

**Will the Mountain Pine Beetle Epidemic Spread from  
Lodgepole Pine into Ponderosa Pine along the Northern Front  
Range Counties of Colorado?**

**Report to the Joint Ecology Working Group**

**Front Range Fuels Roundtable and the  
Colorado Bark Beetle Cooperative**



**Prepared by Jeff Witcosky  
Forest Health Management  
January 26, 2009**

## Executive Summary

The current mountain pine beetle epidemic in northern Colorado started in the late 1990s west of the Continental Divide in lodgepole pine. For the most part the epidemic has been confined to lodgepole pine forests. Over the past four years, mountain pine beetle infestations have developed and expanded in high elevation lodgepole pine forests east of the Continental Divide. By 2007, populations of mountain pine beetle in lodgepole pine forests along the northern Front Range (Boulder, Clear Creek, Gilpin, and Larimer Counties) had reached epidemic levels and were moving into the lodgepole pine/ponderosa pine transition zone. Members of northern Front Range communities have expressed concerns regarding the potential impacts of this beetle epidemic on ponderosa, limber, and Rocky Mountain bristlecone pines. All of these species of pines are acceptable and suitable host trees for the mountain pine beetle.

Examination of the available evidence provides limited support for the continued spread of mountain pine beetle throughout lodgepole pine forests and into ponderosa pine forests along the northern Front Range although we lack any historical parallel for this in Colorado. In recent Colorado history, the mountain pine beetle epidemics in ponderosa pine (Arkansas Valley and South Park in the 1990s and early 2000s and the Front Range in the late 1960s and 1970s) did not lead to substantial spread into adjacent lodgepole pine forests. On the other hand, observations across the west and for southern Wyoming during the current epidemic suggest that spread of the epidemic across the boundary between lodgepole pine and ponderosa pine occurred readily. Finally, the current epidemic in its extent and severity has reinforced the observation that bark beetle epidemics are not identical or similar in all their various characteristics, which contributes to the uncertainty regarding potential impacts of this mountain pine beetle epidemic on Front Range ponderosa pine forests.

Impediments to spread of mountain pine beetle from lodgepole pine into ponderosa pine are not likely to be associated with differences in the defensive chemistry between the two host trees. Whether stand structure and environmental conditions of ponderosa pine forests will influence mountain pine beetle population dynamics during the current epidemic is not clear, but the research of Negron and Popp (2004) and Schmid and others (2007) suggests that these factors will influence the severity of losses observed in ponderosa pine forests.

At this time, our best and most reasonable guess about the impact of mountain pine beetle on the ponderosa pine forests along the northern Front Range conforms to the findings of McCambridge and others (1982) from the last mountain pine beetle epidemic in ponderosa pine in Lory State Park. Initially, it is likely that losses of ponderosa pine may be most severe in areas where large populations of mountain pine beetle are generated in large diameter lodgepole pine forests, which then disperse into adjacent ponderosa pine forests. If active mountain pine beetle infestations are already present in ponderosa pine, these infestations may provide strong pheromone and host terpene cues that result in a rapid buildup of beetles dispersing from adjacent lodgepole pine forests. Long-distance

dispersal of mountain pine beetle from high-elevation lodgepole pine forests will likely contribute to a proliferation of infestations in ponderosa pine stands at all elevations.

This prediction regarding the potential impact of the current mountain pine beetle epidemic on the ponderosa pine cover type along the northern Front Range relies heavily on the modest amount of historic data available for this area. Entomologists are reluctant to extrapolate too far from the impacts of the Lory State Park mountain pine beetle epidemic and its impact on ponderosa pine because the study area is not representative of the entire lower montane ponderosa pine zone. It is likely that overall impacts of the current mountain pine beetle epidemic may vary widely and bear little similarity to the Lory State Park study.

Current policies and objectives of the Front Range Fuels Roundtable appear appropriate for the changing conditions associated with the building mountain pine beetle epidemic on the northern Front Range. This epidemic has caused severe losses of pines in virtually all areas impacted; lodgepole, limber, and Rocky Mountain bristlecone pine losses are increasing rapidly and are predicted to be severe across all high-elevation forests along the northern Front Range. At present, losses in ponderosa pine are elevated due to local beetle populations. These losses will increase significantly as the mountain pine beetle spreads out of lodgepole pine forests and into ponderosa pine forests over the next five to ten years. Absent a severe cold temperature event that kills brood larvae within beetle-infested trees, there is little reason to anticipate a major departure from this pattern as the mountain pine beetle spreads into ponderosa pine.

Nevertheless, restoration/fuels treatment prescriptions should explicitly examine the risk of losing much of the overstory in these stands, particularly where treatments are likely to result in single-storied stands of large diameter trees. Density/basal area reductions associated with restoration/fuels treatment prescriptions should emphasize adopting levels at the lower end of the acceptable range. Lower residual treatment densities or basal areas may prove less vulnerable to losses from mountain pine beetle. Where possible, prescriptions should consider providing for patches of healthy, small diameter (< 7 inches) trees as part of a mosaic to hedge against severe losses in the overstory. Also, prescriptions should consider opportunities for retaining some healthy regeneration and provide for opportunities to obtain additional new regeneration over the next ten to fifteen years.

Once prescriptions and plans are reviewed, restoration/fuels treatments should be implemented with all deliberate speed. Treatment procedures should provide flexibility for identifying and removing/masticating/treating mountain pine beetle-infested trees through the implementation period to account for an unexpected influx of beetles into stands receiving treatment. In high-value settings, resource managers should consider scheduling the timing of treatments for the fall, winter, and early spring months to minimize the mildly attractive host tree odors associated with these treatments.

## Table of Contents

### **Issue – Will the Mountain Pine Beetle Epidemic Spread from Lodgepole Pine into Ponderosa Pine along the Northern Front Range Counties of Colorado? .1**

#### **Mountain Pine Beetle Spread from Lodgepole Pine to Ponderosa Pine .....1**

- A.1 Tree species that serve as hosts for the mountain pine beetle:..... 1
- A.2 The Front Range mountain pine beetle dilemma: ..... 2
- A.3 Is there a scientific basis for the Hopkins Host Selection Principle?..... 2
- A.4 Current status of mountain pine beetle along the northern Front Range ..... 3
- A.5 Historic considerations regarding mountain pine beetle epidemics in Colorado and the West ..... 5
- A.6 Why might it be difficult for the mountain pine beetle to spread from lodgepole pine into ponderosa pine when both tree species are recognized as hosts for this bark beetle?..... 6
- A.7 Are there aspects of mountain pine beetle biology that may make movement between host tree species easier? ..... 8
- A.8 Conclusion – Will mountain pine beetle spread into ponderosa pine along the northern Front Range?..... 8

#### **Potential Losses of Ponderosa Pine to Mountain Pine Beetle.....9**

- B.1 Will losses of ponderosa pine to mountain pine beetle along the northern Front Range be as severe as those observed in lodgepole pine?..... 9
- B.2 Conclusion – Will losses of ponderosa pine be as severe as those observed for lodgepole pine? ..... 10

#### **Restoration/Fuels Treatments and Mountain Pine Beetle.....11**

- C.1 Have the restoration/fuels reduction prescriptions for managing ponderosa pine stands along the Front Range considered fully the implications of a mountain pine beetle epidemic in this forest cover type? In a more general sense, would a mountain pine beetle epidemic affect the policies, partnerships, and original strategies and priorities for restoration and fuels management in ponderosa pine? ..... 11
- C.2 Conclusion – Do restoration/fuels prescriptions for ponderosa pine stands fully consider or account for the potential for a mountain pine beetle epidemic and should these strategies and priorities be re-evaluated due to these changing conditions?..... 13

#### **Appendix – Background Discussion Topics .....15**

- 1. Population phases of the mountain pine beetle..... 15
- 2. Defense mechanisms in pines and variation in pine species defensive chemistry..... 16

3. Host selection and colonization process of eruptive bark beetle species..... 17

4. Mountain pine beetle population effects and the importance of scale..... 18

**Literature Cited .....19**

**Acknowledgements .....23**

**List of Tables .....24**

## **Issue – Will the Mountain Pine Beetle Epidemic Spread from Lodgepole Pine into Ponderosa Pine along the Northern Front Range Counties of Colorado?**

There are three separate elements associated with this issue:

- A. Will the mountain pine beetle spread to another host tree species, ponderosa pine, as populations of beetles move out of the lodgepole pine dominated forests, through the lodgepole pine/ponderosa pine transition zone (ecotone), and into the pure ponderosa pine forests of the Front Range?
- B. If so, will the mountain pine beetle continue to cause losses in ponderosa pine at levels similar to those seen in lodgepole pine?
- C. Have the restoration/fuels reduction prescriptions for managing ponderosa pine stands along the Front Range considered fully the implications of a mountain pine beetle epidemic in this forest cover type? In a more general sense, would a mountain pine beetle epidemic affect the policies, partnerships, and original strategies and priorities for restoration and fuels management in ponderosa pine developed by the Front Range Fuels Roundtable?

The discussion will follow the three topics listed above. However, while addressing the first question it is useful to mention the species of trees that are considered hosts of the mountain pine beetle, Dendroctonus ponderosae, in northern Colorado and southern Wyoming.

