality (Ganz et al., 2002; Fettig et al., 2005; Schwik et al., 2006). Extensive amounts of bark beetle-caused tree mortality may exacerbate problems associated with large fuel loads and fire occurrence in some cover types (Covington and Moore, 1994), but not others (Bebi et al., 2003). Parker et al. (2006) provides an extensive review of the interactions between fire (prescribed and wildfire) and insects in coniferous forests of the interior western USA, which likely has broader applicability.

Following prescribed fire, bark beetles attack ponderosa pines with greater crown damage more frequently than trees with less crown damage. However, trees must have enough green phloem to permit successful colonization by some species, such as western pine beetle (Fischer, 1980; Parker et al., 2006). Wallin et al. (2003) examined the relationships among fire injury, tree physiological condition and tree susceptibility to bark beetles (several species) in northern Arizona. The proportion of successful colonization attempts by *Ips* and *Dendroctonus* spp. was low, but was generally positively related to intensity of crown scorch. Douglas-fir beetles are attracted to trees with only moderate amounts of crown scorch (Furniss, 1965; Flanagan, 1996; Parker et al., 2006). A high percentage of large diameter Douglas-fir that are initially classified as surviving a mixed-severity wildfire may ultimately die due to beetle attack (Weatherby et al., 1994). Similar impacts can occur following more severe prescribed fires. Crown scorch occurring during the growing season may have more severe effects and consequently results in greater risk of insect attack than during the dormant season (Fischer, 1980). McHugh et al. (2003) examined the activity levels of several bark beetle species associated with a spring wildfire, summer wildfire and fall prescribed fire in northern Arizona. The percentage of trees attacked by *Dendroctonus* and *Ips* species was lowest following the fall fire (11% of total trees), intermediate following the summer fire (19%) and highest after the spring fire (41%). Measures of fire severity effects and insect activity were used to develop logistic regression models of tree mortality. In general, tree mortality rates were low until crown damage exceeded 70–80% for unattacked trees, 40–50% for trees with partial (patch or strip) bark beetle attacks, and 30–40% for trees that were mass attacked (McHugh et al., 2003). In the central Sierra Nevada, Schwik et al. (2006) found the probability of bark beetle attack (several species) on pines did not differ between early and late season burns, while the probability of attack on firs was greater following early season burns. Bradley and Tueller (2001) investigated the effects of low intensity, late-season prescribed fire on Jeffrey pine, *P. jeffreyi* Grev. & Balf., and associated short-term responses of bark beetles (several species) in northern California. Results showed a highly significant correlation between burning and bark beetle infestation (Bradley and Tueller, 2001). Over 24% and <1% of trees in prescribed burned and unburned plots were attacked, respectively.

Interactions between pathogenic fungi and bark beetles may also be of importance. For example, fire-scarred boles may be infected by decay fungi (Geiszler et al., 1980). Mountain pine beetle more frequently colonizes lodgepole pine infected with decay (Gara, 1988; Parker et al., 2006).

4. Southern coniferous forests

Bark beetles are among the most destructive pests of southern pine forests and the southern pine beetle is by far the most important tree killer. This species has been the target of more aggressive and sustained direct control programs than any other bark beetle in the USA.

4.1. Tree and stand factors associated with southern pine beetle infestations

Belanger and Malac (1980) and Coster and Searcy (1981) summarized some of the site and stand conditions associated with southern pine beetle infestations (Table 5). Outbreaks have also been associated with climatic factors that stress forests at the landscape level (King, 1972; Kalkstein, 1976), an abundance of susceptible hosts (Hedden, 1978; Coulson, 1979; Mawby and Hain, 1985), and other factors (Coulson, 1980; Turchin et al., 1991). Typically, southern pine beetle outbreaks last 3–4 years before populations decline to endemic or even undetectably low levels, although some persist for decades (Price et al., 1998). Factors which result in population declines are poorly understood, but contributing factors include an increase in natural enemies, interspecific competition with other bark and wood-boring insects, increase in blue stain fungi, lack of susceptible hosts, unfavorable weather conditions or a combination of these and other factors (Moore and Thatcher, 1973; Coulson, 1980; Moser and Dell, 1980; Bridges, 1985; Turchin et al., 1991; Clarke and Billings, 2003; among others).

In early or incipient stages of a southern pine beetle outbreak, resources such as lightning-struck trees are exploited (Hodges and Pickard, 1971; Coulson et al., 1983; Lovelady et al., 1991). These trees serve as focal points of multiple-tree infestations (often termed spots), presumably due to changes in resin flow, monoterpene fractions, carbohydrates and the water content of bark (Hodges and Pickard, 1971; Lorio and Hodges, 1977; Blanche et al., 1985b; Dunn and Lorio, 1993; Tisdale et al., 2003a). Total resin flow is a major factor in conferring resistance to invasion by southern pine beetle and its associated fungi (Brown et al., 1987; Tisdale et al., 2003b). A relationship between the composition and production of oleoresin and water stress (Hodges and Lorio, 1975; Hodges et al., 1979; among others) may explain why oleoresin production is greater in thinned than unthinned loblolly pine stands (Brown et al., 1987). DeAngelis et al. (1986) reported that age and rate of radial growth influenced the formation and development of radial resin ducts, which may explain why decreased radial tree growth and southern pine beetle infestations are correlated

Table 5
Some factors characteristic of stands susceptible to *D. frontalis* attack in the southern USA (adapted from Belanger and Malac, 1980)

Coastal plain	Piedmont	Appalachian mountains
Dense stocking	Dense stocking	Dense stocking, natural regeneration
Declining radial growth	Declining radial growth	Declining radial growth
Poorly drained soils	High clay content	Southern aspects
High percentage of shortleaf and loblolly pine	High percentage of shortleaf pine	High percentage of shortleaf and/or pitch pine

(Coulson et al., 1974). Hodges et al. (1979) compared the chemical and physical properties of the oleoresin in four pine species, loblolly, shortleaf, *P. echinata* Mill., slash, *P. elliottii* Engelm., and longleaf pines, *P. palustris* Mill., and concluded there were differences in their relative susceptibility that were best explained by differences in resin flow characteristics. These traits are significant, predictable and heritable. Efforts to identify and select for high resin flow trees are ongoing (Nebeker et al., 1992; Strom et al., 2002; Roberds et al., 2003).

