

THESIS

EFFECTS OF MOUNTAIN PINE BEETLE ON FOREST STRUCTURE AND FUEL  
LOAD 25-30 YEARS AFTER AN OUTBREAK IN WESTERN COLORADO

Submitted by

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## ABSTRACT

### EFFECTS OF MOUNTAIN PINE BEETLE ON FOREST STRUCTURE AND FUEL LOAD 25-30 YEARS AFTER AN OUTBREAK IN WESTERN COLORADO

Mortality of lodgepole pine (*Pinus contorta* Dougl. Ex. Loud.) caused by mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) has caused concern about long-term forest structure and wildfire hazard changes. In 2010, I identified and sampled areas affected by a 1980s MPB outbreak to quantify forest changes in the 25-30 years following mortality. Stands in Eagle County, Colorado with >30% 1980s lodgepole pine mortality were identified using USDA Forest Service aerial survey maps and inventory data. Stands fell into two forest type groups: lodgepole pine and mixed conifer. I sampled 20 stands to measure forest species and size structure and down woody fuel accumulations. I compared 1980s inventory data to 2010 data to find differences between forest type groups in their post-outbreak changes.

Lodgepole pine stands recovered to pre-outbreak overstory total basal area, density, and species composition by 2010, while in mixed conifer stands basal area and density were significantly less in 2010 than before the outbreak. In mixed conifer stands, lodgepole pine overstory basal area was reduced from 66% of total in the 1980s to 51% in 2010. Understory tree density increased roughly six-fold in both forest types between

the 1980s and 2010. The overall increase in understory density was due to a ten-fold increase in seedling/sapling (trees 0.6 m tall to 3.8 cm dbh) numbers. In lodgepole pine stands, the most abundant species in the 1980s understory was subalpine fir, followed by lodgepole pine. By 2010, lodgepole pine and subalpine fir were the majority of larger understory trees; aspen and subalpine fir were most abundant among smaller understory trees. In mixed conifer stands, subalpine fir and Engelmann spruce consistently dominated all understory size classes in the 1980s and 2010. Total down woody fuel load averaged  $71 \text{ Mg ha}^{-1}$  and did not differ between forest type groups.

Overall, my results suggest that long-term forest recovery trajectories are dependent on pre-outbreak species composition, though understory densities are likely to increase regardless of non-host species abundances. These shifts in species and size composition by 25-30 years after outbreak likely have substantial impacts on forest health, potential fire behavior and ecosystem processes. We speculate that forest recovery following the current MPB outbreak will be similar to observed changes following the 1980s outbreak in these areas.

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## INTRODUCTION

The current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) outbreak in western North America has affected lodgepole pine (*Pinus contorta* Dougl. ex Loud.) throughout much of its range. In Colorado and southern Wyoming, over 1.6 million hectares have been infested by the native MPB (USDA Forest Service and Colorado State Forest Service 2011). Mortality is highly visible and there is serious concern over the outbreak's impacts on future forest conditions and wildfire hazard.

However, there is no consensus on the long-term impacts of MPB on lodgepole pine-dominated forests. This is in part because few studies have measured the long-term consequences of MPB on forest species and size structure or fire hazard. Several studies have quantified short term impacts of MPB (e.g. Amman and Baker 1972, Muir 1993, Sibold et al. 2007, Vyse et al. 2009, Axelson et al. 2010, Collins et al. 2010), and a few have quantified short-term effects and used these to model long-term implications for stand structure and fuel loads (Klutsch et al. 2009, Diskin 2010, Collins et al. 2011). Overall, research suggests post-MPB establishment is likely to be inconsistent and that advance regeneration may be more important than post-disturbance establishment in restocking MPB affected forests (Astrup et al. 2008). It is unclear if forests will continue to be dominated by lodgepole pine or become increasingly dominated by non-host species in the decades following outbreak (e.g., Sibold et al. 2007, Klutsch et al. 2009,



Collins et al. 2011, Diskin 2010, Diskin et al. 2011). Conventional wisdom has held that risk of crown fire necessarily rises following MPB due to increases in dead fuels (e.g., Heinrichs 1983, Lotan et al. 1985, Schmid and Amman 1992). Recent research grounded in fire behavior models has indicated that crown fire hazard likely goes down immediately following MPB mortality due to decreased canopy density of fine fuels as needles fall, and may increase as regeneration grows (e.g., Page and Jenkins 2007b, Jenkins et al. 2008, Simard et al. 2011). Increasing our understanding of the long term implications of MPB on forests is essential to developing and evaluating management proposals.

Management action with the goal of mitigating fire hazard or promoting forest recovery must be based on understanding of the long-term MPB impacts to be effective and avoid unintended ecological and social consequences. We visited areas in western Colorado affected by MPB during the 1980s and assessed vegetation recovery and fuel load accumulated in 20 stands for 25-30 years following outbreak. This allows us assess the long-term impact of MPB on forest composition and fuel complex which can be used to guide management reactions to the current outbreak.

### **Impact of mountain pine beetle on forest species and age structure**

The forest composition following MPB epidemic is a function of the initial forest composition (species and age/size) and beetle-induced mortality. Mountain pine beetles attack all *Pinus* spp., typically killing trees 20 cm diameter at breast height (dbh) and greater (Cole and Amman 1969, Amman and Baker 1972), though they will infest smaller diameter trees when larger trees are scarce (Leatherman et al. 2010). The most

obvious impact of MPB is the initial reduction in live overstory *Pinus* tree numbers and average diameter: in the current outbreak, MPB has killed ~70% of lodgepole pine stands' basal area in many areas (Klutsch et al. 2009, Collins et al. 2010). Smaller lodgepole may grow and become dominant in a stand after the outbreak is over (Romme et al. 1986, Sibold et al. 2007, Klutsch et al. 2009) though it is not clear that older, long-suppressed lodgepole pine trees will release following MPB-caused density reductions.

Non-host species, left unharmed by MPB, will play an important role in post-MPB forest recovery where they make up a substantial portion of the forest. Subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), trembling aspen (*Populus tremuloides*) and occasionally Douglas-fir (*Pseudotsuga menziesii*) are often present in Colorado's lodgepole pine forests. The relative dominance of non-host species will immediately increase as overall forest density decreases due to lodgepole pine mortality (e.g., Roe and Amman 1970, Heath and Alfaro 1990, Sibold et al. 2007, Klutsch et al. 2009, Diskin 2010, Diskin et al. 2011). Dominance of non-host species will further increase if they experience a growth release due to lower stand densities following MPB.

Shifts in species composition will affect potential fire spread and behavior due differences in morphology and species reproductive strategies. Differences among species' typical crown base height (CBH), foliar and branch arrangement, and wind penetration change the potential for fire to spread into and among tree crowns (Rothermel 1972, VanWagner 1977, Scott and Reinhardt 2001). In stands dominated by subalpine fir, Douglas-fir or Engelmann spruce, lower crowns and tighter branch packing increases crown fire hazard as compared to stands dominated by lodgepole. Conversely, areas dominated by aspen have reduced likelihood of crown fire spread due to high canopy

base height and large water content of deciduous leaves (e.g., Turner and Romme 1994). With higher fir and/or spruce abundance, recruitment of these shade tolerant species may rise due to greater seed availability, increasing vertical continuity of fuels and further shifting forest composition away from lodgepole pine.