## **Mountain Pine Beetle Spread from Lodgepole Pine to Ponderosa Pine**

### **A.1 Tree species that serve as hosts for the mountain pine beetle:**

Host tree species of the mountain pine beetle in Colorado and southern Wyoming include lodgepole pine (Pinus contorta), ponderosa pine (P. ponderosa), limber pine (P. flexilis), and Rocky Mountain bristlecone pine (P. aristata). Occasionally, mountain pine beetle will attack and infest piñon pine (P. edulis), when mixed with ponderosa pine, and Engelmann spruce<sup>1</sup>

<sup>1</sup> Engelmann spruce has been attacked and killed by mountain pine beetle in mixed stands with lodgepole pine during the current epidemic, however it remains to be demonstrated whether brood production is successful (but see Huber and others 2009). Stands of pure Engelmann spruce or a spruce-fir mix are not threatened by mountain pine beetle.

(*Picea engelmannii*) when mixed with lodgepole pine. In ornamental settings, Scots pine (*P. sylvestris*) and Austrian pine (*P. nigra*) have been attacked by the mountain pine beetle; whether these two species of trees are suitable hosts remains to be determined.

The current mountain pine beetle epidemic in northern Colorado started in the late 1990s in the vast lodgepole pine forests west of the Continental Divide. For the most part the epidemic has been confined to lodgepole pine, although ponderosa pine stands have been infested and killed along the eastern flank of the Sierra Madre in Carbon County, Wyoming, and ponderosa and limber pines have been killed along the Medicine Bow Mountains in southern Albany County, Wyoming, over the last five years. In certain settings, where lodgepole pine is mixed with Engelmann spruce (riparian zones and the lodgepole pine/spruce-fir ecotone), the mountain pine beetle has attacked and killed spruce trees intermingled with lodgepole pine.

## **A.2 The Front Range mountain pine beetle dilemma:**

The question asked by the members of the Lodgepole Pine Ecology Working Group – will mountain pine beetle spread from lodgepole pine forests to ponderosa pine forests along the northern Front Range of Colorado? – invokes the fundamental element contained in the “Hopkins Host Selection Principle.” This hypothesis was formulated by pioneering forest entomologist A.D. Hopkins (1916, 1917) to address an observation of his regarding infestation patterns of the mountain pine beetle in lodgepole and ponderosa pines in the northern Rocky Mountains during the course of a severe epidemic that extended from about 1909 until 1940.

Hopkins (1916, 1917) observed that “a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted.” In his review of the Hopkins Host Selection Principle (HHSP), Barron (2001) states “Hopkins drew this conclusion from observations concerning the spread of the mountain pine beetle among mixed stands of pine. Outbreaks of the beetle in lodgepole pines rarely spread to adjacent yellow [ponderosa] pines, although both pine species are suitable hosts for the beetle (Hopkins 1916, 1917).” Although the HHSP has taken on a number of different meanings over the years, the most appropriate definition is recognized as “the observation that adult insects may show an enhanced preference for the host species on [in, for our case] which they developed when compared to the general population” (Barron 2001). The origin of this behavior may be (1) genetic, (2) an inherited environmental effect, (3) a behavioral bias developed during the insect’s lifetime, or (4) a combination of these three factors (Barron 2001).

## **A.3 Is there a scientific basis for the Hopkins Host Selection Principle?**

The most relevant experimental test of the HHSP was conducted by Wood (1963) who evaluated this hypothesis with respect to *Ips confusus* in a variety of pine species in California (the bark beetle Wood studied is now recognized by taxonomists as the California fivespined ips, *Ips paraconfusus*, a species separate and distinct from the piñon ips, *Ips confusus*). Wood concluded that the HHSP could not be confirmed for *I. paraconfusus* under experimental conditions because beetles from one host tree species showed no consistent preference when reared in that species

versus two other pine species over 22, 19, or 33 generations in *P. ponderosa*, *P. lambertiana*, and *P. jeffreyi*, respectively. Wood (1963) concluded that the term “Principle” does not appear to be appropriate based on his experimental studies.

In an observational study of three mixed-species stands sustaining mountain pine beetle infestations, Baker and others (1971) presented results that they suggested supported the HHSP. These authors noted that mountain pine beetle developing in lodgepole pine and whitebark pine (*P. albicaulus*) in mixed stands tended to kill more of the dominant species (lodgepole pine in one stand and whitebark pine in the other stand) than the less abundant species of host tree. The authors attributed this pattern of infestation as suggesting that adult beetles exhibited specificity for the tree species in which the beetles completed their larval development. Dean (2007) provided some support for Baker and others when she found that mountain pine beetle appeared to prefer limber pine over lodgepole pine in her study area located in the Medicine Bow Mountains of southern Wyoming (Carbon County).

There is little evidence available in the scientific literature to support the HHSP for the tree-killing species of bark beetles. Nevertheless, the HHSP remains a common discussion point with respect to the on-going mountain pine beetle epidemic in Colorado.

#### **A.4 Current status of mountain pine beetle along the northern Front Range**

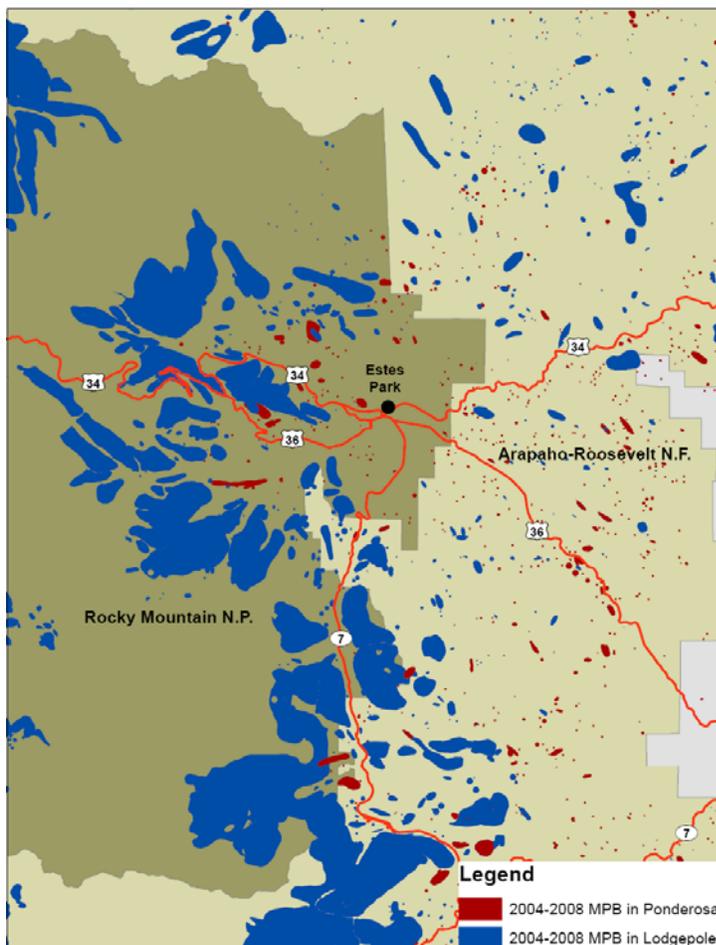
As mountain pine beetle infestations developed and expanded in high-elevation lodgepole pine forests east of the Continental Divide, concerns focused on the potential impacts of this beetle epidemic on ponderosa, limber, and Rocky Mountain bristlecone pines. Populations of mountain pine beetle in the northern Front Range (Boulder, Clear Creek, Gilpin, and Larimer Counties) lodgepole pine forests reached epidemic levels by 2007 (Tables 1, 2) and have begun to spread into the lodgepole pine/ponderosa pine ecotone (Witcosky 2008).

It is important to note that mountain pine beetle populations within the ponderosa pine forest cover type along the northern Front Range were at elevated levels in 2007 as well (Tables 3, 4). The term elevated means that losses of ponderosa pine to mountain pine beetle were higher than normal background-level losses – where beetles attack and infest only weakened or damaged trees – but were much less than the threshold level of tree mortality that signifies epidemic conditions. Utilizing the phases of the population cycle presented by Safranyik and Carroll (2006) [[see Appendix, 1, for discussion of population phases](#)] the mountain pine beetle occurrence in ponderosa pine along the northern Front Range would be classified at the incipient-epidemic population level, a step below the epidemic level.

Also of significance along the Front Range ponderosa pine forests is the relatively conspicuous activity of the pine engraver beetle, *Ips pini*. This bark beetle prefers to attack and kill the canopy portion of ponderosa and lodgepole pines, and is the principal bark beetle killing smaller trees of these two species along the Front Range. The pine engraver increased in abundance in Front Range ponderosa pine forests during the drought period from 1997 – 2003 and has remained at elevated levels through 2008. Where pine engraver beetles attack the canopy portion of larger trees, they provide an opportunity for other bark beetles, like the mountain pine beetle and the sixspined ips, *Ips calligraphus*, to colonize and utilize the lower bole of these pine

engraver-infested trees, which may lead to an increase in the population levels of these two species.

To set the stage for this discussion, epidemic levels of mountain pine beetle are present in high-elevation (> 9,500 ft) lodgepole/limber/Rocky Mountain bristlecone pine forests along the northern Front Range from I-70 north to southern Wyoming. At mid-elevation (8,000 – 9,500 ft), mountain pine beetles are entering the lodgepole pine/ponderosa pine ecotone, especially in Boulder and Larimer Counties (Figure 1). At lower elevations (< 8,000 ft), mountain pine beetles are active and can be found killing healthy ponderosa pines in widely scattered small groups of trees rather than the single-tree or background losses typically associated with low-level, or endemic, beetle populations. Pine engraver beetles are at elevated levels and are contributing to losses of ponderosa pine along the Front Range.

