

Mountain Pine Beetle in High-Elevation Five-Needle White Pine Ecosystems

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Abstract—Across western North America mountain pine beetle, *Dendroctonus ponderosae* (Coleoptera: Curculionidae, Scolytinae), populations are growing at exponential rates in pine ecosystems that span a wide range of elevations. As temperature increased over the past several decades, the flexible, thermally-regulated life-history strategies of mountain pine beetle have allowed for increased population success in numerous habitats. Of particular concern are the high-elevation five-needle white pines that are currently being infested. In a recent study of high-elevation whitebark pine forests, mountain pine beetles from multiple generations were found killing pines within a single summer. These generations included parent beetles that overwintered and emerged to attack new host trees, adult beetles that developed in a single year (univoltine), and adult beetles that required two years for life-cycle completion (semivoltine). The occurrence of univoltine brood emerging from host trees at elevations above 2600 m is potentially due to warming temperatures in recent years. To test if warming temperatures are a contributing factor, mountain pine beetle thermal suitability was simulated using historical temperatures estimated for a single high-elevation whitebark pine site in Wyoming. Although there was substantial variability among years, model predictions for this high-elevation site suggest that thermal conditions in the late 20th and early 21st century have been increasingly conducive to mountain pine beetle univoltine lifecycles, and well within the species cold tolerance limits. Predictions also suggest that in the late 1920s and early 1930s conditions were thermally suitable for mountain pine beetle univoltine lifecycle timing, although extreme cold temperatures in the early 1930s may have resulted in high mountain pine beetle larval mortality. We briefly discuss the implications of these results to past trends in high-elevation white pine mortality. The role of temperature in mountain pine beetle population success, genetic variability among populations, fungal associates, and management implications for high elevation white pine forests are also discussed.

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae), is a phytophagous insect with eruptive population dynamics and an expansive geographic range, extending from southern California USA, north to central British Columbia and recently into eastern Alberta, Canada (Safranyik and others 2010). Mountain pine beetle can attack and successfully reproduce in all *Pinus* species within their geographic range, except Jeffrey pine (*P. jeffreyi*), and larval feeding within the phloem typically results in death of the host tree. In central British Columbia, more than 14 million hectares of lodgepole pine (*P. contorta*), a principle host of mountain pine

beetle, were killed during a decade-long population outbreak that is considered the largest in recorded history (Safranyik and others 2010). In the western United States, more than 12 million hectares of multiple pine species have been affected by the mountain pine beetle in the past decade (figure 1). The fact that suitable pine hosts extend to the north and south of the current geographic range of mountain pine beetle, suggests that climate has historically constrained the geographic distribution of this insect. In the early 21st century, as a result of rising temperatures, there was a significant extension of the mountain pine beetle geographic range in Canada, and populations are now established in lodgepole pine stands that were previously climatically unsuitable (Safranyik and others 2010). Notably, in western Alberta, mountain pine beetle is established in lodgepole pine stands that are close to the boreal zone where jack pine (*P. banksiana*) occurs. The suitability of jack pine for beetle population persistence is unknown, and there is concern that mountain pine beetle range expansion may continue east across the continent.

In addition to geographic range expansion, mountain pine beetle population activity within its historical range has increased in recent years, and outbreaks are currently found in areas where they either were not recorded or were

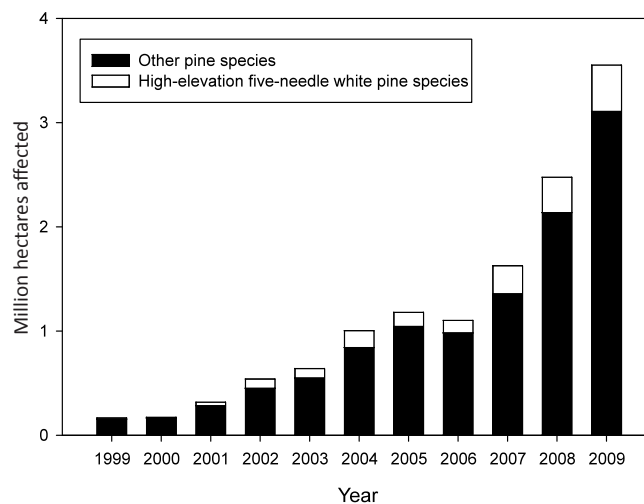


Figure 1. Million hectares of high-elevation five-needle white pine species, and all other pine species, affected by mountain pine beetle from 1999 to 2009 in the western United States. Data from USDA Forest Service, Forest Health Protection.