Shade-intolerant lodgepole pine and aspen may release or establish new regeneration if overstory density declines create canopy gaps that provide favorable light conditions. It has been suggested that aspen will increase in abundance following MPB outbreaks (Klutsch et al. 2009, Nelson 2010, Diskin 2010) because canopy gaps provide sufficient light for aspen growth and may warm the ground enough to encourage suckering. In the short term (1-4 years after outbreak), there is evidence that aspen density and growth increased with MPB severity in Rocky Mountain National Park (Nelson 2010). However, long-term increases in aspen following MPB have not been documented, and ecologically important suckering may be unlikely without mechanical or fire disturbance to roots (Perala 1990).

Lodgepole pine regeneration is most likely where overstory density is sufficiently reduced by MPB mortality. Even in areas with high serotiny, seed availability is not likely to limit regeneration following MPB (Teste et al. 2011). However, many studies report lodgepole regeneration in MPB-affected stands is patchy and slow due to light and substrate limitations (Vyse et al. 2009). This occurs in part because canopy gaps must be sufficiently large to provide adequate light conditions for lodgepole establishment: seedling numbers were inversely proportional to the local overstory basal area in British Columbia (Vyse et al. 2009). Similarly, in Colorado, lodgepole pine regeneration following MPB was significantly higher in areas with  $\geq 50\%$  overstory

mortality (Sibold et al. 2007). In the Canadian Rockies, mossy substrates hinder lodgepole establishment (Astrup et al. 2008). In the central Rockies, regeneration can be inhibited by dense grasses and sedges (Lotan and Critchfield 1990), which have been shown to increase biomass following MPB outbreaks and may further limit lodgepole pine establishment as time passes (Stone and Wolfe 1996).

Advance regeneration can respond to reduced overstory canopy density with rapid growth. In lodgepole pine-dominated forests, advance regeneration often has a large component of shade tolerant species that have successfully established beneath an existing canopy, though lodgepole and aspen may be present (Axelson et al. 2009, Collins et al. 2011). For example, in stands that were 91-100% lodgepole pine, Collins et al. (2011) found 2750 stems per hectare ( $\text{ha}^{-1}$ ) advance regeneration, only 39% of which were lodgepole pine. Even though subalpine fir, aspen and Engelmann spruce made up <10% of stand basal area, they comprised 32%, 29% and 3% of advance regeneration. In mixed species stands, advance regeneration is likely to be even more dominated by the shade-tolerant species present. Advance regeneration will play an important role in vegetation recovery in stands affected by MPB, particularly where substrate or small canopy gap size limits lodgepole pine post-outbreak establishment (Astrup et al. 2008).

### **Impact of mountain pine beetle on forest fuel complex and fire behavior**

Long-standing conventional wisdom dictates that because of high dead fuel loading, there is elevated long-term hazard of severe, stand replacing fire occurrence after a MPB outbreak (Heinrichs 1983, Lotan et al. 1985, Schmid and Amman 1992). In this view, the desiccation of needles, twigs, branches and tree boles following tree death

automatically increases risk of fire occurrence. For this reason, it has been assumed that fires necessarily follow beetle outbreaks in lodgepole pine forests (e.g. Heinrichs 1983, Lotan et al. 1985).

High fuel loads following MPB may not be available to burn due to large fuel diameters and a lack of live vegetation and other fine fuels to act as kindling. Therefore, the effect of a MPB outbreak on fire risk is likely a function of time since outbreak due to the changing fuel arrangement as dead trees disintegrate and vegetation recovers (Lynch et al. 2006, Page and Jenkins 2007b). Fine fuels in the canopy are what allow active crown fire to spread (Van Wagner 1977). When needles are still on the tree, their low moisture may increase the risk of severe fire, relative to a healthy stand (Brown 1975, Knight 1987, Page and Jenkins 2007b, Jenkins et al. 2008). However, crown fire risk may be reduced after tree death due to sagging dead branches even while needles remain on the tree (Simard et al. 2011). Once all needles have fallen from dead trees, usually within four years of tree mortality (Klutsch et al. 2009), it is generally believed probability of crown fire ignition is low because there are no needles to cause fire spread through the canopy (Page and Jenkins 2007b, Jenkins et al. 2008). Because of their size, the dead branches of trees require too much energy to burn, and therefore are not likely to burn in a crown fire without needles to act as kindling. Therefore, risk of severe fire is likely reduced as compared to pre-outbreak fire risk by four years post-outbreak.

As time passes, trees killed by MPB will fall contributing coarse woody debris to surface fuels. However, it is unclear how quickly trees fall following death. In Oregon, 80% of trees fell within 10 years (Mitchell and Preisler 1998), while in British Columbia, on average 45% (with a range of 0 – 80%) of trees were still standing 25 years after they

were killed by MPB (Forest Practices Board 2007). Local precipitation and site conditions likely play a role in determining tree fall rates, making it difficult to predict when trees will fall in Colorado from these site-specific results. Also, because there is a large range of fuel loads in lodgepole pine stands (Romme 1982, Tinker and Knight 2000), it is unclear if the MPB will cause fuels to significantly differ from historical conditions on the stand scale once trees do fall (Klutsch et al. 2009).

Fire hazard may go up with time since MPB as coarse woody debris accumulates from snag fall, and as regeneration size and density increases. Though coarse woody debris is generally unlikely to ignite, it can become available to fire in combination with sufficient fine fuels (Jenkins et al. 2008). There is limited evidence of an increase in fire probability in the decades following MPB. Lynch et al. (2006) found that probability of burning in the 1988 Yellowstone fires was 11% greater in forest affected by MPB 14.5 years earlier than in unaffected forests (Lynch et al. 2006). However, there was no increase in burn probability in areas affected by an outbreak only 6.5 years before the 1988 fires. It is likely that the extra eight years of regeneration, understory growth and MPB-killed tree fall resulted in the 11% increase in burn probability; vegetation had recovered sufficiently to allow fire to spread into MPB affected areas and burn coarse woody debris (Lynch et al. 2006, Kulakowski and Veblen 2007). Despite this evidence of increased fire probability due to MPB activity, other research has failed to find an increase in fire occurrence due to increased fuel loadings as a result of tree mortality (Kulakowski and Veblen 2007).

Although there are mixed conclusions about the impacts of MPB on fire probability, increased surface fuel loads are likely to increase severity and heat residence

time when fire does occur (Turner et al. 1999, Lynch et al. 2006, Kulakowski and Veblen 2007)., In areas that burned in the 1988 Yellowstone fires that had experienced severe MPB mortality ( $\geq 50\%$  trees), severity of fire effects was significantly greater than in areas that were not previously affected by MPB. More moderate MPB mortality (10 -50% trees) reduced fire severity as compared to unaffected areas (Turner et al. 1999). In northwestern Colorado, increased coarse fuel loads due to blowdown and insect outbreak increased fire severity even though fire extent was unaffected (Kulakowski and Veblen 2007). Increased fire severity could have profound implications for seed bank viability, soil organic matter content, erosion and water quality following a fire.