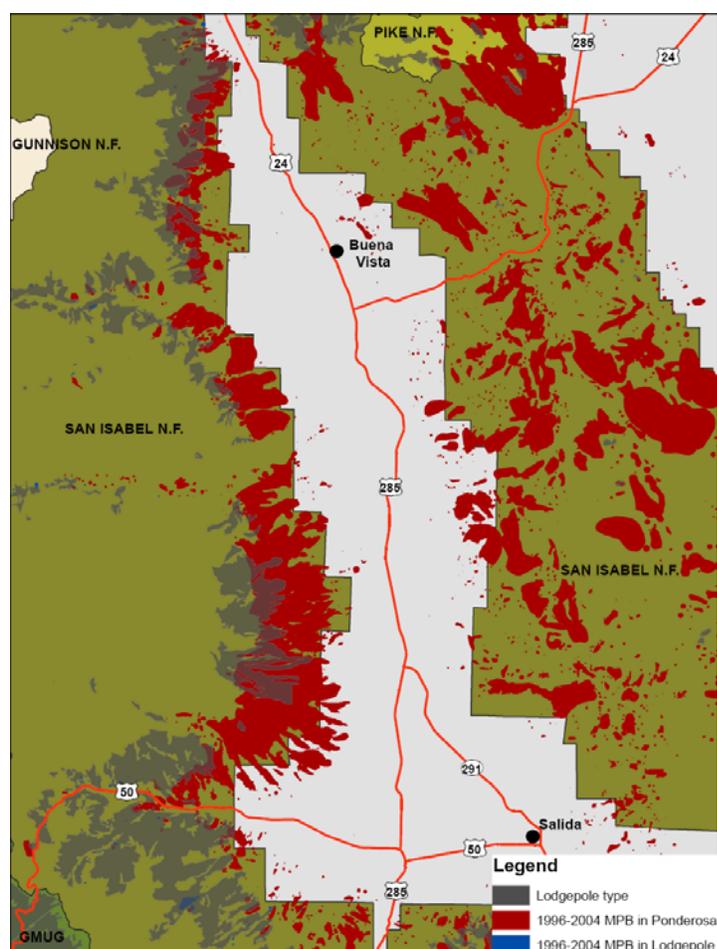


**Figure 1. Mountain Pine Beetle Mortality in western Boulder and Larimer County, Colorado, 2004 – 2008.**

Mountain pine beetle mortality in lodgepole pine (blue), from 2004 through 2008, is widespread along the northern Front Range of Larimer County, near Estes Park, Colorado, and reached epidemic population levels in 2007. Mountain pine beetle mortality in ponderosa pine (red) is increasing and becoming more widespread, however the areas impacted are of much smaller size. Losses of ponderosa pine to mountain pine beetle were at elevated or incipient-epidemic levels in 2007.

## A.5 Historic considerations regarding mountain pine beetle epidemics in Colorado and the West

An historic parallel for mountain pine beetle spreading from lodgepole pine to ponderosa pine in Colorado has never been documented in Colorado. However, there is historical evidence from Colorado that movement of mountain pine beetle from ponderosa pine into lodgepole pine is uncommon during significant epidemics. During the last epidemic on the Front Range from 1965 through 1978, the mountain pine beetle impacted approximately 2,000,000 acres of ponderosa pine forests from Cañon City north to the Colorado-Wyoming state line



**Figure 2. Arkansas Valley-South Park, Colorado, Mountain Pine Beetle Epidemic, 1996 – 2004.**

During the mountain pine beetle epidemic in the Arkansas Valley and adjacent South Park of Colorado (1996-2004) the beetle killed ponderosa pine (red) primarily and only sporadically killed adjacent lodgepole pine (blue). The occurrence of ponderosa pine-dominated stands is not illustrated on the map; lodgepole pine-dominated stands are shown in dark grey. The map combines the aerial survey data of mountain pine beetle mortality in this area from 1996 through 2004.

(McCambridge and others 1982). Aerial detection survey maps prepared during this epidemic suggest that the epidemic impacted the ponderosa pine cover type to a considerable extent but had very limited impact in the lodgepole pine cover type. In the 1996 – 2004 mountain pine beetle epidemic in the Arkansas Valley (Chaffee County) and adjacent South Park (Park County), losses occurred primarily in the ponderosa pine cover type, although there was some

concurrent mortality identified in a few lodgepole pine stands at high elevations in the general vicinity of Arkansas Valley (Figure 2). For the South Park area, Cain and Howell (2005) reported that the mountain pine beetle remained in ponderosa pine and had not impacted adjacent lodgepole pine stands at the time of their survey.

The mountain pine beetle epidemic that developed between 1978 and 1985 in lodgepole pine in Grand and Summit Counties, CO, never reached the Front Range ponderosa pine forests. This epidemic ended, apparently due to high overwintering larval mortality following extremely cold temperatures during the winter of 1984 – 1985 (Lessard and others 1982).

Recent discussions among other forest entomologists throughout the West indicated that movement of mountain pine beetle from lodgepole pine to ponderosa pine has been observed on several occasions although these events were not formally documented. Entomologists indicated that where mountain pine beetle epidemics in lodgepole pine reached a transition zone into ponderosa pine forests the beetle successfully and aggressively spread into ponderosa pine. The mountain pine beetle epidemic underway currently in British Columbia has caused extensive mortality in their ponderosa pine forests adjacent to mountain pine beetle-impacted lodgepole pine forests. In southern Wyoming the mountain pine beetle has infested and killed ponderosa pine stands adjacent to mountain pine beetle-killed lodgepole pine stands along the eastern slope of the Sierra Madre and the southern Medicine Bow Mountains during the current epidemic.

## **A.6 Why might it be difficult for the mountain pine beetle to spread from lodgepole pine into ponderosa pine when both tree species are recognized as hosts for this bark beetle?**

### **(a) Defensive chemicals differ between lodgepole pine and ponderosa pine:**

Oleoresin is contained within the preformed resin canals of pines and is released when these structures are severed during an injury [[see Appendix, 2, for a discussion of conifer defenses](#)]. The oleoresin of pines contains a number of different chemical constituents that contribute to the defensive response. Oleoresin is composed of resin acids and terpene hydrocarbon oil. Oleoresin can suffocate bark beetles by coating and interrupting their respiratory system. One group of defensive chemicals found in the oleoresin of conifers, monoterpenes, exhibit insecticidal or fumigant toxicity to bark beetles. Monoterpenes also vary in their toxicity to bark beetles (see Seybold and others 2006 for discussion and references). Finally, percentages of specific monoterpenes vary among pine species (Table 5), within a single species across its range, and among individuals within a single population.

Mountain pine beetles attacking lodgepole pine will be exposed to high levels of  $\beta$ -phellandrene (69% of monoterpene content), 3-carene (10% of monoterpene content), and  $\beta$ -pinene (9% of monoterpene content) (Smith 2000). In contrast, dominant monoterpenes of ponderosa pine are 3-carene (47%),  $\beta$ -pinene (28%), and myrcene (13%). A change in host tree defensive chemistry between lodgepole pine and ponderosa pine may pose a significant hurdle for beetles spreading from the former host species to the latter host species.

The monoterpene variation between species of pines appears to provide an obvious mechanism that might limit the movement of mountain pine beetle populations from one species of host tree to another species of host tree. However, Raffa and others (1993) concluded that bark beetles can tolerate the oleoresin chemistry of their host trees. In some cases this is even true for non-host tree species (Lee and others 2008).

One probable explanation for a successful transition from lodgepole pine to ponderosa pine is that when mountain pine beetle populations are at epidemic, or eruptive, levels, they may use behavioral strategies that allow them to overcome the deterrent of different host tree defensive chemicals (Wallin and Raffa 2004). Another feature associated with epidemic populations of mountain pine beetle is the observed group-killing pattern of beetle-infested trees. This pattern is associated with a “switching mechanism” of timing of attack and infestation, whereby beetles attack a “focus tree” initially (the first tree in a group to be attacked) and then switch to attack an adjacent “recipient tree” (second or later tree in a group that is attacked) apparently due to the sequential effects of aggregation and anti-aggregation pheromones (Geiszler and Gara 1978, Mitchell and Preisler 1991, Preisler and Mitchell 1993) [[see Appendix 3, for a discussion of host selection in bark beetles](#)]. Geiszler and Gara found that beetles select recipient trees on the basis of diameter and distance from the focus tree. The “switching mechanism” is a simple process that would lead to the infestation of multiple host tree species that occur in mixed species stands, such as those in the lodgepole pine/ponderosa pine ecotone.

The notion that plant defensive chemistry would present an insurmountable barrier to entry of mountain pine beetle into ponderosa pine forests from adjacent lodgepole pine forests seems unlikely over the course of the current epidemic. To date, observations of mountain pine beetle’s success in mixed-host species situations, where lodgepole pine is mixed with limber pine, Rocky Mountain bristlecone pine, or ponderosa pine, all suggest that the beetle will readily surmount the transitional hurdles associated with host tree species other than lodgepole pine. It appears that the mountain pine beetle will likely move through the lodgepole pine /ponderosa pine ecotone and into the pure ponderosa pine forests of the northern Front Range and impact all species of pines in the process.

**(b) Structural differences between lodgepole pine and ponderosa pine stands may alter beetle behavior:**

Once the mountain pine beetle spreads into the pure ponderosa pine forest type, stand structure or the physical environment of these stands may pose significant impediments to sustaining the high beetle populations that have been observed in lodgepole pine forests. Stand structure of ponderosa pine forests along the Front Range tends to differ from that of lodgepole pine, with a greater occurrence of openings and a more variable density and canopy architecture (Negron and Popp 2004).