4.2. *Effectiveness of thinning for preventing southern pine beetle infestations*

Thinning is often recommended as a means to prevent southern pine beetle attack (Bennett, 1968; Belanger and Malac, 1980; Coster and Searcy, 1981; Nebeker, 1981; Nebeker and Hodges, 1983, 1985; Nebeker et al., 1983; Brown et al., 1987). Residual tree density, tree spacing and slash distribution greatly influence the potential for southern pine beetle attack and spot growth to occur (Nebeker and Hodges, 1983, 1985; Fig. 5). Thinning during periods of reduced southern pine beetle activity such as winter, or when beetle populations are at endemic levels, is recommended except under certain conditions (Nebeker et al., 1983). However, thinning can be conducted during periods of beetle activity with limited risk if care is taken to minimize logging damage (Belanger and Malac, 1980) and to avoid concentrations of slash material (Bennett, 1968; Nebeker, 1989). The beneficial effects of thinning on tree vigor last as long as free growth occurs (Zahner and Whitmore, 1960; Smith, 1986a).

Thinning dense stands promotes tree growth and vigor and reduces tree and stand susceptibility to southern pine beetle attack (Nebeker et al., 1983, 1985; Price, 1985; Lorio, 1986), the occurrence of infestations (Coulson et al., 1974; Belanger and Malac, 1980; Hicks et al., 1980; Lorio, 1980; Coster and Searcy, 1981; Mason et al., 1985), and the probability and rate of spot growth once an infestation arises (Johnson and Coster, 1978; Hedden and Billings, 1979; Thatcher et al., 1980; Brown et al., 1987; Cameron and Billings, 1988; Belanger et al., 1993; Turchin et al., 1999a,b; Clarke, 2003; Billings et al., 2006). Numerous efforts have examined the relationship between tree density and southern pine beetle spot initiation and growth (Coulson et al., 1974; Ku et al., 1980; Burkhart et al., 1986; Schowalter and Turchin, 1993; Turchin et al., 1999a; Zhang and Zeide, 1999; Belanger et al., 2000). Others have explicitly examined the relationship between thinning and subsequent amounts of southern pine beetle-caused tree mortality (Nebeker and Hodges, 1983; Brown et al., 1987; Schowalter and Turchin, 1993; Turchin et al., 1999a). In all cases, thinning significantly reduced both the occurrence and subsequent growth of southern pine beetle spots. For example, in an experiment to evaluate the effects of pine and hardwood tree densities (low versus high) on southern pine beetle infestations over a 2-year period, significantly more trees were killed on plots with higher densities of pine trees (Schowalter and Turchin, 1993). The presence of hardwoods did not significantly affect stand susceptibility. In a similar study, Turchin et al. (1999a) examined the effects of four treatments, untreated control, intermediate (i.e., amount harvested) level of thinning with hardwood retention, high level of thinning with hardwood retention and pine retention and hardwood removal, on the amount of southern pine beetle-caused tree mortality. The high level of thinning treatments significantly reduced the rate of spot growth in these stands. Substantially more trees were killed in the control plots versus all the thinning treatments combined (110 versus 28, respectively). Only 10 trees were killed in all three stands that had received a high level of thinning. Brown et al. (1987) studied the effect of three (16.0, 23.0 and 29.8 m^2/ha) thinning treatments and an unthinned control on the amount of southern pine beetle-caused tree mortality in Mississippi. A positive correlation was found between stand density and the number of southern pine beetle-attacked trees. Thinned plots contained trees that were more vigorous as measured by growth rate and oleoresin exudation pressure.

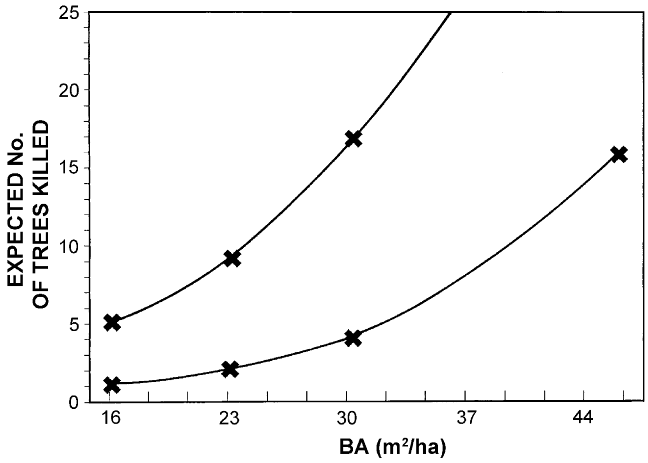


Fig. 5. Initial *D. frontalis* spot size and subsequent tree mortality in relation to density (m^2/ha) following thinning in *P. taeda* forests, Mississippi, USA. Spots of different initial sizes (one or five trees) were created and spot growth was monitored for 4 months (adapted from Nebeker and Hodges, 1985).

Computer models, based on long-term data sets, have been used to examine the relationships between stand structure, southern pine beetle abundance and the economic benefits of thinning (Hedden, 1982; Burkhart et al., 1986; Zhang and Zeide, 1999). Zhang and Zeide (1999) analyzed southern pine beetle infestation data from loblolly pine plantations in several southern states and found the proportion of infested plots increased with stand density. Unlike data presented by Schowalter and Turchin (1993) (see above), stands with an increasing prevalence of hardwoods had significantly less tree mortality. Examining data from 30 randomly selected southern pine beetle spots in a heavily infested area of East Texas, Coulson et al. (1974) found that 85% of spots occurred in stands with >27.5 m^2/ha of basal area. Trees in infested stands exhibited decreased radial growth suggesting decreased vigor. Today, stands with basal areas >27.5 m^2/ha are recommended for thinning to levels <18.3 m^2/ha (Klepzig et al., 2003).

Hedden (1982) evaluated the effects of rotation length and thinning on the amount of southern pine beetle-caused tree mortality in South Carolina. He reported that shorter rotation lengths decreased the probability of spot initiation, and suggested that fewer spots and lower rates of spread would be observed in thinned stands (Hedden, 1982). Other studies (Hedden and Billings, 1979; Nebeker and Hodges, 1983; Burkhart et al., 1986; Brown et al., 1987; Cameron and Billings, 1988) have also demonstrated that stand susceptibility to southern pine beetle infestation, numbers of southern pine beetle spots, and rate and extent of spot growth are all positively correlated with measures of stand density.