Though potential fire hazard in MPB forests has been widely discussed, few studies have quantified the long-term impact of mountain pine beetle on forest fuel complexes or fire behavior. There is little change in surface fuel loads due to MPB activity in the first decade following MPB activity, with the exception of an increase in litter depth (Page and Jenkins 2007a, Klutsch et al. 2009, Simard et al. 2011) and possibly 1-hour fuels (fuels  $\leq 6$  cm diameter) (Page and Jenkins 2007a). By two decades after MPB outbreak in mixed conifer stands in Utah, 10-hour (.6 – 2.5 cm diameter), 100-hour ( 2.5-7.6 cm diameter) and coarse woody debris ( $\geq 7.6$  cm diameter) fuel loads and fuel bed depth increased significantly compared to unaffected areas (Page and Jenkins 2007a). In Wyoming, 1-hour fuels and litter and duff depth declined with increasing time since outbreak, and 10- and 100-hour fuels showed no relationship with time since outbreak. However, coarse woody debris (CWD) did increase with time since MPB outbreak: during initial beetle attack, CWD was  $\sim 20 \text{ Mg ha}^{-1}$ . By 25-30 years post-outbreak, CWD loads were  $\sim 45 \text{ Mg ha}^{-1}$  and by 35 years after MPB CWD had increased

to  $\sim 60 \text{ Mg ha}^{-1}$ , though there was considerable variation among stands in CWD (Simard et al. 2011). Because fine fuels (e.g. needles, leaves, grasses and forbs) and 1-hour fuels drive fire spread, increases in CWD do not present a clear picture that MPB will result in greater risk of fire ignition or spread (Page and Jenkins 2007b). However, these results may be of limited applicability to other areas currently being impacted by MPB. CWD are highly variable in lodgepole pine stands (Romme 1982), and because of the small sample size of fuel load results from Utah ( $n=2$ ) it is not clear that they accurately represent the impact MPB on surface fuel loads. Though from a larger sample of stands ( $n=10$ ), long-term fuel loads from Wyoming only considered nearly pure lodgepole pine areas, while MPB is also impacting mixed species forests. Finally, differences among site characteristics, climates and species composition may result in different fuel loads impacts of MPB.

There is currently little long-term data from which to make conclusive predictions about the future forest structure and fire hazard in MPB-affected forests. There has been a focus on the effects of MPB nearly pure lodgepole pine stands (e.g. Klutsch et al. 2009, Simard et al. 2011), though the trajectory of mixed species stands is likely to be substantially different. Much of the research on future forest conditions following MPB outbreaks relies on modeling based on data from the current outbreak (e.g. Klutsch et al. 2009, Diskin 2010, Collins et al. 2011). There has been no monitoring to comprehensively compare pre-outbreak forest structure to forest structure 20 or more years post-outbreak, though some work has been done to reconstruct past outbreaks in British Columbia (Axelson et al. 2009) and Rocky Mountain National Park (Sibold et al.



2007). There has been no replicated measurement of the fuel complex in stands 20 or more years post-outbreak in mixed conifer forests or forests in Colorado to validate models of future fire hazard.

I examined forest vegetation structure and surface fuel loads in stands that experienced high amounts of mortality during a 1980s MPB outbreak in western Colorado to test predictions of long-term impacts of MPB on stand structure and fuel accumulation. The 1980s outbreak affected many thousands of hectares in Colorado, causing mortality rates similar to the current MPB outbreak in some areas. Both pure lodgepole pine and mixed conifer stands of lodgepole, subalpine fir and Engelmann spruce were affected (Amman and McGregor 1985). I identified stands that were within the area of the 1980s outbreak where Forest Service stand exam data confirmed high mortality rates. I measured structure in these stands using comparable sampling procedures and measured current fuel accumulation in 2010.

I compare stand structure in the 1980s to current stand structure to address the following questions:

1. Do stands recover to pre-outbreak overstory density and species composition in 25-30 years following MPB outbreak? How does current understory tree density and species composition compare to the 1980s understory in these stands?
2. How does initial stand composition impact the forest vegetation recovery in 25-30 years following MPB?
3. What is the fuels complex in stands 25- 30 years after MPB infestation, and does it differ depending on pre-outbreak 1980s species composition?

## **METHODS**

### **Study area**

This study was conducted in the Eagle/Holy Cross Ranger District of the White River National Forest roughly 130 km west of Denver, Colorado, USA (Figure 1). Just west of the continental divide, the area is dominated by mountainous terrain, with a temperate continental climate. Winters are long and cold and summers cool and short. Generally, forest vegetation is dominated by lodgepole pine or aspen at lower elevations and/or southern aspects, with an occasional component of Douglas-fir. At higher elevations and/or more northerly aspects, subalpine fir and Engelmann spruce frequently dominate, though lodgepole and aspen are often also present. Study sites were located from 2650 to 3050 m, with annual precipitation ranging from 520 to 680 mm. The majority of precipitation falls as snow between October and May (PRISM Climate Group 2006).

### **Site selection**

I identified potential study sites that had high levels of mountain pine beetle (MPB) mortality in the 1980s using maps from annual forest health aerial surveys and USDA Forest Service forest inventory data. By intersecting these data sources, I found 132 stands where: 1) MPB activity was observed in aerial surveys no more than 1000 m

from stand center, and 2) forest inventory data showed contemporaneous  $\geq 30\%$  basal area mortality of lodgepole pine. Forest health survey flights record location and intensity of tree mortality on hand-marked maps. The mortality areas recorded by surveys during the 1980s MPB outbreak (1980 to 1987) were digitized into ArcGIS (Dan West, personal communication). These maps provide locations and year by year timing of tree mortality, though spatial accuracy is limited due to the imprecision of hand-drawn polygons. To find more exact information about mortality, we obtained spatially-explicit forest inventory data taken from 1980 to 1988 from the Forest Service's FSVeg database. We looked for areas with a high proportion of standing dead lodgepole pine basal area as an indication of MPB activity because 1980s inventory data did not record MPB or other damage agents. We found 230 stands where standing dead *Pinus contorta* made up  $\geq 30\%$  of total lodgepole pine basal area.

From these 132 potential sites, I randomly selected 50 sites for field inspection. In the field, I looked for evidence that MPB was the agent of 1980s mortality in each stand. I identified older dead lodgepole pine and checked for MPB beetle galleries and sampled wood to check for blue stain. If substantial evidence of 1980s MPB-caused mortality was not found, I rejected the stand. I also verified that each stand's current composition was reasonable given 1980s inventory data and that no substantial biomass removal (such as timber harvest or firewood cutting) had occurred in the half century before 1980s MPB infestation. Twenty stands were selected for sampling.

We repeated forest inventory according to common stand exam data collection protocol in each stand (USDA Forest Service 2007). The repeated forest inventory allowed me to compare current species and age structure to the 1980s stand structure (i.e.,

Smith and Smith 2005). We also measured surface fuel accumulations in each stand to assess fire hazard.