These features are thought to be of significance in relation to bark beetle mass attack because more open stands may: (1) alter or disrupt air currents, and therefore impact the continuity and transport of the aggregation pheromone plume (Bartos and Amman 1989; but see Schmid and others 1992), or (2) alter environmental characteristics, such as increased temperature and light conditions, which may influence beetle behavior directly through flight, landing behavior, or the

propensity for beetles to remain at their landing site and initiate attack (Schmid and others 1991, see Raffa and others 1993 for discussion and references).

These structural properties and environmental conditions of ponderosa pine forests may influence the course of the current mountain pine beetle epidemic as it spreads into these forests. In addition, mountain pine beetles may be subject to greater levels of mortality during dispersal and host selection due to greater exposure to unfavorable environmental conditions. The potential impact of these factors on the mountain pine beetle epidemic is unknown.

### **A.7 Are there aspects of mountain pine beetle biology that may make movement between host tree species easier?**

Eruptive bark beetle species, like the mountain pine beetle, appear to have behavioral traits that allow them to overcome the chemical defenses of well-defended host trees during their epidemic phase, when dispersing beetles are abundant in forest ecosystems [[see Appendix, 4, for a discussion of the importance of scale in bark beetle population dynamics](#)]. Two characteristics of bark beetle behavior during epidemics are notable. First, epidemic populations of host-seeking beetles can respond rapidly and in high numbers to the presence of aggregation pheromones. A rapid rate of mass attack may far exceed the ability of a tree to defend itself against attacking beetles. A pine tree's preformed defenses may be overcome within two to three days of the initiation of a successful mass attack (Raffa and Berryman 1982ab). Second, there appear to be significant changes in the behavior (e.g. declining host discrimination and a decrease in avoidance behavior associated with high concentrations of host monoterpenes) of eruptive bark beetle species during epidemics, where an abundance of beetles acts in a positive feedback process that facilitates successful mass attack and population increase as Wallin and Raffa (2004) found for the spruce beetle, *Dendroctonus rufipennis* (see Raffa and others 2008 for further discussion). The rapid response of high numbers of beetles during mass attack quickly exceeds the threshold level required for successful colonization of a living tree. The benefit of high beetle populations positively enhances the attack, colonization, and reproductive success of the beetle.

### **A.8 Conclusion – Will mountain pine beetle spread into ponderosa pine along the northern Front Range?**

Examination of the available evidence provides limited support concerning the spread of mountain pine beetle from lodgepole pine into ponderosa pine along the northern Front Range. In recent Colorado history, the mountain pine beetle epidemics in ponderosa pine (Arkansas Valley and South Park in the 1990s and early 2000s and the Front Range in the 1970s) did not result in substantial spread into adjacent lodgepole pine forests. On the other hand, observations across the west and for southern Wyoming during the current epidemic suggest that spread of the infestation across the boundary between these two forest cover types will occur readily. Finally, the current epidemic has reinforced the observation that bark beetle epidemics are not identical or similar in all their various characteristics. Historical findings from the mountain pine beetle epidemic in the northern Rocky Mountains during the 1970s have been of limited value in the

current epidemic (see for example, Tishmack and others 2005). The extent and severity of the current mountain pine beetle epidemic add further uncertainty regarding the suitability of historical generalizations from prior epidemics in Colorado.

Impediments to spread of mountain pine beetle from lodgepole pine into ponderosa pine are not likely to be associated with differences in the defensive chemistry between the two host trees. Whether stand structure and environmental conditions of ponderosa pine forests will influence mountain pine beetle population dynamics during the current epidemic is not clear, but the research of Negron and Popp (2004) and Schmid and others (2007) suggests that these factors will influence the severity of losses observed in this forest cover type.

## **Potential Losses of Ponderosa Pine to Mountain Pine Beetle**

### **B.1 Will losses of ponderosa pine to mountain pine beetle along the northern Front Range be as severe as those observed in lodgepole pine?**

A useful starting point for the discussion of potential impacts is the paper published by McCambridge and others (1982) regarding the last mountain pine beetle epidemic (1965 – 1978) in Front Range ponderosa pine forests. At Lory State Park, losses of ponderosa pine during the mountain pine beetle epidemic accounted for approximately one-third of the basal area and approximately 20-25% of the live trees. Tree mortality was patchy, so the authors described losses in areas of “heavy tree kill” and “areas of moderate and scattered mortality.” Overall losses by diameter were in the range of 30-40% for the 7-23 inch diameter classes; losses were lower for smaller diameter trees. Trees larger than 23 inches in diameter were very uncommon in their study area.

For areas where “heavy tree kill” was observed, ponderosa pines 9 inches in diameter or greater sustained mortality in excess of 90% (McCambridge and others 1982). For trees less than 9 inches in diameter, losses ranged from 6% for 3-inch trees, 38% for 5-inch trees, and 68% for 7-inch trees. Although it appeared that losses were reduced in the smaller diameter ponderosa pines, the authors concluded that there was “no tree diameter evident below which ponderosa pine is immune from beetle attack during an outbreak.” The authors concluded that for the Lory State Park epidemic, elevation, site index, aspect, and amount of Douglas-fir mixed with ponderosa pine had no measurable influence on the amount of pine mortality caused by mountain pine beetle.

The discussion of the Lory State Park mountain pine beetle epidemic is of interest due to the variable pattern of mortality observed. This feature was distinctive enough that the authors chose to separate, or classify, their loss statistics based upon the intensity of tree mortality observed. This pattern of patchiness and variable intensity of losses is often observed during mountain pine beetle epidemics in ponderosa pine. In contrast, the pattern of mortality in lodgepole pine during the current epidemic is severe across vast landscapes with little evidence of patchiness. The landscape mortality of ponderosa pine in Lory State Park was probably less than what we have observed in the lodgepole pine cover type, in part, because high-density,

mountain pine beetle-susceptible ponderosa pine stands do not occur over vast continuous acreages.

This difference illustrates one of the difficulties in predicting how the current mountain pine beetle epidemic will play out in ponderosa pine stands. The maintenance of high populations of mountain pine beetle in lodgepole pine will favor a pattern of losses in adjacent ponderosa pine forests similar to those seen in lodgepole pine. To date, losses of ponderosa pine on southern Wyoming sites have been severe where they exist adjacent to severely impacted lodgepole pine stands. However, if features of the ponderosa pine ecosystem on the Front Range contribute to higher levels of beetle mortality, due to reduced survival during dispersal, host selection, mass attack, or brood production, losses of ponderosa pine may resemble those observed by McCambridge and others (1982) or may decline in intensity as the epidemic spreads through these forests.

Another feature to keep in mind regarding the Front Range forests is that dispersing beetle populations may move significant distances across the forest landscape, from high-elevation lodgepole pine forests to low elevation ponderosa pine forests, in patterns that defy simple, short-distance dispersal flight expectations (Jackson and others 2008). Assuming that long-distance dispersal occurs along the Front Range as described by Jackson and others for British Columbia, patterns of dying mountain pine beetle-infested trees with red foliage observed during aerial surveys may not correlate well with patterns of newly infested green trees. While the general pattern of mountain pine beetle infestation within the ponderosa pine cover type over the next several years is likely to be a progression from high elevation to low elevation, the long-distance dispersal capability of the mountain pine beetle will likely also result in the proliferation of mountain pine beetle infestations in ponderosa pine stands at all elevations.

## **B.2 Conclusion – Will losses of ponderosa pine be as severe as those observed for lodgepole pine?**

At this time, our best and most reasonable guess about the impact of mountain pine beetle on the ponderosa pine cover type along the northern Front Range conforms to the findings of McCambridge and others (1982) from the last mountain pine beetle epidemic in ponderosa pine in this area. Initially, it is likely that losses of ponderosa pine may be most severe in areas where large populations of mountain pine beetle are generated in large diameter lodgepole pine forests, which then disperse into adjacent ponderosa pine forests. If active mountain pine beetle infestations are already present in ponderosa pine, these infestations may provide strong pheromone and host terpene cues that result in a rapid buildup of beetles dispersing from adjacent lodgepole pine forests. Long-distance dispersal of mountain pine beetle will likely contribute to a proliferation of infestations in ponderosa pine stands at all elevations.

This prediction regarding the potential impact of the current mountain pine beetle epidemic on ponderosa pine forests along the northern Front Range relies heavily on the modest amount of historic data available for this area. Entomologists are reluctant to extrapolate too far from the impacts of the Lory State Park mountain pine beetle epidemic and its impact on ponderosa pine because the study area is not representative of the entire lower montane ponderosa pine zone due to the limited physiographic area of the park. It is likely that overall impacts of the current

mountain pine beetle epidemic may vary widely and bear little similarity to the Lory State Park study.

It is important to recognize, as well, that environmental conditions (e.g. patterns of rainfall and snowfall, warmer summer temperatures, and warmer winter low temperatures, in addition to the overall increase in large diameter, dense, and older forest stands that can partially be attributed to fire suppression) may have changed bark beetle behavior and population dynamics. If this is true, these changes may exceed the general tendencies and patterns of bark beetle behavior and population dynamics observed and reported in the literature (Raffa and others 2008). This ambivalence has been reinforced over the past decade by an increase in synchronicity of epidemics of multiple species of bark beetles across the entire elevational gradient of coniferous forests in the central and southern Rocky Mountains.

## **Restoration/Fuels Treatments and Mountain Pine Beetle**

### **C.1 Have the restoration/fuels reduction prescriptions for managing ponderosa pine stands along the Front Range considered fully the implications of a mountain pine beetle epidemic in this forest cover type? In a more general sense, would a mountain pine beetle epidemic affect the policies, partnerships, and original strategies and priorities for restoration and fuels management in ponderosa pine?**

The spread of mountain pine beetle populations into ponderosa pine along the northern Front Range introduces a new dimension into the discussion of ponderosa pine restoration treatments and related fuels reduction treatments. At this time, it is prudent to consider the mountain pine beetle as an additional factor during the analysis and evaluation of proposed strategies, prescriptions, and treatments.

