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Tree mortality after synchronized forest insect outbreaks: Effects of tree species, bole diameter, and cutting history

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ABSTRACT

A recent series of bark beetle outbreaks in the Rocky Mountain region of the U.S. is the largest and most intense ever recorded. Factors contributing to tree mortality from bark beetles are complex, but include aspects of forest stand condition. Because stand conditions respond to forest management, evaluating bark beetle-caused tree mortality and changes in forest structural attributes in areas previously subjected to management not only improves mechanistic understanding of beetle-caused changes in forests, but also improves prediction of future bark beetle responses to management regimes. We retrospectively assessed mortality of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*), and stand structure in two watersheds in south-central Wyoming, U.S.A. following outbreaks of mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*), and western balsam beetle (*Dryocoetes confusus*). One watershed received 240 patch cuts (mean area 1.5 ha), a type of group selection cut, six years before the beetle outbreaks began; the other watershed received no active management (control). We conducted surveys of forest vegetation attributes over 27 yrs, during pre-harvest, post-harvest, and post-outbreak periods. After the outbreak, lodgepole pine and Engelmann spruce mortality increased with increasing bole diameters and basal area of each species, but patterns of mortality were influenced by patch-cutting. Large-diameter trees in or near patch cuts tended to escape attack by bark beetles. Away from patch cuts ($\geqslant$15 m), mortality of smaller lodgepole pine was higher compared to the control watershed. Based on our observed patterns of tree mortality, we hypothesize a changing pattern of host selection (i.e., selection for smaller trees) was influenced by stand conditions that created more suitable conditions for bark beetles in areas between patch cuts in the treated watershed. Snag density increased from pre-harvest to post-outbreak periods, but log density was similar, suggesting most dead trees remained standing at the time of data collection. Canopy cover did not decrease as expected, and ground cover did not change substantially from pre-harvest to post-outbreak periods. Patch-cutting improved survival probability of large-diameter lodgepole pine and Engelmann spruce during outbreaks of multiple species of bark beetle, although reduced losses were only realized for trees in or near ($\leqslant$15 m) patch cuts. However, during intense, broad-scale tree mortality events, these benefits may be important in reducing the loss of mature trees to bark beetles and promoting retention of a larger cohort of mature trees post-outbreak.

1. Introduction

Bark beetles, a group of species naturally occurring in coniferous forests of North America, are an important source of habitat modification and heterogeneity in these ecosystems (Schowalter et al., 1981; Franklin et al., 2007). Bark beetle outbreaks, under certain conditions, can result in high tree mortality over extensive areas, leading to cascading changes in structure or species composition of forests (Veblen et al., 1991). Outbreaks can also affect nutrient cycling and hydrologic processes, including water quality (Coulson and Stephen, 2006). Forest vertebrates can also be affected, via changes in resource availability or habitat selection (Martin et al., 2006; Saab et al., 2013). Specifically, insectivores may experience short-term surges in food availability, canopy-sensitive species may be negatively affected a few years after tree

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death, and species associated with abundant logs may find favorable conditions 1–3 decades following the infestation. Beetle-caused tree mortality presents major management challenges in terms of fire risk, hazard trees, and timber production (Samman and Logan, 2000). These challenges may result in significant economic consequences due to altered forest management prioritizing trail and road clearing, or changes in wood fiber characteristics affecting potential wood products for many decades. Therefore, studies of the magnitudes of beetle infestations relative to host species, tree size and cutting history are needed.

During the past two decades conifer forests in the Rocky Mountains experienced one of the most intense and extensive beetle-caused tree mortality events ever recorded. Forests of nearly every coniferous type from New Mexico to British Columbia have been affected. Multiple species of bark beetle have been involved. In Colorado and Wyoming, the primary species have been mountain pine beetle (MPB: *Dendroctonus ponderosae* Hopkins) and spruce beetle (*Dendroctonus rufipennis* Kirby), and to a lesser extent, western balsam beetle (*Dryocoetes confuses* Swaine; Raffa et al., 2008; Bentz et al., 2009). A disturbance of this magnitude necessarily motivates a broad range of ecological and management questions related to bark beetles. These beetle species largely kill individual trees within mature forest stands at low rates during most years but extensive forest mortality events, like that observed recently in the Rockies, occur episodically (Raffa et al., 2008). Except during the most severe outbreaks, small trees are rarely attacked or killed by these species of bark beetles (Bleiker et al., 2003; Fettig et al., 2007). For instance, MPB attack lodgepole pine (*Pinus contorta* Dougl. Ex Loud.) trees <10 cm diameter at breast height (dbh; Roe and Amman, 1970; Shore et al., 2006) at much lower rates than larger trees, demonstrating the influence of individual tree characteristics on bark beetle activity. However, the susceptibility of individual trees >10 cm dbh may differ as a function of stand condition, topography, elevation, tree vigor, weather, and climate, at local and regional scales. Stands with greater tree density or basal area have been shown to be at greater risk of attack by beetles, and risk of attack increases with stand age, percentage of host type, and in stands with a high proportion of large diameter trees (Christiansen et al., 1987; Fettig et al., 2013). Otherwise susceptible stands may resist attack and suffer low tree mortality during years of above-average precipitation indicating the importance of climate in broad-scale mortality events (Chapman et al., 2012; Raffa et al., 2008). Furthermore, brief weather events can have dramatic influence on tree mortality – extreme winter cold that extends over several weeks may significantly reduce beetle-caused tree mortality for several years (Macias Fauria and Johnson, 2009).