## **Data collection**

### ***1980s stand inventory***

Stand inventory data was collected by the USDA Forest Service between 1980 and 1988 according to contemporaneous common stand exam protocol. Five to 18 plot centers were systematically placed on a grid in each stand. At each plot center, a variable radius plot (BAF 6.9, 9.2 or 13.8 m<sup>2</sup> ha<sup>-1</sup>) and a fixed radius plot (13.5 or 8.1 m<sup>2</sup>) were installed. In variable radii plots, used to quantify overstory (trees  $\geq 12.7$  cm dbh) composition, attributes of “in” trees were recorded. Trees are “in” or “out” based on their distance from plot center and their dbh. For each “in” tree, species, status (live or dead) dbh and height were recorded. Understory trees ( $\geq 0.3$  m tall and  $< 12.7$  cm dbh) were measured in fixed radii plots. Tree species, status (live or dead), dbh and height were recorded for trees  $\geq 2.5$  cm and  $< 12.7$  cm dbh. Species-specific counts of live trees  $\geq 0.3$  m tall and  $< 2.5$  cm dbh were recorded by 1-foot height classes.

The exact locations of each plot center had been lost due to Forest Service data reorganization, but the geographic boundaries of each stand (within which plots were measured in the 1980s) were available in 2010. Therefore, though we could not directly repeat plot measurements in 2010, we could sample the same populations (stands) and compare the random sample of plots from each time period to assess stand change through time.

### ***2010 stand inventory and surface fuels***

In each stand, 10 plot centers were located systematically on a grid, from which a 4.6 m<sup>2</sup> ha<sup>-1</sup> BAF variable radius plot, and possibly a 40.5 m<sup>2</sup> fixed-radius plot, and 21.3 m-long Brown's transect were measured (Brown 1974). For each "in" tree we recorded species, status (live or dead), dbh and crown base height (cbh). We also recorded mountain pine beetle activity (1-6, according to stand exam guidelines [USDA Forest Service 2007]) and Hawksworth dwarf mistletoe ratings (Hawksworth 1977) for lodgepole pine overstory trees. We measured heights for two overstory trees per plot. We measured one variable radius plot per 2 hectares, with no less than 6 and no more than 10 plots measured in each stand.

We measured understory trees in 10, 40.5 m<sup>2</sup> and 10, 1.2 m<sup>2</sup> fixed-radius plots per stand. In each 40.5 m<sup>2</sup> fixed-radius plot, live and dead tree species, dbh, cbh, and tree height were recorded for subcanopy trees ( $\geq 3.8$  and  $< 12.7$  cm dbh). Species-specific counts of seedlings/saplings (trees  $\geq 0.6$  m tall and  $< 3.8$  cm dbh) were recorded by height classes: .61 – 1.37 m tall and  $\geq 1.37$  m tall to  $< 3.8$  cm dbh. To assess small seedling (trees .01–0.6 m tall) density, we recorded counts (by species) of trees less than .6 m tall in a 1.2 m<sup>2</sup> fixed-radius plot. We measured heights and sampled a cross-section at root collar of up to 10 randomly selected *Abies lasiocarpa* seedlings/saplings in each stand to determine ages of trees  $< 3.8$  cm dbh. Trees were then aged by counting tree rings under a microscope.

We measured fuels along transects using Brown's planar intercept method to quantify down woody debris accumulations (Brown 1974). Each transect began at plot center and ran along a random azimuth 21.3 m. We measured one transect per 2 ha of

stand area, with no less than 6 and no more than 10 transects measured in each stand. We tallied fine woody debris (dead woody fuels  $\leq 7.62$  cm diameter [FWD]) that intersected varying lengths of transect plane in the following diameter size classes: 0 - .64 cm (1-hour) and .64 – 3.8 cm (10-hour) fuels along the first 1.8 m and 3.8 cm – 7.62 cm (100-hour) fuels along the first 4.6 m. For coarse woody debris (fuels with diameter at transect intersection  $\geq 7.62$  cm [CWD]), we recorded diameter and species (when possible) for all intersections along the 21.3 m transect plane. Fuels that leaned through the transect plane creating an angle  $< 45$  degrees with the ground were included. We recorded fuel bed and duff depth at two points on each transect and recorded the maximum fuel bed depth.

### ***Surface fuel data from stands unaffected by 1980s MPB***

I obtained data for 11 stands in the study area that were unaffected by the 1980s MPB outbreak to estimate the impact of 1980s MPB on dead surface fuel load in forests. I considered stands unaffected by 1980s MPB if  $< 3 \text{ m}^2 \text{ ha}^{-1}$  and  $< 10\%$  of Pico basal area were recorded as dead in 1980s stand exam data. Elevation and average annual precipitation for unaffected stands fell into the same range as sampled stands. Surface fuel load data were collected in 2002 using Brown's planar intercept method (Brown 1974) and summarized to the stand level by the Forest Service.

### **Data analysis**

I summarized and analyzed data using SAS 9.2 software (SAS Institute 2002-2008). Plot tree and fuels transect data were aggregated to the stand level for the 2010 and 1980s data sets. Basal area was calculated to include overstory trees ( $\geq 12.7$  cm dbh).

Dead lodgepole pine tree number and basal area was added to live lodgepole pine tree numbers and basal area to approximate pre-outbreak stand conditions in the 1980s and 2010. Only trees marked as killed in the current MPB outbreak were included in this addition for 2010.

Stands were stratified into initial forest composition types based on species percentages of total stand BA in the 1980s. Lodgepole pine forest type stands (n=8) had >78% basal area in *Pinus contorta* and <11% basal area in *Picea engelmannii/Abies lasiocarpa*. Mixed conifer forest type stands (n=12) had <78% basal area in *Pinus contorta* and >17% basal area in *Picea engelmannii/Abies lasiocarpa* (Figure 2).

“Lodgepole pine” will refer to lodgepole pine stands and “mixed conifer” will refer to mixed conifer stands as defined here for the remainder of this paper. “*Pinus contorta*” will be used when referring to trees of the species commonly known as lodgepole pine.

I used t-tests to compare forest type composition between forest types (lodgepole pine vs. mixed conifer). I used paired t-tests to analyze overstory and understory tree composition changes in lodgepole pine and mixed conifer stands through time. Because Douglas-fir was not present in the understory during the 1980s and comprised  $\leq 1\%$  in 2010, I did not include the species in understory analysis. I pooled variances when equal and using Satterthwaite’s method when variances were unequal. I used Wilcoxon rank sum tests to compare surface fuel load data between forest types (lodgepole pine vs. mixed conifer) and 1980s MPB status (affected vs. unaffected) because the data were not normally distributed.