As mentioned in Section B, above, the last mountain pine beetle epidemic reduced stand basal area and stand density by approximately one-third (McCambridge and others 1982). Losses by diameter class overall were approximately 40% for all trees equal to or greater than 7 inches in diameter. If the current mountain pine beetle epidemic follows this pattern, losses will be significant, but substantial numbers of trees should remain across all diameter classes.

If the mountain pine beetle epidemic follows a pattern similar to that seen in lodgepole pine, there may be reason and need to re-evaluate ponderosa pine restoration treatments and fuels reduction treatments with respect to prescriptive actions and their impact on the smaller diameter classes (< 7 inches) of ponderosa pine. To hedge against severe losses of larger trees, prescriptive treatments may need to favor smaller diameter (< 7 inches) pines in discrete patches, which would allow for some size class variation across the stand but still limit the potential for crown fires to develop due to the presence of ladder fuels associated with smaller trees. Dennis and Sturtevant (2008) provide a useful discussion of forest restoration guidelines for ponderosa pine along the Front Range.

Additionally, a re-examination of prescriptive stand density reduction levels appears appropriate. Negron and Popp (2004) found that susceptibility to mountain pine beetle infestation increased at densities at or above 17.1 m<sup>2</sup>/ha (74 ft<sup>2</sup>/ac) in ponderosa pine stands on the northern Front Range. Restoration and fuels reduction treatments should consider reducing stand basal area to a level

well below the threshold identified by Negron and Popp, for example to 50 – 60 ft<sup>2</sup>/ac. The retention of higher density groups of ponderosa pines within treated stands may create conditions that favor localized mountain pine beetle infestation (Olsen and others 1996). Treatments that result in low density stands also may improve conditions for regeneration, which would be important if losses of the ponderosa pine overstory prove to be severe.

Negron and Popp (2004) noted that larger diameter ponderosa pines were more likely to die in their mountain pine beetle-infested study plots, which is in contrast to the findings of McCambridge and others (1982) for their “areas of moderate and scattered mortality” but not for their areas of “heavy tree kill”. Greater attention to retaining smaller diameter ponderosa pines in restoration and fuels treatments seems prudent given the findings of Negron and Popp. It is conceivable that a majority of the large trees in a restoration/fuels-treated stands could be killed over the course of this epidemic. With the smaller trees removed during the treatment, this outcome would leave these stands in a non-stocked or severely under-stocked condition.

In unmanaged ponderosa pine forests, losses may prove to be more severe in uniformly high density stands than in stands where density is lower and patchiness is greater. Treatments designed to reduce mountain pine beetle impacts may prove less successful when these actions adjoin large areas of unmanaged, high density ponderosa pine forests sustaining losses from mountain pine beetle (Schmid and others 2007, see Fettig and others 2007 for a general discussion).

Management actions undertaken to restore ponderosa pine stands and reduce fuels move stand density characteristics nearer the threshold level identified by Negron and Popp (2004) and should prove beneficial for limiting tree losses to bark beetles (Schmid and others 2007). In this regard, the primary objectives of the Front Range Fuels Treatment Roundtable are in reasonable agreement with current scientific recommendations. However, foresters and land managers should re-examine their stand prescriptions for restoring Front Range ponderosa pine stands to consider the potential effects of a mountain pine beetle epidemic, evaluate stand density and diameter outcomes such that they account for small diameter classes, and address near-term regeneration opportunities.

The focus of restoration treatments near communities and vulnerable watersheds remains an important priority, given the current likelihood of a mountain pine beetle epidemic in ponderosa pine forests along the northern Front Range. Large scale restoration projects, like the South Platte Watershed Restoration Project on federal and private lands in Douglas and Jefferson Counties and smaller projects, like the Bald Mountain restoration project on Parks and Open Space land in Boulder County, will be of special interest assuming that the mountain pine beetle epidemic spreads into these project areas. One major limitation of silvicultural manipulation experiments to reduce mountain pine beetle impacts has to do with the small size of experimental treatment units. The larger, landscape-scale restoration treatments in the South Platte Watershed Project provide a long-sought-after silvicultural manipulation that has eluded bark beetle researchers for decades.

Foresters taking actions to restore Front Range ponderosa pine forests and reduce fuels should access annual Forest Health aerial survey data sets collected jointly by the USDA Forest Service and the Colorado State Forest Service. These data sets are available on-line in ArcGIS format [<http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/download/>]. Overlaying mountain pine beetle mortality areas in ponderosa pine or mortality in adjacent lodgepole pine with high

priority treatment units would provide specialists with an additional tool to prioritize treatment areas where mountain pine beetle is active. However, the aerial survey data should not be used without follow-up ground cruises because conditions on the ground may prove substantially different from those recorded by aerial surveyors. Aerial survey data is always one year in arrears, because aerial surveyors can only reliably identify trees whose needles have faded to a red-brown color after a successful bark beetle attack the previous year. More recently infested trees, whose foliage is still green, cannot be identified by the aerial surveyors.

Removing, masticating, or treating (through bark removal or solar treatment) mountain pine beetle-infested trees in ponderosa pine stands during the implementation of restoration/fuels treatments is a good idea, especially now. This is particularly true in areas where adjacent lodgepole pine stands are experiencing losses now or are likely to experience losses to the mountain pine beetle in the near future; such treatments may limit losses of trees in treated ponderosa pine stands and make these stands less attractive to dispersing mountain pine beetles.

## **C.2 Conclusion – Do restoration/fuels prescriptions for ponderosa pine stands fully consider or account for the potential for a mountain pine beetle epidemic and should these strategies and priorities be re-evaluated due to these changing conditions?**

Current policies and objectives of the Front Range Fuels Roundtable appear appropriate for the changing conditions associated with the building mountain pine beetle epidemic on the Front Range. This epidemic has caused severe losses of pines in virtually all areas impacted; lodgepole, limber, and Rocky Mountain bristlecone pine losses are increasing rapidly and are predicted to be severe across all high-elevation forests along the northern Front Range. At present, losses in ponderosa pine are elevated due to local beetle populations. These losses will increase significantly as the mountain pine beetle spreads out of lodgepole pine forests and into ponderosa pine forests over the next five to ten years. Absent a severe cold temperature event that kills brood larvae within beetle-infested trees, there is little reason to anticipate a major departure from this pattern as the mountain pine beetle spreads into ponderosa pine.

Nevertheless, restoration/fuels treatment prescriptions should explicitly examine the risk of losing much of the overstory in these stands, particularly where treatments are likely to result in single-storied stands of large diameter trees. Density/basal area reductions associated with restoration/fuels treatment prescriptions should emphasize adopting levels at the lower end of the acceptable range. Lower residual treatment densities or basal areas may prove less vulnerable to losses from mountain pine beetle. Where possible, prescriptions should consider providing for patches of healthy, small diameter (< 7 inches) trees as part of a mosaic to hedge against severe losses in the overstory. Also, prescriptions should consider opportunities for retaining some healthy regeneration and provide for opportunities to obtain additional new regeneration over the next ten to fifteen years.

Once prescriptions and plans are reviewed, restoration/fuels treatments should be implemented with all deliberate speed. Treatment procedures should provide flexibility for identifying and removing/masticating/treating mountain pine beetle-infested trees through the implementation period to account for an unexpected influx of beetles into stands during treatment. For high-

value settings, resource managers should consider scheduling the timing of treatments for the fall, winter, and early spring months to minimize the mildly attractive host tree odors associated with these treatments.

## Appendix – Background Discussion Topics

### 1. Population phases of the mountain pine beetle

Safranyik and Carroll (2006) recognize four phases in the population cycle of the mountain pine beetle in lodgepole pine forests: endemic, incipient-epidemic, epidemic (i.e. outbreak) and post-epidemic (i.e. declining) populations. These authors present and discuss a number of characteristics of these four phases:

#### Endemic Populations:

- Beetles are restricted to low-quality host trees with little or no defensive capacity. There are insufficient numbers of beetles to overcome even a single large-diameter tree within a stand.
- The diameter of attacked trees is less than the stand average (although occasional large-diameter trees are attacked following sudden near-lethal stress such as lightning or windthrow).
- Attack densities are very low; often only two or three galleries per tree.
- Attacks are preceded in the current or previous season(s) by attacks from secondary, bole-infesting bark beetle species (e.g. the pine engraver beetle).
- Interspecific competition appears to be an important mortality factor during this population phase of the mountain pine beetle and may be largely responsible for the regulation of population fluctuations.
- Currently attacked trees are not located near brood trees.
- Yearly tree mortality is less than yearly volume growth within a stand.
- Endemic populations are in a dynamic balance with their environment so that, over a number of generations, there is no significant change in population size.

#### Incipient-Epidemic Populations:

- Most of the infested trees have larger diameters.
- Clumps of infested trees are scattered and confined to parts of individual stands
- The groups of infested trees vary considerably in size and number from year to year but tend to grow over time.

#### Epidemic Populations:

- Beetle populations are resilient to proportionally large losses in their numbers. As population size increases (and the infested area expands), the population becomes less and less likely to collapse from adverse factors such as unseasonably cold temperatures.

- Generation mortality is usually in the range of 80% to 95%, corresponding to potential rates of population increase of approximately two- to eightfold each year. The usual annual rate of increase, however, is two- to fourfold over the entire area of the epidemic.
- Infestations are widespread and exist at the landscape scale.
- There are usually large annual increases in both infested areas and numbers of infested trees.