4.3. Effects of prescribed fire treatments on southern bark beetle activity

Relatively little is known of the relationship between prescribed burning and bark beetle responses in the southern USA despite the fact that prescribed burning is frequently used to reduce competition in southern pine forests (McNab, 1977; Wade et al., 1989). Cameron and Billings (1988) reported prescribed burns in young (<10 years) pine plantations in East Texas were associated with increased southern pine beetle incidence. Others have reported increased activity of pine engravers (Santoro et al., 2001) and root beetles (Sullivan et al., 2003). Hanula et al. (2002) compared tree mortality with the abundance of bark and ambrosia beetles, reproduction weevils and wood borers relative to fire severity following a mixed-severity wildfire on the Osceola National Forest in Florida. Mean trap catches of *I. grandicollis* (Eichhoff) and the black turpentine beetle, *D. terebrans* (Olivier), were lower in fire-damaged areas than control stands. Results showed that most tree mortality occurred within 1 year of the fire. Bark beetle populations did not increase in sufficient quantities to attack apparently healthy trees in nearby areas (Hanula et al., 2002). While studies are underway (e.g., Boyle, 2002 as part of the National Fire and Fire Surrogate Study), further efforts are needed to understand these complex interactions.

4.4. Direct control for suppression of southern pine beetle infestations

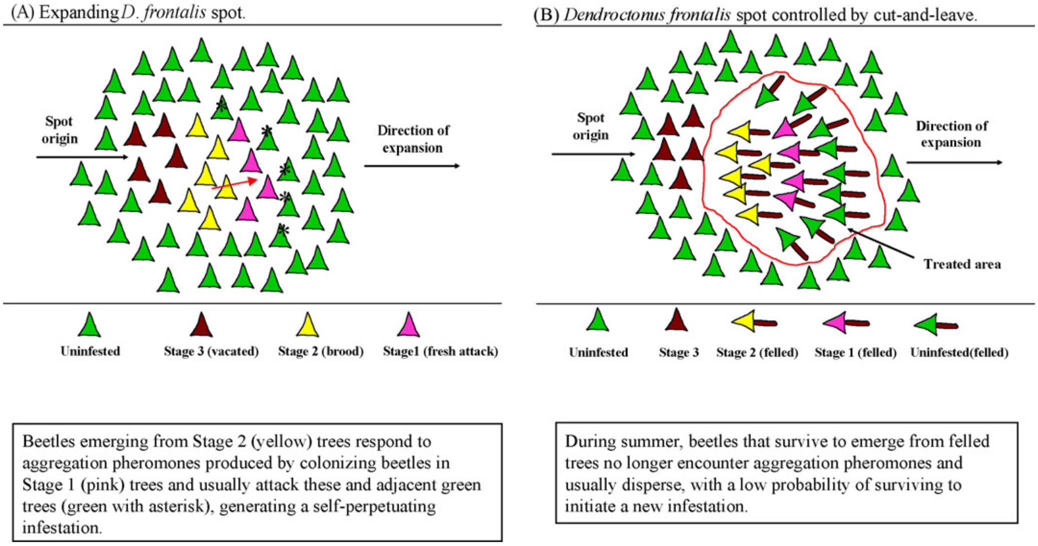
4.4.1. Seasonal behavior of the southern pine beetle as related to direct control

Some discussion of the life history of the southern pine beetle is necessary to fully appreciate how conventional direct control tactics are successful in disrupting spot growth. The southern pine beetle may complete seven generations annually in the Gulf Coast Region (Thatcher and Pickard, 1967) compared to one to four generations per year for most other *Dendroctonus* spp. in the USA (Wood, 1982). This rapid life cycle accommodates a high reproductive potential and an attack behavior that is unique among bark beetles (Coulson, 1979, 1980). During outbreaks, southern pine beetle tends to infest concentrated groups of trees, creating infestations that have the potential to continuously expand over time. These mortality centers may range in size from a few trees at initiation to several thousand hectares under the most favorable of conditions (Fig. 6A and B).


(A) Small, expanding *D. frontalis* spot. (B) Large, expanding *D. frontalis* infestation.


(C) *Dendroctnus frontalis* spots controlled by cut-and-leave. (D) *Dendroctnus frontalis* spot controlled by salvage.

Fig. 6. Expanding (A and B) and controlled (C and D) *D. frontalis* infestations (spots) in *P. taeda* forests, East Texas, USA. Photo: R.F. Billings, Texas Forest Service.


(A) Expanding *D. frontalis* spot.

(B) *Dendroctonus frontalis* spot controlled by cut-and-leave.

Beetles emerging from Stage 2 (yellow) trees respond to aggregation pheromones produced by colonizing beetles in Stage 1 (pink) trees and usually attack these and adjacent green trees (green with asterisk), generating a self-perpetuating infestation.

During summer, beetles that survive to emerge from felled trees no longer encounter aggregation pheromones and usually disperse, with a low probability of surviving to initiate a new infestation.

Fig. 7. Illustrations of an expanding *D. frontalis* spot (A) and one that has been controlled by cut-and-leave tactics (B).

Southern pine beetle may be in flight and capable of attacking trees throughout the year in the Gulf Coast Region (Thatcher and Pickard, 1964, 1967; Billings and Kibbe, 1978; Texas Forest Service, 1978; Coulson, 1980; Moser and Dell, 1980; Billings, 1995). However, the beetle's long-range (>1 km) dispersal capabilities (Turchin and Thoeny, 1993), attack behavior, reproductive potential and longevity vary with season (Thatcher and Pickard, 1967; Coster et al., 1977a; Hedden and Billings, 1977; Coppedge et al., 1994; among others). Dispersal typically begins in March or April (Billings, 1988a, 1997) in the absence of aggregation pheromone production within overwintering spots. This produces a large aerial population that leads to long-range dispersal and initiation of new spots often in previously uninfested areas (Coulson et al., 1972; Texas Forest Service, 1980).

During the spring, new spots are initiated by pioneer southern pine beetles that locate and aggregate on stressed or previously weakened trees (Vité et al., 1964; Gara, 1967; Coster et al., 1977b). Spring-dispersing beetle populations generally encounter optimal conditions for pheromone plume dispersion beneath the forest canopy (Fares et al., 1980) and often occur at a sufficient level to infest numerous trees in rapid succession. These new infestations are detected by aerial surveyors once crown fade becomes visible in June–August (Doggett, 1971; Coulson et al., 1972; Billings and Kibbe, 1978; Billings, 1979; Billings and Pase, 1979a; Billings and Doggett, 1980; Fig. 6A) and are the primary targets of suppression programs in summer and fall (Billings, 1995).