## RESULTS

### Overstory

All 20 stands were well stocked in the 1980s before MPB outbreak. Lodgepole pine and mixed conifer stands did not differ significantly in overstory basal area or density, with an overall average of 862 overstory trees ha<sup>-1</sup> and basal area of 36 m<sup>2</sup> ha<sup>-1</sup> (Table 1, Figure 3). Overstory species composition varied between forest types. In lodgepole pine stands, basal areas averaged 89% *Pinus contorta*. Average basal area in mixed conifer stands were 66% *Pinus contorta*, 19% *Abies lasiocarpa*, and 11% *Picea engelmannii*. Mixed conifer stands had significantly less *Pinus contorta* but significantly more *Abies lasiocarpa* and *Picea engelmannii* basal area than lodgepole pine stands. Average stand diameters (ASD) for *Pinus contorta* and non-host species did not differ between lodgepole pine and mixed conifer stands before the 1980s MPB outbreak. In lodgepole pine, ASD for overstory *Pinus contorta* and non-host tree species was 24.6±1.8 and 22.6±4.0 cm dbh, while in mixed conifer ASD for *Pinus contorta* and non-host tree species was 25.0±0.7 and 24.5±1.5 cm dbh.

There was significant mortality due to the 1980s MPB outbreak in both lodgepole pine and mixed conifer stands. A similar portion of *Pinus contorta* overstory was killed in both stand types, but lodgepole pine stands lost a larger portion of total overstory due to the 1980s MPB outbreak. The amount of 1980s MPB mortality (in trees and basal area



ha<sup>-1</sup>) was not significantly different between forest types (Table 1). In lodgepole pine stands, an average of 303 *P. contorta* trees with 13.8 m<sup>2</sup> ha<sup>-1</sup> basal area were killed (Figure 3, Table 2). *Pinus contorta* ASD in lodgepole pine stands was significantly lowered by the outbreak, from 24.6±1.8 to 23.6±1.7 cm dbh ( $P=.0353$ ). In mixed conifer stands, average MPB mortality was 214 *P. contorta* trees ha<sup>-1</sup>, or 10.7 m<sup>2</sup> ha<sup>-1</sup> basal area (Figure 3, Table 2). *Pinus contorta* ASD in mixed conifer stands was not significantly changed by the 1980s outbreak (25.0±0.7 cm before, 25.1±0.8 cm after,  $P=.8142$ ). In lodgepole pine stands, mortality was 46% of *P. contorta* overstory basal area, or 41% of total stand basal area. In mixed conifer stands 43% of *P. contorta* was killed, but this amounted to only 28% of total stand basal area. Consequently, mixed conifer stands had significantly more live basal area than lodgepole pine stands immediately after the outbreak, though there was no significant difference between lodgepole pine or mixed conifer stands in their live *P. contorta* basal area or trees ha<sup>-1</sup> (Table 1). Therefore, forest type species composition differences were exaggerated by the 1980s MPB mortality. Live basal area was 81% *P. contorta* in lodgepole pine stands while in mixed conifer stands live basal area was 53% *P. contorta* immediately following the outbreak. After the 1980s outbreak, ASD of *P. contorta* did not differ between forest types.

Lodgepole pine stands recovered to pre-1980s outbreak basal area and density by 2010 (Table 2, Figure 3). The overstory recovery in lodgepole pine stands was due to growth of existing *P. contorta* overstory trees and growth of smaller *P. contorta* trees into the overstory size class. *Pinus contorta* basal area increased by 89% and tree numbers increased by 66% during the 25-30 years since outbreak. *P. contorta* ASD was 25.0±1.1 cm before the current outbreak, which was not significantly different from ASD before

the 1980s MPB outbreak ( $P=.7664$ ). There was no significant difference in non-host species overstory basal area, density or ASD from the 1980s to today in lodgepole pine stands. By 2010, *P. contorta* made up an average of 84% of overstory basal area and 81% of trees, only 5% and 1% less than before the 1980s outbreak. ASD of non-host species was  $22.2\pm 2.0$  cm in 2010, not significantly from than non-host species ASD of  $22.6\pm 4.0$  cm in the 1980s.

In contrast, in mixed conifer stands the overstory did not recover to pre outbreak conditions during the 25-30 years following 1980s MPB mortality, even though mixed conifer stands had a significantly greater basal area immediately following the 1980s outbreak than lodgepole pine stands (Table 2, Figure 3). There was no significant increase in basal area or density by 2010 in mixed conifer stands, and average total overstory basal area and tree densities in 2010 were significantly less than before the 1980s MPB outbreak. The overstory reduction was driven by the loss of the *P. contorta* component from these stands; there was no significant change in non-host tree species' basal area or density. Non-host ASD was  $24.9\pm 1.1$  cm, not significantly different from 1980s non-host ASD ( $P=.8797$ ). Though *P. contorta* was 66% and 60% of the basal area and trees  $\text{ha}^{-1}$  before the 1980s outbreak, *P. contorta* made up only 51% and 44% of total basal area and overstory trees  $\text{ha}^{-1}$  by 25-30 years later. Therefore, the 1980s outbreak resulted in a significant long-term decrease in total and *P. contorta* basal area and density in mixed conifer stands.

The current MPB outbreak had a greater impact on lodgepole pine stands than mixed conifer stands, though there was significant mortality in both forest types (Table 1, Figure 3). In lodgepole pine stands, MPB killed 40% of *P. contorta* and 48% of *P.*

*contorta* basal area, reducing total basal area 44%. In mixed conifer stands, MPB killed 32% of *P. contorta* trees and 35% of *P. contorta* basal area, reducing total basal area by only 18%. Mortality from the current outbreak significantly reduced *P. contorta* ASD in both forest types, from 25.0±1.1 to 22.9±0.8 cm in lodgepole pine ( $P<.0001$ ) and from 24.9±1.0 to 23.9±0.9 cm in mixed conifer stands ( $P=.0205$ ).

Together, the 1980s and the 2000s MPB outbreaks have resulted in a significant loss of total overstory and *P. contorta* basal area and tree density in both forest types (Table 2, Figure 3). Nearly all of this net basal area and density reduction has been due to the current outbreak in lodgepole pine stands. In mixed conifer stands, the 1980s outbreak resulted in a permanent reduction in basal area and tree density which, when added to mortality from the current outbreak, has significantly reduced total overstory basal area and density in these stands since before the 1980s MPB.

## **Understory**

There was a large increase in understory density in all stands in the 25-30 years since MPB outbreak. Average density of seedlings/saplings (>.6 m tall and <3.8 cm dbh) increased ten-fold in both forest type groups, from 239 to 2374 trees ha<sup>-1</sup> in lodgepole pine and from 651 to 7713 trees ha<sup>-1</sup> in mixed conifer (Table 3, Figure 4). There was no increase in subcanopy (trees 3.8 – 12.7 cm dbh) tree number in either forest type group during this time (Table 3). In lodgepole pine, the relative abundances of shade intolerant species (*Pinus contorta* and *Populus tremuloides*) increased, though *Abies lasiocarpa* was dominant in the small seedling (trees .01 -.6 m tall) size class. In mixed conifer stands, shade tolerant spruce and fir continued to dominate of all understory size classes.

Shade tolerant species increased dominance in progressively smaller size classes in both forest type groups.

In lodgepole pine stands in the 1980s, there was an average of 207 subcanopy trees ha<sup>-1</sup>; *Abies lasiocarpa* was most abundant followed by *Pinus contorta* (Table 3). In 2010, *Pinus contorta* had the highest relative abundance in the subcanopy, followed by *Abies lasiocarpa*. However, there was no significant increase in any species subcanopy numbers. This may be a result of trees growing out of the subcanopy into the overstory.