recorded infrequently (Gibson and others 2008). In particular, mountain pine beetle populations are currently affecting high-elevation five-needle white pine species including whitebark pine (*Pinus albicaulis*), limber pine (*P. flexilis*), foxtail pine (*P. balfouriana*), western white pine (*P. monticola*), Rocky Mountain bristlecone pine (*P. aristata*), Great Basin bristlecone pine (*P. longaeva*), and southwestern white pine (*P. strobiformis*). Mountain pine beetle macrofossils were found in lake sediment cores in Montana at time periods during the Holocene when whitebark pine was also predominate suggesting a long association of bark beetles and high-elevation white pines, although the frequency and intensity of historical outbreaks can not be inferred from these data (Brunelle and others 2008). While tree death associated with mountain pine beetle was observed in some whitebark pine ecosystems during intermittent warm periods in the 20th century (Arno 1986; Kipfmueller and others 2002; Perkins and Swetnam 1996), population activity at high elevations was not typically sustained due to a lack of seasonal thermal input that is required for population growth (Amman 1973).

Increasing temperature and shifts in precipitation patterns associated with climate change are likely contributing to the recent widespread death of five-needle white pines, which perform critical keystone functions in high-elevation ecosystems (Logan and Powell 2001). Temperature directly influences mountain pine beetle development and survival (Bentz and others 1991; Régnière and Bentz 2007), and shifts in precipitation can affect host tree vigor and defense mechanisms (Raffa and others 2008), the principle determinates of beetle attack success. Other factors that are contributing to high-elevation white pine decline include replacement by, and competition with, other tree species often following fire exclusion (Keane and Parsons 2010) and the exotic disease white pine blister rust caused by *Cronartium ribicola* (Schwandt and others 2010).

In this paper, we focus our discussion on mountain pine beetle, exploring the influence of temperature on beetle population dynamics and potential outbreak activity in high-elevation white pine forests. Using established models of thermally-dependent beetle physiological processes and current and historical temperatures, we provide predictions of mountain pine beetle population success over the last century at a single high-elevation whitebark pine site. We also present a brief overview of fungal species that are closely associated with the beetle (in other words, symbionts) and can influence mountain pine beetle population dynamics, genetic variability among mountain pine beetle populations, and management options for protection of high-elevation five-needle white pines against mountain pine beetle attack.

Temperature Affects Mountain Pine Beetle Population Success

Mountain pine beetle adults attack host trees in the summer, mate, and oviposit eggs under the bark. After the eggs hatch, individuals develop through four larval instars as

they feed through the phloem and then pupate to become an adult beetle that emerges from the tree to attack a new pine host. Like all insects, mountain pine beetle developmental timing is greatly affected by temperature and each life-stage has specific thermal requirements (Bentz and others 1991). The timing of tree attack and length of a generation are both dependent on annual temperature patterns as they influence life-stage specific developmental thresholds and ultimately the synchronicity of adult emergence (Logan and Bentz 1999). Emergence timing is a critical determinant of whether the number of adults attacking individual trees are sufficient to overcome host defenses, thereby allowing for successful host colonization and reproduction (Powell and Bentz 2009). A one-year (univoltine) generation time, which reduces the time individuals spend exposed to mortality factors, is considered optimal for mountain pine beetle population growth (Safranyik 1978). Annual thermal patterns can also influence mountain pine beetle survival through control of metabolites that are important for tolerating cold temperatures (Bentz and Mullins 1999; Safranyik and Linton 1998).