A large southern pine beetle spot develops when pheromone production is successfully maintained for 30–40 days by beetles immigrating into the area and/or by re-emergent parent beetles attacking new trees. The spot then contains brood trees with southern pine beetles of all life stages. In response to the pheromones emanating from freshly attacked trees, new adults and re-emerging parents attack additional trees on the periphery of the spot from which they emerged (Vité et al., 1964; Gara and Coster, 1968; Coster and Johnson, 1979; Payne, 1980). This synchrony between beetle emergence and pheromone production leads to spot growth (Gara, 1967; Texas Forest Service, 1978; Hedden and Billings, 1979; Schowalter et al., 1981a) (Fig. 7A), in which even healthy host trees often succumb to attack.

The majority of newly established spots are <50 trees in size (Leushner et al., 1976) and many quickly become inactive (Billings, 1974). Spot growth is the primary mode of southern pine beetle survival during the hot summer months (June–September), a period when long-range dispersal is curtailed and few new spots are initiated (Hedden and Billings, 1979). In the fall, emerging beetles tend to fly longer distances to attack individual trees and small groups of trees (Thatcher and Pickard, 1964). During winter, when temperatures >15.6 °C (Moser and Dell, 1980), emerging southern pine beetle often attack uninfested portions of the same trees from which they emerged (Thatcher and Pickard, 1967).

Once single spots become established and exceed a certain size threshold (about 30 infested trees), they may rapidly expand and persist for multiple beetle generations, until direct control, lack of hosts or other factors intervene (Coulson et al., 1972; Hedden and Billings, 1979; Coulson, 1980; Cameron and Billings, 1988). Expanding spots typically represent <25% of all spots detected during outbreaks, but account for >60% of timber losses (Leushner et al., 1976; Texas Forest Service, 1980) (Fig. 6B). In the northern limits of southern pine beetle's range, there are fewer generations (3–5) and winter conditions terminate all beetle activity. During cold winters beetle survivorship may be significantly reduced (McClelland and Hain, 1979).

4.4.2. *Direct control tactics of southern pine beetle spots by silvicultural manipulations*

Direct control has changed considerably over the years (Billings, 1980a). Current efforts focus on mechanically disrupting the unique attack behavior of southern pine beetle that leads to the development of continuously, expanding spots.

Forest managers must first identify spots which are most likely to expand and then treat this subset of the entire population (Billings, 1974; Billings and Doggett, 1980; Billings and Ward, 1984). Several practical spot growth models have been developed to predict tree losses (Billings and Hynum, 1980; Reed et al., 1981; Hedden, 1985; Stephen and Lih, 1985).

Salvage (sanitation) removal (St. George and Beal, 1929; Morris and Copony, 1974; Texas Forest Service, 1976; Swain and Remion, 1981), one of the oldest southern pine beetle control tactics, continues to be the most recommended. By harvesting and utilizing southern pine beetle-infested trees, plus a buffer strip of uninfested trees, landowners can halt spot growth and recover some of the economic loss (Fig. 6C, D). Broods within trees are removed and eliminated if logs are promptly and properly processed (Texas Forest Service, 1976). Unfortunately, timely salvage is often not possible during southern pine beetle outbreaks (Billings, 1980a). In this case, the best alternative is to treat expanding infestations with cut-and-leave tactics.

Cut-and-leave (Texas Forest Service, 1975; Billings, 1980a,b) is a control method developed to halt the expansion of southern pine beetle spots that cannot be promptly salvaged. The tactic consists of felling all freshly attacked and brood-bearing trees toward the center of an infestation. In addition, a horseshoe-shaped buffer of uninfested trees at the spot's expanding front is felled to help disrupt pheromone production and recruitment of other southern pine beetle (Fig. 7B). Typically, the width of the buffer is equivalent to the height of the average tree in the stand, although actual buffer width (3–90 m) varies depending on spot size and rate of growth. All infested trees are left on site, but may be harvested at a later date. If done promptly and properly, cut-and-leave results in a small opening in the stand having little economic impact (Figs. 6C and 7B). Initially, this tactic was recommended for application only during the hot summer months (May–October) on small spots with <50 infested trees (Texas Forest Service, 1975; Billings and Pase, 1979b). However, out of necessity, cut-and-leave has been successfully applied to spots of varying sizes during all seasons (Billings, 1988b, 1995, 2001; Billings and Schmidtke, 2002; Clarke and Billings, 2003; Billings et al., 2004).

Survival of southern pine beetle brood in felled (leave) trees may be reduced by direct solar radiation (St. George and Beal, 1929), changes in moisture conditions (Gaumer and Gara, 1967; Ollieu, 1969; Palmer and Coster, 1978), increased predation (Baker, 1977) or competition from other wood-boring species (Billings, 1988b, 2001). However, survivorship varies by stage of development, season, geographic location, bark thickness and abiotic conditions (Hodges and Thatcher, 1976; Baker, 1977; Hertel and Wallace, 1983).

If applied correctly, cut-and-leave is effective principally because it disrupts the spot growth process preventing further tree losses (Fig. 6C). Felling freshly attacked trees and adjacent buffer trees serves to disrupt the production of aggregation pheromones and host odors required for continual spot growth (Gara, 1967; Billings, 1980b). Uninfested trees immediately adjacent to trees undergoing bark beetle attack are eliminated in the buffer strip, further discouraging spot growth (Gara, 1967; Johnson and Coster, 1978). Beetles that survive to disperse from treated spots during summer months have reduced energy reserves (Hedden and Billings, 1977; Coppedge et al., 1994) and a lower probability of survival (Coulson, 1980). Felled trees are rapidly colonized by *Ips* bark beetles, particularly in subtropical climates, thus increasing competition and reducing survival of southern pine beetle broods. Finally, the lack of a large aerial southern pine beetle population during summer months outside of established spots makes it unlikely for immigrating southern pine beetles to initiate new spots (Billings, 1980a, 1995).

Direct control is considered to be a short-term response to reduce tree losses once an infestation develops (Billings, 1980a,b; Swain and Remion, 1981). With the possible exception of a recent outbreak in Nicaragua (Billings, 2001), there is little evidence that suppression of individual spots will influence a large-scale outbreak. Clearly, effective southern pine beetle management involves other critical components such as monitoring, risk and hazard rating (Lorio, 1978; Lorio et al., 1982; Hicks and Mason, 1982; Thatcher et al., 1982; Billings et al., 1985; Clarke, 2003) and proper forest management. To that end, the maintenance of adequate tree vigor by whatever combination of silvicultural practices is best suited to the site is important.