No seedling/sapling *Pinus contorta* or *Populus tremuloides* were reported in lodgepole pine stands in the 1980s, but these species were present in 2010. However, only *Populus tremuloides* made up a substantial percentage (62%) of seedlings/saplings density. *Pinus contorta* comprised only 7% of seedlings/saplings in lodgepole stands in 2010. *Abies lasiocarpa* dominance of seedlings/saplings numbers declined from 90% in the 1980s to 28% in 2010, though *A. lasiocarpa* was still the second most abundant seedling/sapling species in 2010. *Picea engelmannii* seedling/sapling numbers increased significantly since the 1980s, but made up only 2% of the seedlings/saplings ha<sup>-1</sup> by 2010, as compared to 10% in the 1980s. However, shade tolerant species density dwarfed that of *Populus tremuloides* in the small seedlings size class (trees .01 - .6 m tall). *Abies lasiocarpa* was 79% and *Picea engelmannii* 4% of 7013 small seedlings ha<sup>-1</sup> in 2010. *Populus tremuloides* and *Pinus contorta* were only 16% and 1% of small seedlings, despite their larger relative abundances in the seedling/sapling size class (Table 3).

In mixed conifer stands, an average of 654 subcanopy trees ha<sup>-1</sup> were reported in 1980s stand inventory data. The subcanopy was 62% *Abies lasiocarpa*, 18% *Picea engelmannii*, 10% *Pinus contorta* and 9% *Populus tremuloides*. There were not

significantly more subcanopy trees in 2010, and species' relative abundances remained similar to 1980's (Table 3). *Pinus contorta* subcanopy density increase was nearly significant ( $P=.0533$ ), from 66 to 145 trees  $\text{ha}^{-1}$ , but the species still made up only 17% of the subcanopy by 2010.

*Abies lasiocarpa* dominated the seedling/sapling size class in mixed conifer stands during the 1980s and in 2010 (Table 3, Figure 4). Of the average 651 seedlings/saplings  $\text{ha}^{-1}$  recorded in inventory data in the 1980s, 82% were *Abies lasiocarpa*. By 2010, total seedlings/saplings in mixed conifer stands had increased to an average of 7713 trees  $\text{ha}^{-1}$ . Densities of all species except *Pinus contorta* increased significantly. The largest density increase was of *Abies lasiocarpa*, which increased by an order of magnitude from the 1980s to 2010. *Picea engelmannii* average densities increased roughly six fold. Yet, *Picea engelmannii* was only a small portion of the total seedlings/saplings  $\text{ha}^{-1}$  in 2010 due to the large numbers of *A. lasiocarpa* in these stands. In 2010, the seedling/sapling size class was 88% *Abies lasiocarpa*, 6% *Picea engelmannii*, 3% *Pinus contorta* and 3% *Populus tremuloides*. *Abies lasiocarpa* was even more dominant among small seedlings in 2010, comprising on average 91% of the over 25,000 trees  $\text{ha}^{-1}$  (Table 3).

*Abies lasiocarpa* seedlings/saplings were significantly younger in lodgepole pine stands than in mixed conifer stands ( $P<.0001$ , Figure 5). In lodgepole pine stands, the median age was 29 years, indicating that nearly half of the *A. lasiocarpa* seedlings/saplings currently present established since the 1980s MPB outbreak (Figure 5). In contrast, the median age of *A. lasiocarpa* in mixed conifer stands was 74 and 75% of trees were older than 25, the majority of which established prior to 1980s MPB.

## Forest floor

Total dead surface fuel loads did not differ significantly between initial forest type groups (63 and 78 Mg ha<sup>-1</sup> in lodgepole pine and mixed conifer, respectively) (Table 4). There was a large variation in average total fuel loads among stands. In lodgepole pine stands, stand total fuel load averages ranged from 37 to 124 Mg ha<sup>-1</sup>. In mixed conifer, stand total fuel load averages ranged from 48 to 100 Mg ha<sup>-1</sup>. Total coarse woody debris ( $\geq 7.62$  cm diameter [CWD]) and fine woody debris ( $< 7.62$  cm diameter [FWD]) loads also were not different between forest types. However, there was significantly more rotten coarse woody debris in mixed conifer stands (33 Mg ha<sup>-1</sup>) than in lodgepole pine stands (8 Mg ha<sup>-1</sup>,  $P=0.001$ ). Duff and fuel bed depths were not different between forest types, but maximum fuel bed depth was significantly greater in lodgepole pine than in mixed conifer forest. Average overstory crown base height (CBH) in lodgepole pine was  $8.3 \pm 0.8$  m, significantly greater than in mixed conifer stands ( $5.5 \pm 0.5$  m,  $P=.0064$ ).

We found that stands affected by the 1980s outbreak had significantly higher total fuel loads (78 Mg ha<sup>-1</sup>) than stands unaffected by the 1980s outbreak (48 Mg ha<sup>-1</sup>) (Table 4, Figure 6). However, unaffected stands did have high average total fuel loads that ranged from 22 to 101 Mg ha<sup>-1</sup>. Stands affected by the 1980s MPB had significantly more CWD and 1-hr fuels, but significantly less 100-hr fuels than unaffected stands. Fuel bed depth and duff depth were not significantly different in affected stands than in unaffected stands.

## DISCUSSION

Forest stands with high rates of MPB mortality in the 1980s were fully stocked when remeasured 25-30 years later. However, forest structure was different from 1980s pre-outbreak conditions in all stands. The outbreak had a greater long-term impact on the overstory in mixed conifer stands. In lodgepole pine stands, overstory conditions had returned to pre-outbreak conditions, but understory density had increased substantially by 2010. In mixed conifer stands, overstory density, basal area and *Pinus contorta* component never recovered to pre-outbreak conditions, and understory densities also increased by nearly an order of magnitude. The current (2000's) outbreak has killed a similar proportion of *Pinus contorta* as was killed in the 1980s both forest types. Therefore, we speculate that forest recovery following the current MPB outbreak will be similar to observed changes following the 1980s outbreak in these areas.

Basal area recovery in lodgepole pine stands was due to growth of existing overstory *P. contorta* and growth of surviving *P. contorta* into the overstory. The majority of the 89% increase in basal area following the 1980s outbreak was likely due to upgrowth from smaller size classes, because overstory tree numbers increased by 66% during this time. Post-1980s outbreak live tree density is the likely driver of the overstory recovery differences between forest types. In lodgepole pine stands, high mortality of large *P. contorta* resulted in stands with low overall basal area post-outbreak, resulting in less competition and high light levels for *P. contorta* growth. Growth of overstory *P.*

*contorta* and upgrowth of established understory *P. contorta* may have precluded significant increases in non-host basal area in lodgepole pine stands. Species composition in lodgepole pine stands was not considerably different from pre-outbreak conditions by 25-30 years later—stands were 84% *P. contorta* in 2010 and 88% *P. contorta* before the 1980s MPB outbreak. Recovery of stands to pre-outbreak overstory density and species composition in lodgepole pine stands is consistent with Diskin (2010) who found lodgepole pine stands recovered basal area and maintained *P. contorta* dominance 50 years after outbreak in a simulation.