In mid-elevation lodgepole pine forests, the mountain pine beetle life-cycle is consistently univoltine, which means that a single generation is completed within one year (Amman and Cole 1983; Safranyik and Carroll 2006). The timing of beetle emergence from hosts in these forests can also be remarkably synchronous. For example, in a lodgepole pine forest at 2042 m, greater than 90 percent of adults emerged during a period of 15 days in each of the three years that emergence was monitored (2001, 2002, and 2003) (Bentz 2006). In contrast, at several high elevation whitebark pine sites (2652 to 2926 m) in 2004 and 2005, mountain pine beetle emerged at each site over a period greater than 60 days (Bentz and Schen-Langenheim 2007). Moreover, mountain pine beetle life-cycle timing in the individual whitebark pine trees monitored at the high-elevation sites was both univoltine and semivoltine (in other words, one generation of beetles develops every two years). At both the high-elevation whitebark pine site and the mid-elevation lodgepole pine site, at least some proportion of parent adults survived the winter and emerged in early summer (Bentz, unpublished data). Although the ability of these parents to oviposit additional eggs has not been fully investigated, it is known that they can attack live host trees (DeLeon and others 1934). Collectively, these data suggest that mountain pine beetle has a flexible life-history, and that beetles from multiple generations may be killing pines within a single summer. At high elevations, parent beetles that overwintered in hosts, adults produced from a univoltine life-cycle (eggs laid the previous summer), and adults produced from semivoltine life-cycles (eggs laid two summers ago) emerged within the same summer to attack whitebark pines. A mixture of adults produced from univoltine life-cycles and parent beetles that overwintered attacked lower elevation lodgepole pines. Because mountain pine beetle populations were at outbreak levels in both the mid-elevation lodgepole pine and high elevation whitebark pine sites, these data also suggest that a strictly univoltine life-cycle is not necessary for population

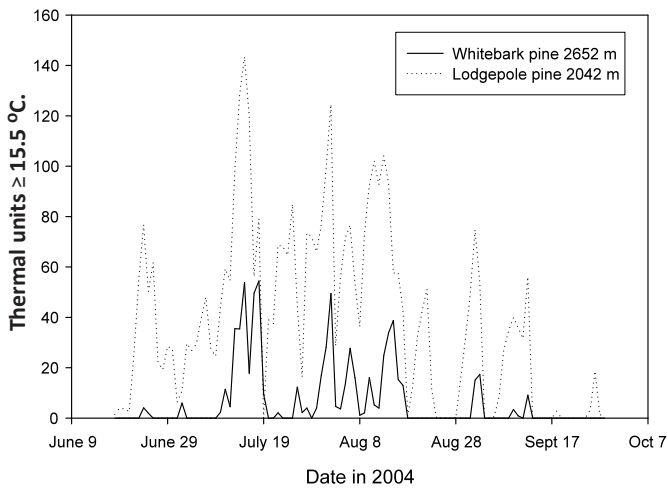


Figure 2. Air temperature recorded in a mountain pine beetle-infested lodgepole pine forest at 2042 m (Sawtooth National Recreation Area, ID) and an infested whitebark pine forest at 2652 m (Targhee National Forest, ID). Shown are daily thermal units $\geq 15.5^{\circ}\text{C}$ during the summer of 2004.

outbreaks. Thermal patterns that differ between the elevations (figure 2) undoubtedly influence mountain pine beetle life-cycle and emergence timing.

With the exception of warm periods during the 20th century (Perkins and Swetnam 1996), high-elevation white pine ecosystems were considered thermally unsuitable for mountain pine beetle population growth. Low temperatures at the high-elevation sites resulted in beetle life-cycles that historically required two or even three years for completion resulting in poor survival and low population growth (Amman 1973). However, our data suggests that at least some proportion of mountain pine beetle populations were able to complete a univoltine life-cycle in recent years at elevations above 2600 m (Bentz and Schen-Langenheim 2007). Amman (1973) observed that five-needle white pine forests at these elevations produced only semivoltine life-cycles in the early 1970's. Increasing temperature associated with climate change may have been a positive influence on mountain pine beetle population activity in high-elevation white pine forests in the early 21st century. We used mechanistic models that describe the relationship between temperature and mountain pine beetle development time (Bentz and others 1991; Gilbert and others 2004; Logan and Amman 1986) and cold-induced mortality (Régnière and Bentz 2007) to investigate this hypothesis.

These mechanistic models describe ecologically important and thermally-regulated traits that underlie population success (for example, development time and cold-temperature survival), and use hourly records of temperature from multiple years as input. We used these models to investigate trends in mountain pine beetle population success at a single high-elevation site over the past century. Hourly temperature for the years 1920 to 2008 were estimated using daily air temperature data collected in one mountain pine beetle-infested whitebark pine site near Togwotee Pass, WY (2950 m) from 2003 to 2005, and daily temperature data