4.4.3. *Effectiveness of direct control tactics*

In our experience, direct control of southern pine beetle infestations is quite effective if applied before infestations grow large. Concerns that cut-and-leave tactics increase the occurrence of spots in locations adjacent to newly treated areas appear largely unfounded. Billings and Pase (1979b) reported that the incidence of new infestations was significantly reduced in the vicinity of spots controlled by cut-and-leave during summer months. Spot proliferation was observed during fall treatments. Fitzgerald et al. (1994) reported no significant difference in spot proliferation between cut-and-leave and cut-and-remove tactics on the Sam Houston National Forest in Texas. Cronin et al. (1999) demonstrated that cut-and-leave may increase the numbers of southern pine beetle flying outside treated areas compared to untreated spots, and suggested that emigrating beetles may survive by joining untreated spots nearby, indicating the need to treat all expanding spots in a given area to eliminate natural pheromone sources that might attract dispersing beetles.

Morris and Copony (1974) reported on the effectiveness of intensive salvage in Virginia. In 1973, salvage was promptly applied on the Cumberland State Forest to all expanding southern pine beetle spots. Spot density was reduced by 77.4% (27.9 versus 6.8 spots/405 ha). However, on adjacent private lands where little control was applied, spot density increased by 30%. Average spot size was over four times greater on private lands (26.9 trees versus 6.3 trees) despite less susceptible stand conditions (Morris and Copony, 1974). In early 1983, prompt direct control of southern pine beetle spots on the Four Notch RARE II Study Area, Sam Houston National Forest was delayed for several months by protests from concerned groups

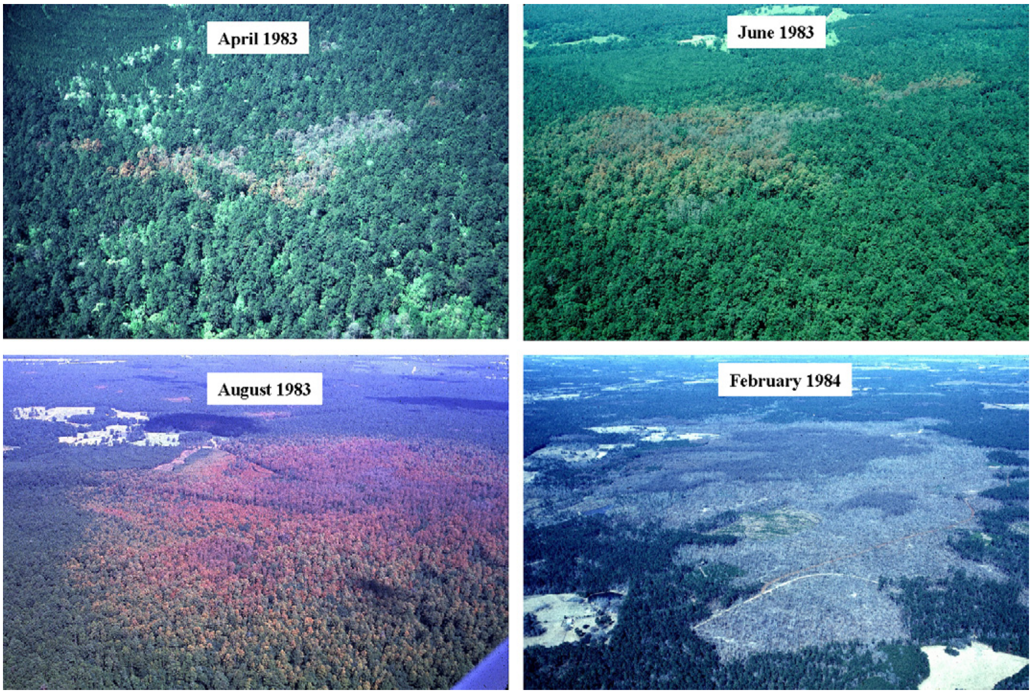


Fig. 8. *Dendroctonus frontalis* outbreak on the Four Notch RARE II Study Area, East Texas, USA, 1983–1984. Photo: R.F. Billings, Texas Forest Service.

(Miles, 1987). During that time, several small, uncontrolled spots in a dense stand of loblolly pine converged to create a massive southern pine beetle infestation that grew by 15 m per day along a 4.8 km front (USDA Forest Service, 1987; Fig. 8). The infestation was halted by cutting a 76.2 m wide buffer strip of recently infested and uninfested trees around the periphery, followed by helicopter logging to reduce overwintering populations (Billings, 1986). These delayed actions resulted in the loss of 1,498 ha of pine (valued at US $4,000,000 in 1986) and eliminated the area for wilderness consideration (Billings, 1986). During that same year, a southern pine beetle outbreak occurred on nearby Huntsville State Park, a 842 ha preserve of 60–70-year-old loblolly pine. Infestation density averaged 20 spots/405 ha of host type compared to seven spots on the Four Notch. At Huntsville State Park, spots were promptly controlled and total tree losses were limited to about 32 ha (Billings and Varner, 1986). These data provide strong evidence supporting the value of timely direct control to minimize losses from southern pine beetle infestations.

DeSteiguer et al. (1987) conducted an economic analysis of southern pine beetle control programs. Potential losses, in the absence of control, were estimated using the Clembeetle spot growth model (Hedden, 1985). The authors confirmed that substantial benefits could be realized from control of southern pine beetle spots on commercial forest lands. Similarly, Redmond and Nettleton (1990) conducted an economic analysis of southern pine beetle suppression efforts (cut-and-remove or cut-and-leave) on the national forests within the Gulf Coastal Plain. Actual suppression costs were compared with estimates of potential timber losses without suppression obtained by using the Arkansas spot growth model (Stephen and Lih, 1985). The authors reported benefit:cost ratios of 3.9:1 (based on a 4% discount rate) and 2.6:1 (based on a 7.125% discount rate) (Redmond and Nettleton, 1990).

Potential benefits of prompt direct control were dramatically demonstrated in the 1990–1994 southern pine beetle outbreak in East Texas. Losses on five recently designated wildernesses (12,811 ha) where little or no direct control was applied were compared to losses on the surrounding 242,817 ha of national forests (Angelina, Davy Crockett, Sam Houston, and Sabine NF) where expanding spots were promptly controlled by cut-and-remove, cut-and-leave, and to a much lesser extent, cut-and-spray with insecticides (Billings, 1998; Clarke and Billings, 2003). Initial density of southern pine beetle spots was higher on the national forests compared to adjacent wilderness. Nevertheless, more than 40% of the host type was killed on the wilderness areas versus <2% on the national forests (Billings, 1995, 1998; Clarke and Billings, 2003).