### **Post-Epidemic Populations:**

- The size distribution of trees attacked by post-epidemic populations may be different from that attacked during epidemics.
- Many trees may only be partially attacked due to the smaller size of the beetle population and the rate of accumulation of attacks may be reduced. Brood survival will be reduced due to the expression of host resistance resulting from an insufficient mass attack.
- Interspecific competition for food and space, as well as predation and parasitism, may become important factors affecting populations. Where collapse of the epidemic is primarily due to local depletion of suitable hosts, subsequent generations of beetles are forced to breed in trees of reduced nutritional quality or increased resistance and will likely suffer mortalities of similar magnitude as those occurring in endemic populations.
- Large populations of secondary bark beetles, such as the pine engraver and twig beetles (Evenden and Gibson 1940), which built up in portions of the bole not utilized by the mountain pine beetle during the epidemic, may kill large numbers of pine trees, mainly in the smaller diameter classes.

## **2. Defense mechanisms in pines and variation in pine species defensive chemistry**

When mountain pine beetle populations are at low levels, or endemic levels, healthy host tree defenses pose a formidable challenge for beetles seeking trees in which to breed and reproduce. Under these conditions, beetles infest the very few trees across the landscape that have been damaged by physical forces (wind, lightning, etc., see Gandhi and others 2007) or are impacted by disease, defoliation, or drought, situations where the defense capabilities of the tree may be compromised or limited.

As mountain pine beetles increase to epidemic levels, the number of dying or weakened trees in the forest is rapidly depleted and the beetles must contend with and overcome the more capable defenses of healthy living trees. The defenses of pines are grouped into two systems: (1) constitutive, that is a system of preformed resin canals embedded in the living tissues of the tree, and (2) inducible, that is the chemical defense system of living tissues of the tree that responds following injury (Franceschi and others 2005). Pines have both constitutive and inducible oleoresin defense responses to colonization by bark beetles, but the constitutive system appears to be more important (Nebeker and others 1993).

Pine trees have a constitutive or preformed defense system of resin ducts filled with oleoresin. Oleoresin is produced by the tissues of the tree and secreted into the resin ducts where it is maintained under pressure by the living cells surrounding the resin ducts. The constitutive

defense system delivers a variety of chemicals (monoterpenes, diterpene acids, and stilbene phenolics) to the site of a wound when resin canals are severed, such as during a bark beetle attack (see Franceschi and others 2005). The capacity of the tree to respond to injury through the production and secretion of oleoresin is influenced by the moisture status of the tree (the ability of the tree to maintain high oleoresin exudation pressure requires conditions of good soil moisture availability). Tree defensive chemicals also may be limited due to competing demands on carbohydrate food resources during periods of rapid tree growth.

An injury, such as that caused by an attacking beetle, may activate the second type of defense in pine trees – the inducible defense system. In response to injury, the inducible defense system can inundate injured tissues and adjacent healthy tissues with defensive chemicals that may have insecticidal, repellent, or fungistatic properties (Raffa and Berryman 1982a,b, Raffa and others 2005). These defensive chemicals change tissue conditions and make the environment surrounding the beetle gallery less suitable for continued development of the beetles, their offspring, or the important species of fungi carried by the beetle that are critical for the nutrition of the developing brood (see Raffa and Berryman 1982a, b, 1983a,b, and Raffa and others 1993 for further discussion).

### **3. Host selection and colonization process of eruptive bark beetle species**

Wood (1982) provides a general discussion of the host selection and colonization process by bark beetles, particularly those species like the mountain pine beetle, which exhibit eruptive population dynamics where healthy trees are attacked and killed. The four steps identified by Wood are: (1) dispersal; (2) host selection; (3) concentration; and (4) establishment. A more comprehensive model of bark beetle host selection behavior [item (2), above] has been presented by Graves and others (2008) to account for alternative hypotheses of host selection: (a) undirected flight followed by landing in response to visual cues, leading to feeding and associated host evaluation and acceptance or rejection; or (b) directed flight guided by long-range olfaction followed by landing, feeding and host evaluation and acceptance.

Newly emerged beetles leave brood trees and disperse. Flight may be required before beetles respond to pheromones. In the most aggressive bark beetles, such as the mountain pine beetle, adults appear to land randomly on trees to evaluate whether to initiate attack.

Host selection by flying, dispersing mountain pine beetles begins with visual cues associated with vertical silhouettes of the trees. Once on the bark surface, beetles appear to evaluate the host using olfactory and chemical cues through contact or by penetrating the bark and tasting the phloem. Beetles may resume flight if the tree is not a host tree.

Concentration of mountain pine beetles via mass attack is triggered by the release of aggregation pheromones when pioneer beetles attack suitable host trees. Aggregation pheromones are released into the air around trees, and along with host tree monoterpenes (pheromone co-attractants), provide a potent chemical attractant for dispersing male and female mountain pine beetles. Responding beetles orient upwind and fly towards the source of the pheromones. Rapid response by large numbers of beetles overwhelms the tree's defensive systems and the resulting colonized phloem becomes a favorable habitat for establishment.

Establishment occurs as mountain pine beetles occupy the habitat provided by the tree as it succumbs to mass attack. As beetles occupy the habitat, later stage behavioral chemicals such as anti-aggregation pheromones or fungal-produced compounds result in the cessation of further beetle attacks. Trees adjacent to a mass attacked tree may come under mass attack due to a strong response by the dispersing beetle population (“switching mechanism” of Geiszler and Gara 1978).

#### **4. Mountain pine beetle population effects and the importance of scale**

The significance of a spread into a different species of host tree and cover type should be viewed across the scale of the ecological effects associated with the mountain pine beetle. Ecological processes operate at many different levels, from the level of an individual bark beetle gallery (typically multiple centimeters in size), to tree-level (square meters in size), to stand-level (hectares in size), and potentially to the level of entire landscapes (kilometers in size) (Raffa and others 2008). With regard to the discussion of scale presented by Raffa and others, our current mountain pine beetle epidemic has passed through the critical thresholds of gallery establishment, individual tree, and forest stand levels, and has reached the level where landscape processes are affected.

At the stand level within the lodgepole pine/ponderosa pine ecotone, mountain pine beetles will experience both host tree species side-by-side. This challenge will test the mountain pine beetle’s ability to transition to a new host species with a considerably different mix of defensive chemicals. Bridging the host tree species transition will be facilitated by the size of the attacking beetle population available to infest these mixed stands. Because the mountain pine beetle population has erupted to the level of landscape effects, the lower level thresholds associated with tree defensive chemistry versus individual attack success (gallery scale), surmounting tree resistance with an attack density adequate to ensure survival (tree scale), and proliferation of mass attacked trees (stand scale), are not thought to pose a significant limit to expansion and will likely be readily overcome as the beetle spreads into the lodgepole pine/ponderosa pine ecotone.

Landscape scale losses of mixed species pine forests on the eastern side of the Continental Divide provide support for the prediction in the previous paragraph. The mountain pine beetle has attacked and killed limber and Rocky Mountain bristlecone pines in the course of the beetle’s expansion through high-elevation lodgepole pine forests along the northern Front Range. Relative losses for each of these species have never been determined, so there are no data to suggest that the mountain pine beetle is taking one species at a rate greater than it is represented in these stands. Mountain pine beetle spread into the lodgepole pine/ponderosa pine ecotone is progressing in a similar fashion where the beetle has been present.

The positive feedback mechanisms that reinforce and sustain the high population levels characteristic of this epidemic will be key factors in determining whether the mountain pine beetle impacts the ponderosa pine cover type at the landscape scale. It would be necessary to break these positive feedback mechanisms to alter the probable course of the epidemic. For this to occur, fundamental aspects of survival during dispersal of adults may be the factor of most importance (see figure 3 in Raffa and others 2008).

## Literature Cited

- Baker, B.H.; Amman, G.D.; Trostle, G.C. 1971. Does the mountain pine beetle change hosts in mixed lodgepole and whitebark pine stands. Research Note INT-151. Ogden, UT. U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 7p.
- Barron, A.B. 2001. The life and death of Hopkins' Host-Selection Principle. *J. Insect Behavior* 14: 725-737.
- Bartos, D.L.; Amman, G. D. 1989. Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestations. Res. Pap. INT-400, USDA Forest Service, Intermountain Research Station, Ogden, U.T. 10p.
- Cain, R.J.; Howell, B.E. 2005. Biological evaluation of mountain pine beetle activity on the Black Trout Analysis Area of South Park Ranger District, Pike-San Isabel National Forests and Comanche and Cimarron National Grasslands, 2005. Biological Evaluation R2-05-04. USDA Forest Service, Region 2, Forest Health Management. 36p.
- Dean, D.K. 2007. Host utilization by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), in mixed stands of limber pine, *Pinus flexilis* James, and lodgepole pine, *Pinus contorta latifolia* Engelman. Masters Thesis, University of Wyoming. 55 p.
- Dennis, F.C.; Sturtevant, B. 2008. Forest restoration guidelines in ponderosa pine on the Front Range of Colorado. Colorado State University and Colorado Forest Restoration Institute, Fort Collins, CO. 8 p. [http://www.cfri.colostate.edu/docs/guidelines\\_web.pdf](http://www.cfri.colostate.edu/docs/guidelines_web.pdf)
- Evenden, J.C.; Gibson, A.L. 1940. A destructive infestation in lodgepole pine stands by the mountain pine beetle. *Journal of Forestry* 38: 271-275.
- Fettig, C.J.; Klepzig, K.D.; Billings, R.F.; Munson, A.S.; Nebeker, T.E.; Negron, J.F.; Nowak, J.T. 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. *Forest Ecology and Management* 238: 24-53.
- Franceschi, V.R.; Kronkene, P.; Christiansen, E.; Krekling, T. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* 167: 353-376.
- Gandhi, K.J.K.; Gilmore, D.W.; Katovich, S.A.; Mattson, W.J.; Spence, J.R.; Seybold, S.J. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. *Environmental Reviews* 15: 113-152.
- Geiszler, D.R.; Gara, R.I. 1978. Mountain pine beetle attack dynamics in lodgepole pine. P. 182-187 in Berryman, A.A., G.D. Amman, and R.W. Stark (eds.) *Theory and practice of*

