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Climate, weather, and recent mountain pine beetle outbreaks in the western United States

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ABSTRACT

Recent outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) have impacted large areas of western North America. Climate and weather conditions influence beetle population dynamics, and managers and policymakers are concerned about the potential effects of climate change on outbreaks. Here we studied five locations with extensive outbreaks in lodgepole pine (*Pinus contorta*) forests across the western United States. Using observations and modeling, we quantified means and changes relative to prior years of three climate or weather factors associated with outbreaks: (1) year-round temperatures that affect adaptive seasonality; (2) low temperatures that induce mortality of overwintering beetles; and (3) drought stress of host trees. Climate variable means varied among locations, indicating the beetle's tolerance to different climate during outbreaks. Analyses of climate or weather factors as outbreaks progressed revealed that year-round temperatures during outbreaks were typically higher than in prior years, and outbreak years lacked very low winter temperatures that often occurred in prior years. Drought was present at each location during some time of an outbreak, and increases in beetle-caused tree mortality at lower beetle population levels (as indicated by killed trees) were usually coincident with drought. Furthermore, drought was not required to maintain large outbreaks; in several locations, relief from drought during periods of high tree mortality did not cause subsequent declines in tree mortality. We did not find strong evidence that maladaptive seasonality, cold-induced mortality, or drought stress was responsible for decreases in tree mortality, suggesting the role of host depletion. Large variability in the relationships between climate or weather variables and outbreaks suggests that different climate and weather factors may have been limiting outbreaks at different times and that these factors did not influence beetle-caused tree mortality similarly among locations. Our results increase understanding of the climate and weather factors that influence beetle outbreaks and their variability in space and time and will lead to more accurate predictions of future patterns of outbreaks that consider future climate.

1. Introduction

Native bark beetle (Coleoptera: Curculionidae, Scolytinae) outbreaks are natural processes of forested ecosystems of western North America. However, recent outbreaks of some bark beetles are the largest in recorded history and have exceeded previously documented ranges, impacts, and frequencies (Carroll et al., 2004b; Raffa et al., 2008; Logan et al., 2010; Safranyik et al., 2010). Notable among these species is the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), whose outbreaks have impacted millions of hectares of lodgepole (*Pinus contorta*) and other pine forests across western North America (Meddens et al., 2012). A challenge for current forest management is to predict beetle outbreaks given probable climate change in the coming decades.

Climate and weather influence outbreaks of mountain pine beetle through three main factors: (1) adaptive seasonality; (2) cold-induced mortality; and (3) drought stress on host tree species. These factors manifest themselves through changes in the physiology and life history traits of the beetle as well as through changes in host tree physiology (Safranyik and Carroll, 2006; Bentz et al., 2010). The first factor, adaptive seasonality, results from the conditions of univoltinism (one-year life cycle) as well as synchronous adult emergence and life cycle timing (Bentz et al., 1991; Logan and Bentz, 1999; Logan and Powell, 2001). Temperature directly controls life stage development rates of mountain pine beetle, including progression through egg, larvae, pupae, and adult life stages (Logan and Bentz, 1999; Logan and Powell, 2001; Safranyik and Carroll, 2006). Maladaptive seasonality, such as fractional voltinism (two- or three-year life cycles) found in colder environments, can limit the outbreak potential of mountain pine beetles (Amman, 1973; Logan and Powell, 2009). Genetic variability in sensitivity to temperatures has been demonstrated for different mountain pine beetle populations (Bentz et al., 2001, 2011a).

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Low summer temperatures impacting synchronous adult emergence and life cycle timing hindered the building of an incipient beetle population in central Idaho in 1993, highlighting the potential of this factor to influence beetle populations (Logan and Powell, 2009).

The second factor is beetle larvae mortality from very low temperatures during the cold season (including late fall, winter, and early spring). Low temperatures during this time have contributed to population declines of mountain pine beetle across its range (Evenden and Gibson, 1940; Lessard et al., 1987; Safranyik and Linton, 1991; Kipfmueller et al., 2002; Bentz et al., 2011b), can determine thermal boundaries of available habitat (Safranyik, 1978; Logan and Powell, 2009), and can reduce outbreak probability (Sambaraju et al., 2012). During large outbreaks, however, cold-induced mortality events may act to slow down outbreaks, not completely stop them (Evenden and Gibson, 1940; Hopping and Mathers, 1945; Safranyik, 1978). Overwintering larvae progressively gain cold tolerance with decreasing temperatures (Bentz and Mullins, 1999), and mortality thresholds have been developed in laboratory studies (Wygant, 1940; Bentz and Mullins, 1999). Using a model of winter survival developed by Régnière and Bentz (2007), Safranyik et al. (2010) proposed that population growth occurs when the modeled winter survival probability is greater than 0.2; probabilities below that threshold lead to declines in population.