Photos documenting the rapid development of uncontrolled southern pine beetle infestations on Indian Mounds Wilderness in Sabine County, Texas, which eventually attained 3035 ha, are shown in Fig. 9. These photos illustrate the magnitude of tree losses that can rapidly occur when a no-control policy is adopted or direct control is delayed (Billings, 1995).

4.4.4. Limitations of southern pine beetle direct control programs

Southern pine beetle is a native forest insect and a natural component of southern forest ecosystems. Eradication is neither possible nor desirable and periodic outbreaks will occur as long as susceptible forests and favorable climatic conditions exist. Such outbreaks are favored by: (1) a preponderance of private land ownership in the southern USA, which leads to a variety of management objectives and

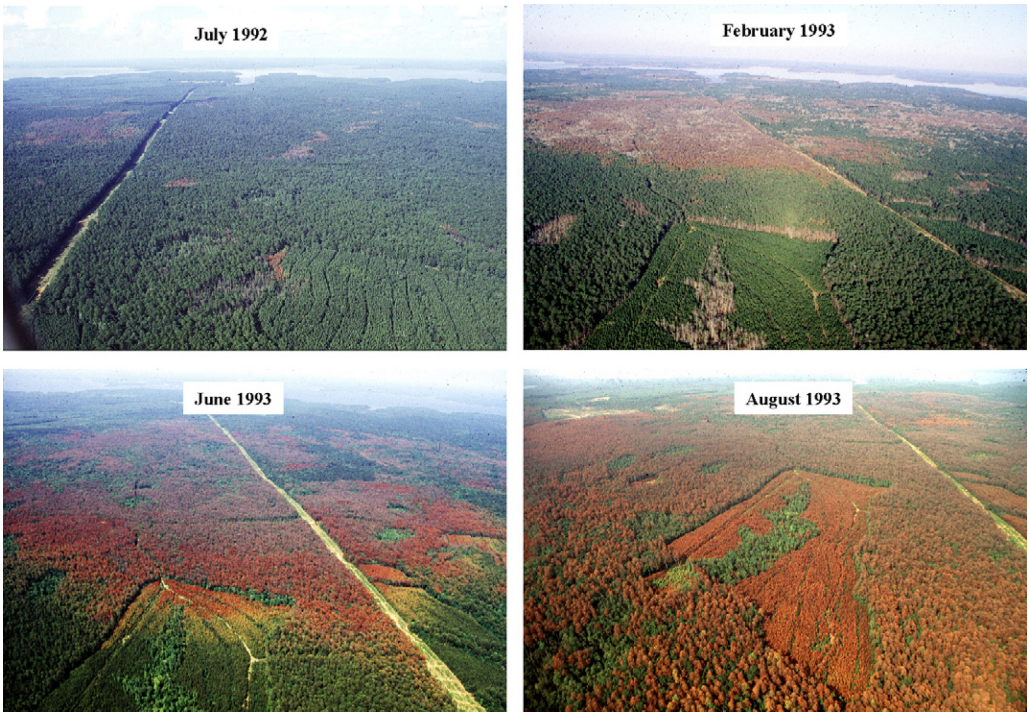


Fig. 9. *Dendroctonus frontalis* outbreak on the Indian Mounds Wilderness Area, Sabine National Forest, East Texas, USA, 1992–1993. Photo: R.F. Billings, Texas Forest Service.

levels of southern pine beetle awareness (Billings, 1980a), (2) social or political constraints that may affect implementation of appropriate and timely forest management practices (USDA Forest Service, 1987), (3) rotation lengths and high stand densities that negatively influence host vigor and thus stand susceptibility (Carter et al., 1991; Clarke et al., 2000), (4) federal wilderness areas where little or no direct control is permitted (Clarke and Billings, 2003), (5) lack of markets and labor in some areas for applying direct control in a timely manner, and (6) frequent occurrence of other disturbances that periodically stress trees at the stand and landscape level (King, 1972; Kalkstein, 1976; Clarke et al., 2000).

4.5. Other bark beetles in the southern USA

In terms of impacts on pine forests in the southern USA, bark beetles of the genus *Ips* are also of concern (Drooz, 1985; Riley and Goyer, 1988). However, none of the species in this genus is nearly as aggressive as the southern pine beetle in killing healthy trees. As a result, the amount of literature published on *Ips* spp. is a fraction of that found on southern pine beetle (Foltz et al., 1984). Generally, four species are of concern and, while there are differences in their biology, each typically attacks slash and felled or severely stressed trees, but also occasionally apparently healthy trees (Drooz, 1985). The sixspined ips, *I. calligraphus* (Germar), is usually among the first to attack severely drought-stressed trees. The eastern fivespined ips may also colonize drought-stressed pines and has become a major pest in other countries where it was accidentally introduced (Morgan, 1989). The small southern pine engraver, *I. avulsus* (Eichhoff), generally colonizes the tops and limbs of trees attacked by other bark beetles. It is unique among pine engravers in maintaining a close association with a fungus upon which it relies for nutrition (Klepzig et al., 2001). The pine engraver is a transcontinental species (Furniss and Carolin, 1977; see Section 3.3.4).

These beetles primarily attack stressed trees particularly on unmanaged lands. In this situation, the beetles serve to thin pine forests leaving more vigorous trees and actually decreasing the risk of subsequent southern pine beetle infestations (Thatcher, 1960; Paine et al., 1981; Clarke et al., 2000; Ward and Mistretta, 2002). On managed lands, outbreaks of pine engravers occur infrequently, and then mainly in dense, unthinned young pine stands. While more infestations may be seen after burning or thinning, these increases are usually temporary and do not outweigh the long-term benefits of these management activities (Ward and Mistretta, 2002).

Slash or damaged host material is important as it serves as sources of infestation growth, particularly in areas of high beetle populations. Even when populations are low, damaged trees serve as refugia from which new infestations may originate (Flamm et al., 1993). Thus, silvicultural practices that reduce the amount of such material are important. In general, practitioners are encouraged to avoid leaving logging debris in contact with or close to residual trees, to remove harvested timber from a stand as soon as possible and to minimize damage to residual trees (Williston et al., 1981; Connor and Wilkinson, 1983; Nebeker et al., 1985). Further preventive measures include planting appropriate tree species (i.e., those naturally adapted to the site) at appropriate spacing intervals (i.e., those of lower density to reduce the amount of inter-tree competition occurring until intermediate treatments are employed), thinning stands to maintain residual tree vigor (Brown et al., 1987), and prompt removal of potential breeding material (Connor and Wilkinson, 1983). The effects of other silvicultural treatments, such as fertilization, on the susceptibility of pines to bark beetle attack are unclear (Warren et al., 1999; Klepzig et al., 2005). Even with application of proper silvicultural practices, infestations may progress to outbreak status. In these cases, preventive measures are no longer effective. Removal of *Ips*-infested and recently killed trees can be an effective means to minimize further tree losses (Connor and Wilkinson, 1983), but also causes additional disturbance that may enable populations to persist and perhaps expand. The black turpentine beetle can also be of concern, but generally exhibits a preference for weakened trees, such as those damaged by fire, worked for naval stores (i.e., turpentine production), or infested by other bark beetles.