In mixed conifer stands, *Pinus contorta* basal area and tree densities did not increase after the 1980s outbreak. There was also no increase in density or basal area of non-host species during this time, resulting in a significantly lower total basal area from before the 1980s to before the current outbreak. This density and basal area decline is likely due to the increase in disease-prone *Abies lasiocarpa* stocking, and consequent increases in mortality (Alexander et al. 1990). The stocking decline in mixed conifer stands contradicts predictions that *Pinus contorta* mixed with subalpine fir and spruce will recover quickly due to high surviving tree density and basal area (i.e., Diskin et al. 2011). Indeed, mixed conifer stands did have higher surviving density and basal area than lodgepole pine stands following the 1980s outbreak. However, our results indicate that higher residual basal area/density in mixed conifer stands may actually hinder overstory stocking recovery. Competition between surviving overstory *Pinus contorta* and non-host species may have remained great following the MPB outbreak due to relatively high survival, preventing substantial growth. Understory *P. contorta* and non-host species present during the 1980s in mixed conifer stands may not have had sufficient light to



grow into the overstory due to high remaining overstory basal area and density.

Uprgrowth of *P. contorta* into the overstory may have also been prevented by competition with high densities of shade tolerant *Abies lasiocarpa* and *Picea engelmannii*. Growth rates of shade-tolerant non-host species *Abies lasiocarpa* and *Picea engelmannii* tend to be less than *Pinus contorta* (Alexander et al. 1990, Alexander and Shepperd 1990, Lotan and Critchfield 1990, Perala 1990), which could have also made growth difficult to detect. It is also possible that sampling error was too great for modest basal area growth or tree number increases to be detected because we did not remeasure exact trees recorded in the 1980s. However, the lack of growth in basal area may simply be due to a shift from a developed “mature” stand to a stand which is essentially in its early developmental stages due to lack of old, large trees (Schmid and Amman 1992) and therefore has lower basal area growth rates.

In mixed conifer stands species composition has shifted from before the 1980s outbreak. *Abies lasiocarpa* and *Picea engelmannii* relative basal area has increased from 33% before the 1980s outbreak to 49% before the current outbreak. This is consistent with studies that show MPB speeds transition to late successional species in seral lodgepole pine stands (e.g., Roe and Amman 1970, Amman 1977, Schmid and Amman 1992). The increase in *Abies lasiocarpa* and *Picea engelmannii* in stands may result in higher proportions of these species in the understory due to seed availability (Vyse et al. 2009), though it is not clear that understory numbers and species composition are clearly related to overstory species composition (Coates et al. 2006). Higher densities of trees with low crown base heights also increases crown fire hazard and may affect water yield due to increased snow interception (Robert Hubbard, personal communication).

Understory tree densities were high in both forest types in 2010, though mixed conifer stands' understories continued to be much denser than lodgepole pine stands' in as in the 1980s. Understory tree numbers far exceeded minimum post-harvest stocking requirement of 370 trees ha<sup>-1</sup> set by the USDA Forest Service (USDA Forest Service 1997). However, the majority of understory trees were species other than *Pinus contorta* in both forest types, though *Pinus contorta* were the majority of larger understory (subcanopy) trees in lodgepole pine stands. Significant increases in understory tree density represent a substantial shift in tree size distribution in both lodgepole pine and mixed conifer stands. The ten-fold seedling/sapling density increase is likely to impact subcanopy and overstory density in the future. In the 1980s, subcanopy and seedling/sapling densities were roughly equal. By 2010, subcanopy densities had not significantly increased compared to 1980s densities in either forest type group—presumably because there were not higher densities of smaller trees in the 1980s that were able to grow into the subcanopy by 2010. However, in 2010 seedlings/saplings outnumber subcanopy trees by roughly ten times in both forest types. Similarly, there are about three times more small seedlings than seedlings/saplings. Therefore, as time passes, it is reasonable to expect that densities of larger trees to increase accordingly as trees grow into larger size classes.

Differences between lodgepole pine and mixed conifer stands' overstory species compositions and basal areas immediately following the 1980s MPB outbreak likely had implications for understory response. Lower surviving tree basal area following the outbreak in lodgepole pine stands likely allowed more light to the forest floor than in mixed conifer stands. Gaps allow light to reach the forest floor, providing light conditions

that *Pinus contorta* needs for establishment and growth (Lotan and Critchfield 1990). Similarly, increased light availability likely allowed *Populus tremuloides* numbers to increase in the seedling/sapling class (Perala 1990). Shade-tolerant *Abies lasiocarpa* and *Picea engelmannii* trees were also establish in lodgepole pine stands following the outbreak. These species were more prevalent in the smallest understory size classes, as has been observed elsewhere in Colorado (Collins et al. 2011). This is presumably because they were able to take advantage of lower-light environments than *Pinus contorta* or *Populus tremuloides*. The majority of *Abies lasiocarpa* established following the 1980s outbreak, as 50% of the *A. lasiocarpa* seedlings/saplings were less than 30 years old in lodgepole stands. Therefore, it is possible that *Abies lasiocarpa*, and perhaps *Populus tremuloides*, will be the dominant species in lodgepole pine stands in the future.

In mixed conifer stands higher surviving basal area following the 1980s MPB outbreak likely resulted in stands with lower light availability at the forest floor. Also, the substantial shade tolerant advance regeneration present in the 1980s (~600 spruce and fir seedlings/saplings ha<sup>-1</sup>) was poised to capture resources freed by MPB-caused mortality and were able to grow into larger size classes. This growth release of shade tolerant species further limited forest floor light levels. Therefore, areas conducive to shade intolerant species regeneration or growth were likely scarce, resulting in no significant increase in *Pinus contorta* or *Populus tremuloides* and the overwhelming dominance of shade-tolerant species in all understory size classes. This is consistent with trends in Rocky Mountain National Park and British Columbia, where lower total overstory mortality resulted in little *Pinus contorta* or *Populus tremuloides* regeneration density (Sibold et al. 2007, Vyse et al. 2009, Nelson 2010).

Overall, post-MPB trajectories are consistent with the long-held view that MPB speeds shifts species dominance away from *Pinus contorta* to other non-host species present (Roe and Amman 1970, Amman 1977, Schmid and Amman 1992). Lodgepole pine stands overstory remains similar to before the 1980s outbreak. However, in 2010 stands had high densities in the understory though they had little advance regeneration in the 1980s. In the recovery from the current MPB outbreak, this advance regeneration, dominated by *Abies lasiocarpa* and *Populus tremuloides*, not *Pinus contorta*, will experience a growth release and is likely to be the most important source of growing stock for the future forest (Astrup et al. 2008). Furthermore, *Abies lasiocarpa* will continue to regenerate as the forest recovers from the current outbreak and understory light availability is reduced. *Pinus contorta* and *Populus tremuloides* may not have sufficient light conditions for growth into the overstory or continued regeneration. The compound effect of multiple outbreaks may result in a shift in dominance away from *P. contorta* towards *Abies lasiocarpa* in the long-term, barring fire occurrence. In mixed conifer stands, where *Pinus contorta* was only 51% of stand basal area and there were relatively few *P. contorta* in the understory, stands were likely the formerly dominant *P. contorta* component even before the current MPB outbreak. There will likely be few surviving *P. contorta* in the overstory due to current MPB outbreak mortality. There is little *Pinus contorta* advance regeneration and likely to be little post-outbreak establishment. This will hasten the transition to forest heavily dominated by *A. lasiocarpa* and *P. engelmannii* in these stands, even though 66% of their basal area was *P. contorta* in the 1980s.