from a nearby site (Moran, WY, 2072 m) that is part of the Historical Climatology Network (HCN). Two years of daily maximum and minimum temperature from the whitebark pine site were regressed against daily maximum and minimum temperature data from the HCN site for the same time period (Proc Mixed, SAS Institute) (daily maximum $R^2 = 0.9090$; daily minimum $R^2 = 0.6970$; $df = 754$). The resulting regression parameters were then applied to historical daily temperature recorded at the HCN site between 1920 and 2008 to estimate daily maximum and minimum temperature at the high-elevation whitebark pine site. Hourly temperatures were estimated from the daily maximum and minimum temperatures using a sine wave function. Estimated hourly temperatures were then used to drive a mountain pine beetle phenology model (Gilbert and others 2004) and mountain pine beetle cold tolerance model (Régnière and Bentz 2007). The annual proportion of univoltine mountain pine beetle and annual probability of cold temperature-related survival from 1920 to 2008 were predicted. A LOESS curve was fit to the annual predictions to approximate trends throughout the modeled time period.

Model results over the 78 year period indicated substantial variability in annual probability of beetle survival among years, which is likely the result of variability in the annual temperature pattern that drives accumulation of polyols responsible for larval cold tolerance (Bentz and Mullins 1999). We also predicted annual peaks in population univoltinism that were separated by years dominated by a semivoltine life-cycle. One hundred percent univoltinism was not predicted for any of the simulated years. Model results suggest that during the late 1920s and early 1930s thermal regimes at the high-elevation whitebark pine site were particularly favorable for univoltine mountain pine beetle life-cycle development (figure 3). A high proportion of individuals with a univoltine life-cycle, relative to a semivoltine life-cycle, can result in increased mountain pine beetle population success (Amman 1973). These findings are supported by tree-ring studies indicating mountain pine beetle killed whitebark pine during this same time period at several locations in the northern Rocky Mountains (Kipfmüller and others 2002; Perkins and Swetnam 1996) (figure 4), and also in southern mountain ranges of British Columbia and Alberta (Jackson and Campbell 2008; Wong and others, submitted).

Cold tolerance model predictions suggest that winter temperatures in 1933 may have caused significant mountain pine beetle mortality at the high-elevation whitebark pine site near Togwotee Pass, WY. Tree-ring data also suggest a reduction in mountain pine beetle-caused whitebark pine deaths in MT and ID following 1933 (figure 4). Although temperatures during the growing season were favorable for univoltine life-cycle development and mountain pine beetle population growth from the late-1920s into the late-1930s, extreme cold temperatures probably resulted in high levels of larval mortality during this time period.

Considering the more recent weather record, model predictions suggest a generally increasing trend during the late 20th and early 21st century (in other words, from around 1990 to 2008) in thermal regimes conducive to univoltine

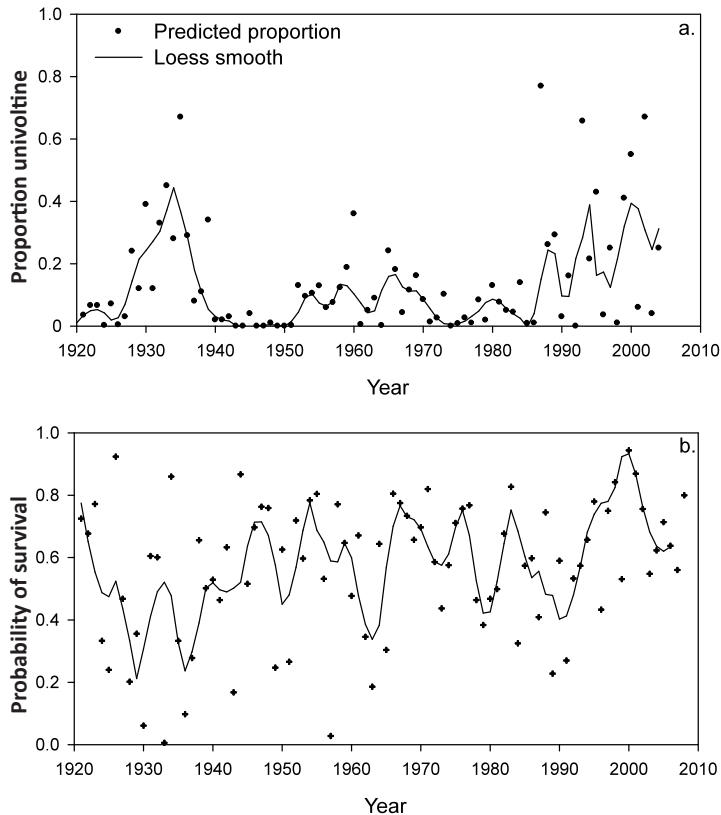


Figure 3. Predicted annual (a) proportion univoltine mountain pine beetle and (b) probability of mountain pine beetle cold temperature-related survival from 1920 through 2008 for a whitebark pine site near Togwotee Pass, WY (2950 m). The solid line is a LOESS smooth approximation to the annual model predictions.