5. Mechanistic explanations on the effectiveness of thinning treatments for preventing bark beetle infestations

Thinning not only affects the vigor of residual trees influencing resin chemistry, flow and oleoresin exudation pressure (Vité and Wood, 1961; Reid et al., 1967; Lorio and Hodges, 1968; Smith, 1975; Hodges et al., 1979; Raffa and Berryman, 1983), but also the physical environment within these stands. Shepherd (1966) discussed the influence of heat and light intensity on how beetles locate and orient to host trees during attack. Increased temperatures and windspeeds are common within thinned stands (Bartos, 1988; Amman, 1989; Bartos and Amman, 1989; Schmid et al., 1992, 1995; Amman and Logan, 1998; Hindmarch and Reid, 2001b) and may accelerate the development of certain bark beetle species and force them to overwinter in stages that are more susceptible to freezing (Amman, 1973, 1989), or cause turbulences that disrupt pheromone plumes used for recruiting conspecifics during initial phases of host tree colonization. Thistle et al. (2004, 2005) examined the near-field canopy dispersion of tracer gases, as a surrogate for bark beetle pheromones, within the trunk space of trees. They showed that when surface layers are stable (e.g., during low wind velocities) the tracer plume remained concentrated and showed directional consistency due to suppression of turbulent mixing. Low density stands result in unstable layers and multi-directional traces that dilute pheromone concentrations and could result in reductions in beetle aggregation. A significant number of pioneer beetles are required to overcome host defenses (see Section 2). A lack of beetle recruitment often results in unsuccessful attacks.

Safranyik (1978) discussed the role of climate on the abundance and distribution of mountain pine beetle stating changes in microclimate could influence mountain pine beetle behavior and thus stand susceptibility. Microclimate also influences beetle fecundity and fitness, phenology and voltanism as well as that of predators, parasites and competitors. Competitive ratios between predator and prey may be altered in ways that are difficult to predict (Price, 1997).

Some authors have suggested that thinning strategies designed to reduce stand susceptibility to bark beetle attack must address residual inter-tree spacing. Geiszler and Gara (1978) stated that as inter-tree distance increases the risk to adjacent trees decreases, and an infestation within the stand will likely not continue when some critical threshold distance is met. Gara and Coster (1968) reported that southern pine beetle spot expansion was unlikely in stands that had an inter-tree spacing of 6.1–7.5 m. Johnson and Coster (1978) reported the probability of southern pine beetle attack decreased with the distance between trees in small to moderate size spots with only one or a few pheromone plume sources (i.e., individual trees in early stages of the attack sequence). However, Preisler and Mitchell (1993) showed that wider spacings did not interfere with host finding when mountain pine beetle populations became epidemic in lodgepole pine stands. In British Columbia, Whitehead and Russo (2005) suggested increases in resin production were not as important in reducing mountain pine beetle-caused tree mortality at the stand level as reductions in the number of initiated attacks, which is more likely associated with inter-tree spacing.

The physical environment is also thought to influence the spacing and distribution of beetles within thinned stands (Amman, 1989). Schmitz et al. (1989) sampled the flight behavior of mountain pine beetle in thinned and unthinned stands in Montana. Most beetles were caught in the least intensely thinned plots and unthinned control, which had the most tree mortality (McGregor et al., 1987). Safranyik et al. (2004) analyzed the number of bark beetles (several species) captured in spaced and unmanaged mature lodgepole pine in British Columbia. Unlike some studies in lodgepole (Schmitz et al., 1989) and ponderosa pine (Zausen et al., 2005), but in agreement with others (Sánchez-Martínez and Wagner, 2002), significantly more bark beetles (several species) were captured in thinned stands.

Trap catches may be of limited value in assessing the effectiveness of thinning treatments for preventing bark beetle infestations. An understanding of the relationship between trap catch and levels of bark beetle-caused tree mortality is necessary, but generally unavailable for most species. This is likely due to temporal variation in host vigor and thus large variation in the critical minimum number of beetles required to mass attack a tree and overcome host defenses. An exception is a system developed for the southern pine beetle (Billings, 1988a), which has proven to be reasonably accurate for forecasting population trends (increasing, declining or static) and expected infestation levels (low, moderate, high or outbreak) but is limited to large spatial scales. The model incorporates trap catch data (mean daily catch of southern pine beetle and the ratio of southern pine beetle to a common predator, *Thanasimus dubius* (F.) (Coleoptera: Cleridae)) from multiple-funnel traps baited with synthetic pheromones and kairomones.

6. Integrating silvicultural treatments with other bark beetle management strategies

A detailed discussion of other bark beetle control techniques is beyond the scope of this review, however, several have been integrated with vegetation management practices and are worthy of brief mention here. Dispersing adults of several bark beetle species are attracted to trap trees (Nagel et al., 1957; Lister et al., 1976; Schmid and Frye, 1976; Gibson, 1984; among others). This method involves the use of living or felled trees that are usually baited with attractive semiochemicals and harvested or otherwise removed prior to emergence of the developing brood (Wood et al., 1985), or treated with insecticides to kill arriving beetles (Smith, 1986b). Bentz and Munson (2000) successfully suppressed increasing spruce beetle populations confined to a localized area in northern Utah through the use of trap trees, sanitation harvests and other treatments. Suppression of bark beetle populations may also involve attracting beetles, usually by placement of aggregation pheromones, to certain areas in which they can be collected (Shea and Neustein, 1995) or treated in a controlled manner (Ross and Daterman, 1997a,b; Thier and Patterson, 1997; Laidlaw et al., 2003; among others).