- mountain pine beetle management in lodgepole pine forests. Washington State University, Pullman, WA. 224 p.
- Graves, A.D.; Holsten, E.H.; Ascerno, M.E.; Zogas, K.; Hard, J.S.; Huber, D.P.W.; Blanchette, R.; Seybold, S.J. 2008. Protection of spruce from colonization by the bark beetle, Ips perturbatus, in Alaska. *Forest Ecology and Management* 256: 1825-1839.
- Hopkins, A.D. 1916. Economic investigations of the scolytid bark and timber beetles of North America. U.S. Department of Agriculture Program of Work for 1917. p. 353.
- Hopkins, A.D. 1917. A discussion of C. G. Hewitt's paper on "Insect Behavior." *J. Econ. Entomol.* 10: 92-93.
- Huber, D.P.W.; Aukema, B.H.; Hodgkinson, R.S.; Lindgren, S. 2009. Successful colonization, reproduction, and new generation emergence in live interior hybrid spruce Picea engelmannii x glauca by mountain pine beetle Dendroctonus ponderosae. *Agricultural and Forest Entomology* 11: 83-89.
- Jackson, P.L.; Straussfogel, D.; Lindgren, B.S.; Mitchell, S.; Murphy, B. 2008. Radar observation and aerial capture of mountain pine beetle, Dendroctonus ponderosae Hopk. (Coleoptera: Scolytidae), above the forest canopy. Mountain Pine Beetle Working Paper 2007-02. Canadian Forest Service, Pacific Forestry Centre. 32 p.  
[http://bookstore.cfs.nrcan.gc.ca/catalog\\_e.php?Catalog=28839](http://bookstore.cfs.nrcan.gc.ca/catalog_e.php?Catalog=28839)
- Lee, J.C.; Flint, M.L.; Seybold, S.J. 2008. Suitability of pines and other conifers as hosts for the invasive Mediterranean pine engraver (Coleoptera: Scolytidae) in North America. *J. Econ. Entomol.* 101: 829-837.
- Lessard, G.; Hildebrand, D.; Haneman, D.E. 1987. Forest pest conditions in the Rocky Mountain Region 1986. Unpublished office report. USDA Forest Service, Rocky Mountain Region. Timber, Forest Pest and Cooperative Forest Management, Lakewood, CO. 11p.
- McCambridge, W. F.; Hawksworth, F. G.; Edminster, C. B.; Laut, J. G. 1982. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. Research Paper RM-235, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 7p.  
[http://www.fs.fed.us/rm/pubs\\_rm/rm\\_rp235.html](http://www.fs.fed.us/rm/pubs_rm/rm_rp235.html)
- Mitchell, R.G.; Preisler, H.K. 1991. Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. *Forest Science* 37: 1390-1408.
- Nebeker, T.E.; Hodges, J.D.; Blanche, C.A. 1993. Host response to bark beetle and pathogen colonization. In: Schowalter, T.D., Filip, G.M. (eds) *Beetle-pathogen interactions in conifer forests*. Academic Press, New York. Pp. 157-173.
- Negron, J. F.; Popp, J. B. 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. *Forest Ecology and Management* 191: 17-27.

- Olsen, W. K.; Schmid, J. M.; Mata, S. A. 1996. Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. *Forest Science* 42: 310-327.
- Preisler, H.K.; Mitchell, R.G. 1993. Colonization patterns of the mountain pine beetle in thinned and unthinned lodgepole pine stands. *Forest Science* 39: 528-545.
- Pureswaran, D.S.; Gries, R.; Borden, J.H. 2004. Quantitative variation in monoterpenes in four species of conifers. *Biochemical Systematics and Ecology* 32: 1109-1136.
- Raffa, K.F.; Berryman, A.A. 1982a. Physiological differences between lodgepole pines resistant and susceptible to the mountain pine beetle and associated microorganisms. *Environ. Entomol.* 11: 486-492.
- Raffa, K.F.; Berryman, A.A. 1982b. Gustatory cues in the orientation of Dendroctonus ponderosae. *Can. Entomol.* 114: 97-103.
- Raffa, K.F.; Berryman, A.A. 1983a. The role of host plant resistance in the colonization behavior and ecology of bark beetle. *Ecol. Monogr.* 53: 27-49.
- Raffa, K.F.; Berryman, A.A. 1983b. Physiological aspects of lodgepole pine wound responses to a fungal symbiont of the mountain pine beetle, Dendroctonus ponderosae. *Can. Entomol.* 115: 723-734.
- Raffa, K.F.; Phillips, T.W.; Salom, S.M. 1993. Strategies and mechanisms of host colonization by bark beetles. In: Schowalter, T.D., Filip, G.M. (eds). *Beetle-pathogen interactions in conifer forests*. Academic Press, New York. Pp. 103-128.
- Raffa, K.F.; Aukema, B.H.; Erbilgin, N.; Klepzig, K.D; Wallin, K.F. 2005. Interactions among conifer terpenoids and bark beetles across multiple levels of scale: An attempt to understand links between population patterns and physiological processes. *Recent Advances in Phytochemistry* 39: 80-118.
- Raffa, K.F.; Aukema, B.H.; Bentz, B.J.; Carroll, A.L.; Hicke, J.A.; Turner, M.G.; Romme, W.H. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience* 58: 501-517.
- Safranyik, L.; Carroll, A.L.. 2006. The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik, L. and Wilson, W.R. (eds). *The mountain pine beetle: A synthesis of biology, management, and impacts on lodgepole pine*. Natural Resources Canada, Canadian Forest Service. Pp 3-66.  
[http://bookstore.cfs.nrcan.gc.ca/Catalog\\_e.php?catalog=26116](http://bookstore.cfs.nrcan.gc.ca/Catalog_e.php?catalog=26116)
- Schmid, J.M.; Mata, S.A.; Schmidt, R.A. 1991. Bark temperature patterns in ponderosa pine stands and their possible effects on mountain pine beetle behavior. *Can. J. For. Res.* 21: 1439-1446.

- Schmid, J.M.; Matta, S.A.; Allen, D.C. 1992. Potential influences of horizontal and vertical air movement in ponderosa pine stands on mountain pine beetle dispersal. Research Note RM-516, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 4p.
- Schmid, J.M.; Matta, S.A.; Kessler, R.R.; Popp, J.B. 2007. The influence of partial cutting on mountain pine beetle-caused tree mortality in Black Hills ponderosa pine stands. Research Paper RMRS-RP-68, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 19p.
- Seybold, S.J.; Huber, D.P.W.; Lee, J.C.; Graves, A.D.; Bohlmann, J. 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. *Phytochem Rev* 5: 143-178.
- Smith, R.H. 2000. Xylem monoterpenes of pines: Distribution, variation, genetics, function. Gen. Tech. Rept. PSW-GTR-177. USDA Forest Service, Pacific Southwest Research Station, Albany, CA. 454p.
- Tishmack, J.; Mata, S. A.; Schmid, J. M.; Porth, L. 2005. Mountain pine beetle emergence from lodgepole pine at different elevations near Fraser, CO, Res. Note RMRS-RN-27. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 5 p.
- United States Geological Survey. 2000. Colorado gap analysis project: A geographic approach to planning for biological diversity. Final Report. 118 p.
- Wallin, K.F.; Raffa, K.F. 2004. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecological Monographs* 74: 101-116.
- Witcosky, J.J. 2008. Status of mountain pine beetle populations in lodgepole, limber, Rocky Mountain bristlecone, and ponderosa pine stands in the northern Front Range of Colorado, LSC-08-06. Service Trip Report LSC-08-06. USDA Forest Service, Region 2, Forest Health Management. 26p.
- Wood, D.L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Ann. Rev. Entomol.* 27: 411-44.
- Wood, D.L. 1963. Studies on host selection by Ips confusus. University of California Publications in Entomology 27: 241-282.
- Zavarin, E.; Cool, L.G.; Snajberk, K. 1993. Geographic variability of Pinus flexilis xylem monoterpenes. *Biochemical Systematics and Ecology* 21: 381-387.

## **Acknowledgements**

A previous version of this document was reviewed by: John Schmid, Steve Seybold, Jose Negrón, Dave Leatherman, Ingrid, Aguayo, Wayne Shepperd, Ken Gibson, Andris Eglitis, Susan Gray, Sheryl Costello, Bob Cain, Jenny Briggs, and Scott Golden.