life-cycles and cold temperature-related beetle survival at our high-elevation whitebark pine site. Mechanistic model projections of mountain pine beetle population success in whitebark pine habitats of British Columbia produced similar results—the percentage of whitebark pine's range highly susceptible to beetle outbreaks was projected to double, increasing to 20 percent over the next century (Campbell and Carroll 2007). Projections of future warming suggest this increasing trend in thermal suitability for mountain pine beetle will continue throughout this century in high-elevation five-needle white pine forests (Bentz and others 2010; Hicke and others 2006).

Genetic Variability Among Mountain Pine Beetle Populations

The geographic distribution of mountain pine beetle extends across pronounced latitudinal temperature gradients. One result of this widespread distribution is phenotypic and genetic variability in thermally-regulated traits such as beetle developmental timing (Bentz and others 2001; Bentz and others 2011). In replicated common garden rearing experiments using mountain pine beetle populations from multiple

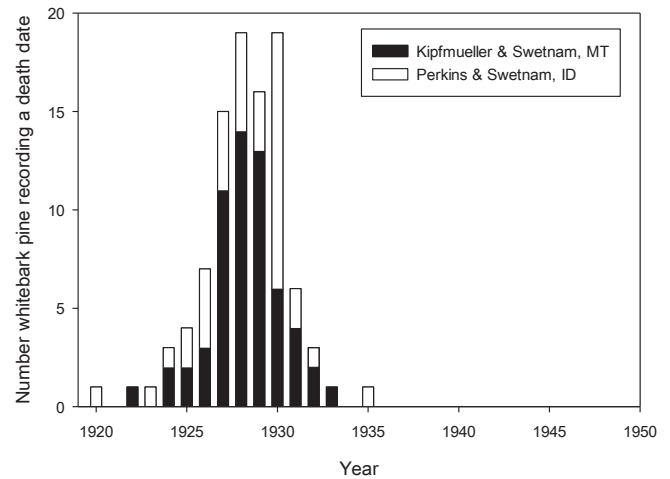


Figure 4. Number of whitebark pine recording a death date due to mountain pine beetle at several high elevation sites in Montana (Kipfmüller and others 2002) and Idaho (Perkins and Swetnam 1996). Death dates were determined using dendrochronology, and gallery patterns on the exposed tree bole were used to assign mountain pine beetle as the mortality agent.

latitudes reared at multiple temperatures, temperature contributed to substantial variation among populations in development time suggesting a role for phenotypic plasticity. Source population (in other words, the geographic location where the population was collected) was also significant in explaining differences in development time, an indication of genetic variation among latitudinally-separated populations that have adapted to local thermal regimes (Bentz and others 2011). An interesting result from these common garden experiments was that mountain pine beetle from Idaho developed faster, at a common optimal temperature, than mountain pine beetle from either a high-elevation southwestern white pine forest in Arizona (Bentz, unpublished data) or a pinyon pine (*P. monophylla*) forest in southern California (Bentz and others 2011). If we assume the univoltine life-cycle is optimal for beetle population growth (Logan and Bentz 1999), results from these studies suggest that time constraints in growth season have selected for fast development rates of one or more life-stages in more northern latitudes and for slow rates or different developmental thresholds in southern latitudes. Thus, a generation would be completed annually in both climates, with synchronous brood adult emergence at a suitable time of year. The optimal genotypes and phenotypes, however, will depend on the thermal habitat occupied, and could vary substantially across the elevational and latitudinal range of the species.

Plasticity in mountain pine beetle thermal response has allowed for close tracking of changing environmental conditions, thereby providing avenues for mountain pine beetle range expansion in Canada, and population eruptions in mid-elevation forests of multiple pine species (for example, lodgepole pine and ponderosa pine) and high-elevation five-needle white pine forests including whitebark pine and limber pine among others. As the climate continues to change, however, populations at all elevations may be increasingly

exposed to conditions that exceed the capacity of existing phenotypic plasticity to maintain synchrony with environmental conditions. The limits within which mountain pine beetle can maintain its capacity to adapt to continued climate warming across all elevations is currently unknown. Moreover, evidence of adaptation in thermally-regulated life-history traits to local climates (Bentz and others 2011) suggests that mountain pine beetle response to a changing climate will differ across the geographic range of this insect.