Insecticides are available for protecting individual, high-value trees from bark beetle attack (Haverty et al., 1998). Some solar treatments are effective for reducing adult and brood (several species) survival in infested logs (Buffam and Lucht, 1968; Negrón et al., 2001) and may influence the number of newly attacked trees on a localized basis. Biological control has been investigated (Stephen and Dahlsten, 1976; Dahlsten and Whitmore, 1989; Kulhavy and Miller, 1989; Mathews and Stephen, 1997; Stephen and Browne, 2000), but is not used operationally. Behavioral chemicals are effective for managing some bark beetle species (Ross and Daterman, 1997a; Skillen et al., 1997). For example, applications of synthetic verbenone, an anitaggregation pheromone, have been effective in disrupting southern pine beetle spots (Payne and Billings, 1988, 1989; Payne et al., 1992; Billings and Upton, 1993; Billings et al., 1997; Clarke et al., 1999). This novel approach is even more effective when combined with the felling of all freshly attacked and brood trees within a spot (Payne and Billings, 1988; Billings and Upton, 1993).

7. Implications of landscape level dynamics on bark beetle populations and management

Landscape ecology considers interactions between spatial patterns and ecological processes (Turner, 2005). Coulson et al. (1999) summarized the scale and periodicity of southern pine beetle outbreaks defining them as ‘‘autogenic disturbances that are normally observed at the mesoscale (100–1,000,000 ha) landscape as levels of herbivory above an average or expected amount.’’ As with all bark beetles, the abundance and distribution of susceptible hosts play important roles. Bark beetle populations increase and outbreaks occur when favorable environmental and host conditions coincide (Rykiel et al., 1988; Coulson et al., 1999). The spatial arrangement of forest stands is also important (Coulson et al., 1999). For example, in some areas, large forested landscapes contain little heterogeneity resulting in a landscape with contiguous areas simultaneously susceptible to certain outbreaks (Samman and Logan, 2000). Management activities are available to reduce susceptibility (see Sections 3.3, 3.4, 4.2 and 4.3) (Samman and Logan, 2000), but must be considered at both the stand and landscape level (Schmid and Mata, 2005). This approach calls for a comprehensive strategy addressing the distribution of multiple land uses. It is important to note that even a course of no action is not without consequence and may lead to drastic changes at the landscape level (see Fig. 9). Clearly, additional research is needed to determine the short and long-term implications of vegetation management treatments on bark beetle populations and associated levels of tree mortality at appropriate spatial scales (Billings and Bryant, 1983; Billings et al., 1985; Coulson et al., 1989, 1999; Samman and Logan, 2000; Dymond et al., 2006; Wulder et al., 2006).

The maintenance of desirable (or sustainable) forest conditions may require multiple disturbances (Schowalter et al., 1981b; Waldron et al., in press). For example, a thorough modeling effort of southern pine beetle-affected forests in the Appalachian Mountains suggested that while southern pine beetle plays an important role in maintaining these systems, the beetle could eventually lead to the replacement of xeric pine forests by other tree species if fire is not reintroduced (Waldron et al., in press). Complex and interacting climatic, topographic and biological features require careful consideration and planning of restoration efforts in such forests (Waldron et al., in press). Attempts to understand the direct impacts of climate change on the landscape ecology of bark beetles (Hansen et al., 1973; Kalkstein, 1976; Michaels, 1984; Logan et al., 1995; Reeve et al., 1995; McNulty et al., 1997; Gan, 2004; Tran et al., in press) have in some cases led to the prediction of serious socio-economic impacts (McNulty et al., 1997; Gan, 2004; Logan and Powell, 2004).

8. Conclusions

Recent epidemics of some native forest insects have exceeded historical records. Efforts to avoid such catastrophic events focus on returning the forest landscape to a normative relationship with natural disturbance agents. A variety of vegetation management practices are available to prevent epidemics from occurring and expanding when properly instituted at appropriate spatial and temporal scales. Experience has shown that even a course of no action is not without consequence. The review of existing bodies of empirical and anecdotal evidence concerning variations in host susceptibility to bark beetle infestation by thinning and other vegetation management practices leads to several conclusions:

(1) Native tree-killing bark beetles are a natural component of forest ecosystems. Eradication is neither possible nor desirable and periodic outbreaks will occur as long as susceptible forests and favorable climatic conditions exist. Changes in forest structure and composition by natural processes and management practices have led to increased competition among trees for water, nutrients and growing space thereby increasing susceptibility to bark beetles and other forest insects. As trees become stressed, their insect resistance mechanisms are compromised. Trees of low

vigor are more susceptible to bark beetle attack. Efforts to prevent undesirable levels of bark beetle-caused tree mortality must change stand susceptibility through reductions in tree competition, disruption of pheromone plumes thus negatively affecting host-finding, and reductions in the fecundity, fitness and survivorship of target bark beetle species.

(2) Forested landscapes that contain little heterogeneity promote the creation of large contiguous areas susceptible to similar insect outbreaks. Efforts to prevent undesirable levels of bark beetle-caused tree mortality at the landscape level must also account for the spatial distribution of both cover types and stand ages. In many areas, treatments should be implemented to increase heterogeneity.

(3) Sufficient literature exists concerning tree and stand susceptibility to bark beetle infestations as related to thinning and other vegetation management practices for most forest cover types. However, information is lacking or incomplete for some cover types and common bark beetle species. Additional research is required to address these knowledge gaps.

(4) Factors involving tree density are consistently associated with the occurrence and severity of bark beetle infestations. Management to reduce stand or landscape-level susceptibility to bark beetles must address factors related to tree density. Accordingly, thinning has long been advocated as a preventative measure to reduce the amount of bark beetle-caused tree mortality and its effectiveness for this purpose is supported by the scientific literature. Some studies of the efficacy of thinning have failed to detect significant differences among treatments, and others are limited to anecdotal evidence. However, to date there are no reports of significant increases in the amount of *Dendroctonus* spp.-caused tree mortality in response to thinning treatments. Thinning also redistributes growing space to desirable trees, utilizes anticipated mortality resulting from stem exclusion, encourages regeneration, creates early cash flows, and reduces risks associated with fire and diseases.

(5) Certain bark beetles are attracted to thinning residues. Published guidelines are available to minimize bark beetle activity in response to thinning residues.

(6) Sublethal heating of critical plant tissue can stress trees, and increase their susceptibility to insect attack. Prescribed burns must be planned and executed carefully to minimize injury to desirable residual trees while still fulfilling management objectives. Prescriptions should be considered that result in reduced stand susceptibility.

(7) The effectiveness of direct control techniques varies among bark beetle species. Direct control (i.e., cut-and-remove, cut-and-leave) is especially effective for controlling the spread of southern pine beetle infestations because of its unique life cycle and attack behavior.

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