## List of Tables

- Table 1.** Cumulative (1996 through 2007) acres of lodgepole pine containing one or more trees killed by the mountain pine beetle (MPB) in Boulder, Clear Creek, Gilpin and Larimer Counties, CO, in the lodgepole pine forest cover type and in other forest cover types.
- Table 2.** Cumulative (1996 through 2007) privately owned and National Forest acres of lodgepole pine containing one or more trees killed by the mountain pine beetle (MPB) in Boulder, Clear Creek, Gilpin, and Larimer Counties, CO, in the lodgepole pine forest cover type and in other forest cover types.
- Table 3.** Cumulative (1996 through 2007) acres of ponderosa pine containing one or more trees killed by the mountain pine beetle (MPB) in Boulder, Clear Creek, Gilpin and Larimer Counties, CO, in the ponderosa pine forest cover type and in other forest cover types.
- Table 4.** Cumulative (1996 through 2007) privately owned and National Forest acres of ponderosa pine containing one or more trees killed by the mountain pine beetle (MPB) in Boulder, Clear Creek, Gilpin, and Larimer Counties, CO, in the ponderosa pine forest cover type and in other forest cover types.
- Table 5.** Terpene composition of limber, lodgepole, ponderosa, and Rocky Mountain bristlecone pines and Engelmann spruce.

**Table 1.** Cumulative (1996 through 2007) acres of lodgepole pine containing one or more trees killed by the mountain pine beetle (MPB) in Boulder, Clear Creek, Gilpin and Larimer Counties, CO, in the lodgepole pine forest cover type<sup>1</sup> and in other forest cover types<sup>2</sup>.

County, State	All Forest Ownerships				
	Acreage in Lodgepole Pine Cover Type <sup>1</sup>	Acreage in Lodgepole Pine Cover Type Impacted by MPB	Percent of Lodgepole Pine Cover Type Impacted by MPB	Acreage in Other Forest Cover Types <sup>2</sup> Impacted by MPB	Acreage of Lodgepole Pine Impacted by MPB in all Forest Cover Types
Boulder, CO	44,100	9,000	20%	18,200	27,200
Clear Creek, CO	69,300	8,700	13%	25,500	34,200
Gilpin, CO	48,600	10,600	22%	6,600	17,200
Larimer, CO	365,000	78,400	21%	45,600	124,000

<sup>1</sup> Lodgepole pine forest cover type characterized in the Colorado Gap Analysis Project, United States Geological Survey, 2000.

<sup>2</sup> Other forest cover types where lodgepole pine makes up a variable but small portion of the overstory trees. These forest cover types may be classified as aspen, Rocky Mountain bristlecone and limber pines, Douglas-fir, ponderosa pine, or spruce-fir.

**Table 2.** Cumulative (1996 through 2007) privately owned and National Forest acres of lodgepole pine containing one or more trees killed by the mountain pine beetle (MPB) in Boulder, Clear Creek, Gilpin, and Larimer Counties, CO, in the lodgepole pine forest cover type<sup>1</sup> and in other forest cover types<sup>2</sup>.

County, State	Private Forest Ownership				National Forest Ownership			
	Acreage in Lodgepole Pine Cover Type <sup>1</sup>	Acreage in Lodgepole Pine Cover Type Impacted by MPB	Percent of Lodgepole Pine Cover Type Impacted by MPB	Acreage in Other Forest Cover Types <sup>2</sup> Impacted by MPB	Acreage in Lodgepole Pine Cover Type <sup>1</sup>	Acreage in Lodgepole Pine Cover Type Impacted by MPB	Percent of Lodgepole Pine Cover Type Impacted by MPB	Acreage in Other Forest Cover Types <sup>2</sup> Impacted by MPB
Boulder, CO	17,511	1,900	11%	4,700	23,508	5,700	24%	15,700
Clear Creek, CO	27,311	1,500	5%	6,500	36,222	6,600	18%	23,900
Gilpin, CO	26,763	4,800	18%	8,300	18,233	5,700	31%	8,800
Larimer, CO	39,132	2,500	6%	7,500	310,384	73,500	24%	93,500

<sup>1</sup> Lodgepole pine forest cover type characterized in the Colorado Gap Analysis Project, United States Geological Survey, 2000.

<sup>2</sup> Other forest cover types where lodgepole pine makes up a variable but small portion of the overstory trees. These forest cover types may be classified as aspen, Rocky Mountain bristlecone and limber pines, Douglas-fir, ponderosa pine, or spruce-fir.

**Table 3.** Cumulative (1996 through 2007) acres of ponderosa pine containing one or more trees killed by the mountain pine beetle (MPB) in Boulder, Clear Creek, Gilpin and Larimer Counties, CO, in the ponderosa pine forest cover type<sup>1</sup> and in other forest cover types<sup>2</sup>.

County, State	All Forest Ownerships				
	Acreage in Ponderosa Pine Cover Type <sup>1</sup>	Acreage in Ponderosa Pine Cover Type Impacted by MPB	Percent of Ponderosa Pine Cover Type Impacted by MPB	Acreage in Other Forest Cover Types <sup>2</sup> Impacted by MPB	Acreage of Ponderosa Pine Impacted by MPB in all Forest Cover Types
Boulder, CO	146,956	15,600	11%	3,300	18,900
Clear Creek, CO	23,464	770	3%	3,200	3,970
Gilpin, CO	7,257	310	4%	2,000	2,310
Larimer, CO	384,752	28,600	7%	20,200	48,800

<sup>1</sup> Ponderosa pine forest cover type characterized in the Colorado Gap Analysis Project, United States Geological Survey, 2000.

<sup>2</sup> Other forest cover types where ponderosa pine makes up a variable but small portion of the overstory trees. These forest cover types may be classified as aspen, Rocky Mountain bristlecone and limber pines, Douglas-fir, lodgepole pine, or spruce-fir.

**Table 4.** Cumulative (1996 through 2007) privately owned and National Forest acres of ponderosa pine containing one or more trees killed by the mountain pine beetle (MPB) in Boulder, Clear Creek, Gilpin, and Larimer Counties, CO, in the ponderosa pine forest cover type<sup>1</sup> and in other forest cover types<sup>2</sup>.

County, State	Private Forest Ownership				National Forest Ownership			
	Acreage in Ponderosa Pine Cover Type <sup>1</sup>	Acreage in Ponderosa Pine Cover Type Impacted by MPB	Percent of Ponderosa Pine Cover Type Impacted by MPB	Acreage in Other Forest Cover Types <sup>2</sup> Impacted by MPB	Acreage in Ponderosa Pine Cover Type <sup>1</sup>	Acreage in Ponderosa Pine Cover Type Impacted by MPB	Percent of Ponderosa Pine Cover Type Impacted by MPB	Acreage in Other Forest Cover Types <sup>2</sup> Impacted by MPB
Boulder, CO	80,434	9,000	11%	1,500	59,781	5,600	9%	1,800
Clear Creek, CO	17,345	490	3%	1,610	2,876	50	2%	1,050
Gilpin, CO	3,733	80	2%	1,620	751	1	1%	69
Larimer, CO	191,866	11,600	6%	2,000	159,673	14,400	9%	16,600

<sup>1</sup> Ponderosa pine forest cover type characterized in the Colorado Gap Analysis Project, United States Geological Survey, 2000.

<sup>2</sup> Other forest cover types where ponderosa pine makes up a variable but small portion of the overstory trees. These forest cover types may be classified as aspen, Rocky Mountain bristlecone and limber pines, Douglas-fir, lodgepole pine, or spruce-fir.

**Table 5.** Terpene components of limber, lodgepole, ponderosa, and Rocky Mountain bristlecone pines and Engelmann spruce.

Source	Tree Species	Location	Terepene Components (Percent)						
			$\alpha$ -pinene	$\beta$ -pinene	camphene	3-carene	$\rho$ -cymene	limonene	myrcene
Smith, 2000	Rocky Mountain Bristlecone Pine	Colorado, New Mexico	6.0	6.0	0.1	73.1		4.5	2.5
Zvarin, 1993	Limber Pine	Boulder, CO	16.8	4.1	0.2		0.8	25.6	5.5
Zvarin, 1993	Limber Pine	Chaffee, CO	57.2	10.8	0.8	1.7	1.2	16.5	3.1
Zvarin, 1993	Limber Pine	Weld, CO	28.6	6.2	0.3	9.0	1.0	41.1	3.7
Zvarin, 1993	Limber Pine	Mean (24 locations)	52.6	10.8	0.8	9.5	0.6	14.7	4.4
Smith, 2000	Lodgepole Pine (var latifolia)	Front Range, CO	5.6	8.7		9.7		1.6	1.9
Smith, 2000	Ponderosa Pine (var scopulorum)	Colorado, Wyoming	6.0	27.5		46.5		3.0	13.0
Pureswaran, 2004	Engelmann Spruce	British Columbia	52.8	23.2		8.8			

**Table 5 (cont.).** Terpene components of limber, lodgepole, ponderosa, and Rocky Mountain bristlecone pines and Engelmann spruce.

Source	Tree Species	Location	Terpene Components (Percent)						
			$\beta$ -phellandrene	sabinene	$\gamma$ -terpinene	terpinolene	tricyclene	$\eta$ -undecane	others
Smith, 2000	Rocky Mountain Bristlecone Pine	Colorado, New Mexico		0.0	0.3	3.5			
Zvarin, 1993	Limber Pine	Boulder, CO		1.5	0.5	2.5	0.0	1.0	
Zvarin, 1993	Limber Pine	Chaffee, CO		0.5	1.0	2.3	1.9	0.2	
Zvarin, 1993	Limber Pine	Weld, CO		1.9	1.5	3.6	0.0	1.0	
Zvarin, 1993	Limber Pine	Mean (24 locations)		0.7	0.5	1.3	0.1	4.1	
Smith, 2000	Lodgepole Pine (var latifolia)	Front Range, CO		2.5		0.3			
Smith, 2000	Ponderosa Pine (var scopulorum)	Colorado, Wyoming							
Pureswaran, 2004	Engelmann Spruce	British Columbia	5.7						9.4