The third factor is drought stress on host trees. Drought affects the capability of a host tree to defend itself against bark beetle attack (Raffa and Berryman, 1983; McDowell et al., 2011). Warmer summers and drought conditions were associated with previous bark beetle outbreaks in North America, including spruce beetle (*Dendroctonus rufipennis*) (Berg et al., 2006; Hebertson and Jenkins, 2008), pinyon ips beetle (*Ips confusus*) (Breshears et al., 2005), and mountain pine beetle (Safranyik et al., 1975; Thomson and Shrimpton, 1984; Raffa et al., 2008; Thomson, 2009; Chapman et al., 2012). Increased host tree vigor increases resistance to attack by mountain pine beetle (Mitchell et al., 1983), and growth rate responses to climatic water deficit and drought influenced patterns of pine mortality in California (Millar et al., 2007, 2012). Not all documented outbreaks, however, correspond with drought conditions (Beal, 1943; Powell, 1969; Crookston, 1977). Furthermore, drought may negatively influence beetle populations because decreased survival and brood production occurs in depleted or dried phloem tissue (reduced phloem thickness) of host trees (Amman, 1972; Safranyik and Carroll, 2006).

Models have been developed to simulate the role that climate or weather plays in mountain pine beetle outbreaks. Process models based on insect physiology and climate or weather data have been developed for predicting adaptive seasonality (Bentz et al., 1991; Logan and Powell, 2001) and cold-induced mortality (Régnière and Bentz, 2007). These models have been used to predict current and future climate suitability for the beetle (Bentz et al., 2010; Safranyik et al., 2010), but lack evaluation across much of the beetle's range. Statistical models have identified relationships between beetle metrics such as area affected, trees killed, or population growth rate and climate or weather metrics using correlation, regression, or other statistical modeling (Kipfmueller et al., 2002; Aukema et al., 2008; Evangelista et al., 2011; Jewett et al., 2011; Preisler et al., 2012).

Descriptive and graphically focused methods showing climate or weather patterns related to mountain pine beetle outbreaks have also been conducted (Powell, 1969; Thomson and Shrimpton, 1984), and may be better at establishing the nature of relationships than explicitly quantifying them (Thomson and Shrimpton, 1984). Powell (1969) averaged conditions five years before, during, and five years after outbreaks in western Canada in the 1900s and found mixed results regarding the influence of climate or weather on outbreaks. Such an analysis may highlight general differences in climate among time periods, but may also mask interannual variations in weather important to beetle and host tree ecology.

Although much is understood about the role of climate and weather in influencing beetle outbreaks, gaps remain that limit our understanding and therefore ability to predict future changes in outbreak regimes. Mountain pine beetle populations exhibit variability in traits related to climate and weather, such as temperature sensitivity of development rates (Bentz et al., 2001, 2011a), yet more information is needed to ascertain differences among populations across the beetle's range. Analyses documenting patterns of climate and weather before, during, and after outbreaks of mountain pine beetle at multiple locations in the United States have not been conducted. Although the causes of population declines of some previous beetle outbreaks have been reported in the literature (Safranyik and Linton, 1991; Stahl et al., 2006), causes of decline are understudied and likely involve multiple factors, including host tree availability, cold-induced mortality, and maladaptive seasonality.

To address these gaps, we conducted a study of the patterns of climate and weather factors at five locations of recent (since 1980) mountain pine beetle outbreaks across the western US. We analyzed patterns of climate and weather variables and tree mortality during the progression of outbreaks. Our objectives were to: (1) compare climate means during outbreaks among locations; (2) document the temporal patterns of weather factors for decades before, during, and after outbreaks; and (3) examine the relationship between interannual changes in weather factors and changes in beetle-caused tree mortality during outbreaks.

2. Materials and methods

2.1. Study locations

We studied five major mountain pine beetle outbreaks in lodgepole pine forests across the western US in Utah, Colorado, Idaho, Montana, and Oregon (Fig. 1). Locations were chosen by examining the cumulative beetle outbreak extent within lodgepole pine from all years of acquired aerial survey maps, USFS Forest Insect and Disease Condition Reports (e.g., USDA, 1977; Man, 2010), lodgepole pine host range (Little, 1971b), outbreak initiation and collapse locations, and the number of trees killed within a location. Study locations varied in size and elevation (Table S1).

2.2. Data used in analysis

We analyzed the number of lodgepole pine trees killed by mountain pine beetles. Aerial survey data collected by US and Canadian agencies have been used to document and investigate large-scale patterns of forest insect outbreaks (Peltonen et al., 2002; Aukema et al., 2008; Powell and Bentz, 2009). Observers in aircraft map damage polygons, attribute tree mortality to disturbance agents, and estimate attack severity (number of trees killed). Spatial location errors, errors in discerning host tree type, and errors discerning host tree mortality are inherent using aerial detection survey techniques and therefore convey uncertainties, but these databases provide high spatial coverage of forest disturbance (Aukema et al., 2008; Powell and Bentz, 2009). We used 1-km gridded data sets of tree mortality in Washington and Oregon from 1980 to 2008 (Preisler et al., 2012) and throughout western North America from 1997 to 2010 (lower estimate of Meddens et al., 2012). To extend the period of tree mortality prior to 1997, we obtained polygonal aerial survey maps from USFS Regions 1 and 4 (UT, ID, MT) from 1991 to 1996 and USFS Region 2 (CO, WY) from 1995 to 1996. Aerial surveys were not always flown in all areas