Mountain Pine Beetle Fungal Associates

Mountain pine beetle population dynamics are influenced by a close association with several fungal species that are introduced into a tree upon beetle colonization (Klepzig and Six 2004; Lee and others 2006). The relationship between mountain pine beetles and their fungal associates is often described as symbiotic, as they have evolved morphological adaptations to assist in the transport of specific associates, derive nutritional and defensive benefits from them, or both (Klepzig and Six 2004). The association of mountain pine beetle with various fungal species is integral to their survival. For example, developing mountain pine beetle larvae acquire vital nutrients (for example, nitrogen and ergosterol), which are not found in host tree tissue, by feeding on at least two fungi, *Grossmannia clavigera* and *Ophiostoma montium*, the hyphae of which spread throughout the phloem and sapwood following inoculation into the tree by attacking beetles (Adams and Six 2006). Although both fungi are important, one species (*G. clavigera*) supports faster brood development, larger body size, and higher brood production than does the other (Bleiker and Six 2007). Each fungus possesses different thermal ranges for optimal growth and survival, and seasonal temperature can dictate which fungal species is ultimately vectored by dispersing beetles (Six and Bentz 2007). *Grossmannia clavigera* can survive colder temperatures than *O. montium*, and *O. montium* grows better than *G. clavigera* at warmer temperatures (Rice and others 2008). Based on the observed thermal tolerances of each fungal species, we would expect to find a higher proportion of beetles carrying *G. clavigera* at high-elevation sites although this relationship has not been investigated. Because benefits to mountain pine beetle are not the same for each fungal species, ongoing temperature changes in high-elevation pine forests could indirectly affect mountain pine beetle population success through direct effects on their fungal symbionts.

Management Implications

Lodgepole pine is often considered the main host of mountain pine beetle (Safranyik and Carroll 2006). Baker and others (1971) found that mountain pine beetle attacked proportionately more lodgepole pine than whitebark pine in mixed high-elevation stands of Wyoming, although Waring and Six (2005) found that mountain pine beetle appeared to prefer whitebark pine to lodgepole pine at a site in Montana.

Reduced precipitation and increased temperature associated with climate change may differentially affect host tree species. Little is known about responses of pine trees at any elevation to changing environmental conditions and how this may influence defensive response to mountain pine beetle attack. Future management and restoration of high-elevation pine forests would benefit from a better understanding of how geographic location, site condition, host tree species, and differential host tree defensive response to changing abiotic conditions influence mountain pine beetle attack success and brood production in high-elevation pine forests.

Widespread deaths of high-elevation five-needle white pine due to a combination of mountain pine beetle and the exotic disease white pine blister rust, caused by *Cronartium ribicola* (Geils and Volger, these Proceedings; Tomback and others, these Proceedings), is threatening the existence of these species in many parts of their range. Protection of blister rust resistant trees from mountain pine beetle attack is crucial for continued collection of genetic material for development of rust-resistant strains, in addition to out-planting in heavily-affected areas. Although protection of high-elevation five-needle pines against mountain pine beetle attacks is difficult, in part due to the isolated location of high elevation ecosystems, there are options for protection of individual trees and stands. In particular, properly applied insecticide, applied annually, on the bole of living trees can provide protection (Hastings and others 2001). Semiochemical treatment using verbenone in stands (Perkins and others, these Proceedings) and on individual trees (Kegley and Gibson 2009) can also reduce high-elevation five-needle pine mortality due to mountain pine beetle. Aerial application of verbenone flakes in whitebark pine stands has also shown efficacy in reducing mountain pine beetle attacks over large areas (Gillette and others, unpublished data). Research on removing currently infested brood trees along with verbenone flake application to improve residual whitebark pine protection is on-going. These and other management options are described in detail in other sections of these Proceedings. In addition to stand and tree-level tactics for protection of high-elevation pines, population monitoring is a crucial aspect of restoration and conservation of high-elevation ecosystems (Macfarlane and others 2010).

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein.