Partial cutting in systems dominated by lodgepole pine and ponderosa pine (*P. ponderosae* Dougl. Ex Laws.) has effectively reduced mortality rates from MPB (MacGregor et al., 1987; Amman et al., 1988; Schmid and Mata, 2005). Similarly, mortality from spruce beetles was significantly reduced in stands of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) treated with partial-cutting (Hansen et al., 2010). Therefore, partial cutting has emerged as a potential tool for reducing total tree mortality in landscapes at risk for infestation. However, the efficacy of partial cutting in reducing bark beetle-caused mortality may be influenced by remaining levels of growing stock, patterns of tree grouping, stand structure, and landscape context, as well as beetle demography and behavior (Olsen et al., 1996; Schmid and Mata, 2005; Fettig et al., 2007). Structural characteristics in post-harvest stands can influence microclimate, which is perhaps even more important than structural characteristics *per se* because it strongly affects beetle behavior and whether a suitable host tree is attacked (Bartos and Amman, 1989). In managed stands, bark beetles may be deterred by microclimate features such as warmer temperatures, lower humidity, and higher wind speeds than in unmanaged stands. These factors may inhibit larval development or the spread of pheromone plumes used to coordinate tree attacks with other individuals (Amman and Logan, 1998; Thistle et al., 2004). Thus, an evaluation of specific partial cutting techniques is essential to determine how overall tree mortality rates may be affected.

Beginning in approximately 1996, MPB populations erupted in north-central Colorado and south-central Wyoming (Harris et al., 2001). Since approximately 2005, MPB populations have been at epidemic levels in mountains of southern Wyoming (Harris, 2006). As of 2012, over 1.7 million ha of pine (*Pinus* spp.) – dominated forests in south-central Wyoming and Colorado had been affected by this series of outbreaks (Harris, 2013). Additional outbreaks of other bark beetle species occurred concurrently with the initial MPB outbreak. Spruce beetle activity began with a large blowdown event in 1997 near Steamboat Springs, Colorado. As of 2012, spruce beetles had affected >420,000 ha in south-central Wyoming and Colorado. In the same region, western balsam bark beetle, a species implicated in mortality of subalpine fir, had affected >95,000 ha (Harris et al., 2001, USDA Forest Service, http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/).

The occurrence of these bark beetle outbreaks in two watersheds where pre-outbreak data on forest structure and composition were collected presented the opportunity to evaluate whether patch-cutting, a type of group selection cut, influenced subsequent tree mortality or stand structure. Our objectives were to compare changes in tree mortality and structural attributes over time between patch-cut and uncut stands in treatment and control watersheds. We also tested for the previously demonstrated relationship between basal area and mortality rate of the same species. We include pre-epidemic data to evaluate whether changes in forest characteristics caused by the beetle epidemic were affected by forest management.

2. Materials and methods

2.1. Study site

Our study was conducted in the Sierra Madre Mountains of south-central Wyoming, in the Medicine Bow National Forest near the town of Encampment. Mean annual temperature during the period 1982–1986 was estimated to be 1 °C, and ranges from −10 °C in January to 12.9 °C in July. Mean annual precipitation is 87 cm, about 70% of which falls as snow (Bevenger and Troendle, 1987).

The study site comprised the Coon Creek and adjacent East Fork, Encampment River ("East Fork") watersheds (Fig. 1). These watersheds were the site of a water yield augmentation project, begun in 1985 and completed in the 1990s, designed to evaluate the efficacy of one timber harvest technique to increase surface water yield at the scale of large basins (Troendle et al., 2001). Paired watersheds covering 1673 ha (Coon Creek) and 908 ha (East Fork) were selected based on similar size, aspect, elevation, and timber cover. Mean aspect for Coon Creek is 266° and for East Fork is 197°, and elevation for both watersheds ranges between 2682 and 3322 m (Troendle et al., 2001). During 1990–1992, 240 small patch cuts (mean area 1.5 ha; range: 0.1–7.0 ha) were created in Coon Creek while East Fork remained untreated. Within Coon Creek, a 985-ha portion considered to be the sampling area received 155 patch cuts and a system of access roads (total length = 31.5 km). Within patch cuts, most trees >15 cm dbh were removed, leaving fewer than 10 trees/ha (Hayward et al., 1999). Some advanced regeneration was retained, but as much as 95% of volume was removed. Patch cuts were distributed uniformly throughout the treated area, resulting in cut areas that were 53 m from the nearest neighbor, on average (Troendle et al., 2001). Prior to harvest, both watersheds