Fuel loads in stands impacted by 1980s MPB were large and highly variable and were relatively consistent with post-MPB fuel loads two or more decades after outbreak elsewhere (i.e., Page and Jenkins 2007a, Simard et al. 2011). There were 72 Mg/ha average total surface fuel load, 86% of which was from CWD. The average CWD load of  $62 \pm 5$  Mg/ha agreed with CWD loads measured 35 years post epidemic by Simard et al. (2011) and projected by Klutsch et al (2009) with 80% tree fall rate ( $\sim 60$  Mg/ha and 64 Mg/ha), but was nearly 40 Mg/ha less than observed in Utah 20 years post MPB epidemic (Page and Jenkins 2007). Observed fuel loads in the 1, 10 and 100 hour classes agreed reasonably well (within  $\sim 2$  Mg/ha) with long-term fuel load measurements reported by Page and Jenkins (2007), Simard et al (2011) and projections by Klutsch et al (2009). Surprisingly, despite the large difference in forest composition, there was little difference in down surface fuel loads between lodgepole pine stands and mixed conifer stands, though there was significantly more rotten CWD in mixed conifer stands. This discrepancy between mixed conifer and lodgepole pine stands may be due to different CWD decay rates due to species composition and moisture and temperature differences (Kueppers et al. 2004).

Mountain pine beetle significantly increased total fuel loads as compared to unaffected stands, even though fuel loads were also high and variable in unaffected stands. There were significantly less 100-hour and 1-hour fuels in stands affected by 1980s MPB than unaffected stands. This contradicts studies which reported much lower FWD loads in stands unaffected by MPB, which concluded that in the long term, MPB activity increases 10 and 100 hour (Page and Jenkins 2007a) and 1- and 10-hour fuels significantly (Klutsch et al 2009). However, FWD loads were substantially higher in my

unaffected stands than in unaffected stands in these studies and may explain the inconsistent results. Also, woody debris accumulation, especially of larger fuels (2.6 cm diameter and greater), has been shown to be extremely variable and unpredictable following tree death in Colorado subalpine forest (Bigler and Veblen 2011).

Observed increases in CWD loads due to MPB are likely to impact fire behavior and severity. In Oregon, down logs provided the main corridors for fire spread in a prescribed fire in lodgepole pine forest (Agee 1981). Severity of fire impacts and heat residence time typically goes up with fuel loading (Turner et al. 1999, Lynch et al. 2006, Kulakowski and Veblen 2007). Observed fuel loads were composed primarily by large diameter logs and may therefore be unlikely to burn without sufficient fine fuels from low canopy base heights, understory trees, shrubs, grasses and forbs (Jenkins et al. 2008). However, seedlings/saplings increased ten-fold in all stands from the 1980s to today, greatly increasing ladder fuels. This increase resulted in 3.3 times more seedlings/saplings in mixed conifer than in lodgepole pine stands because of differences in understory density in the 1980s. Considering the difference between lodgepole pine and mixed conifer stands in tree species and understory density today, it is reasonable to expect that these two forest types would experience substantially different fire behavior despite similar dead surface fuel loads. In lodgepole pine stands, a lower density of fuels near the surface may prohibit fire spread and ignition of large fuels. Higher overstory crown base height also reduces crown fire potential. In mixed conifer stands, extremely high densities of understory trees, as well as lower overstory crown base heights typical to shade tolerant *Abies lasiocarpa* and *Picea engelmannii* provides greater vertical continuity of fuels increasing crown fire hazard. Dense understory vegetation may

provide sufficient fuels for fire spread and ignition of coarse down surface fuels resulting from the 1980s MPB outbreak. Therefore, it seems likely that forest species composition differences prior to MPB outbreak are likely to have long-term consequences on potential fire behavior.

The long-term impacts of the 1980s MPB outbreak on these stands differed depending on pre-outbreak species composition. Lodgepole pine stands remain dominated by *Pinus contorta*, though increasing densities of shade tolerant trees in the understory foreshadow possible future increases in overstory *Abies lasiocarpa* and *Picea engelmannii*. The MPB outbreak seems to have set mixed conifer stands on a speedy trajectory to permanent reduced *Pinus contorta* dominance, which will only be compounded by the current outbreak. All stands experienced increases in dead fuel loads and understory tree density, though mixed conifer stands had far denser understory vegetation which could lead to more severe fire behavior. However, because this study was conducted only on specific stands in western Colorado, the long-term impacts of MPB observed in these stands may not occur elsewhere.

The different trajectories of these forests highlight the importance of considering pre-MPB forest composition when considering mitigation of the current outbreak. Because funds are limited and only 20% of affected areas are likely to be actively managed due to legal and operational constraints (Collins et al. 2010), it is important to carefully plan treatments and choose treatment areas strategically. In lodgepole pine stands, mitigation may not be necessary to ensure future *P. contorta* dominance 25-30 years down the line. However, in long term, with multiple MPB outbreaks, these areas

may become increasingly dominated by shade tolerant species with continued absence of fire. In mixed conifer areas, stand composition is shifted towards shade tolerant species immediately, and continues to be by 2-3 decades following MPB mortality. Total stand basal area suffers a long-term reduction in these stands. High understory tree densities also put mixed conifer stands at greater risk of stand replacing fire. Therefore, if reducing fire hazard and maintaining *Pinus contorta* are desired, focusing mitigation on areas with higher components of spruce and fir will likely render the greatest benefit.



## REFERENCES

Agee, J.K. 1981. Initial effects of prescribed fire in a climax *Pinus contorta* forest: Crater Lake National Park, National Park Service Report CPSU/UW 81-3. College of Forest Resources, University of Washington, Seattle. 10 p.

Amman, G.D. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: Impact on succession. *In*: Mattson, W.J., ed. Arthropods in forest ecosystems: Proceedings of the 15<sup>th</sup> international congress of entomology. Springer-Verlag: 3-18.

Amman, G. and B.H. Baker. 1972. Mountain pine beetle influence on lodgepole pine stand structure. *Journal of Forestry*, 70(4):204-209.

Amman, G.D. and M.D. McGregor. 1985. The beetle. *In*: McGregor, M.D. and D.M. Cole, eds. *Integrating Management Strategies for the Mountain Pine Beetle with Multiple-Resource Management of Lodgepole Pine Forests*. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT. General Technical Report INT-174. 68 p.

Alexander, R.R., R.C. Shearer and W.D. Shepperd. 1990. *Abies lasiocarpa* (Hook.) Nutt. Subalpine Fir. *In*: Burns, R. M. and Honkala, B. H., tech. coords. *Silvics of North America. Volume 1, Conifers*. Washington, DC: USDA Forest Service. pp. 87-120.

Alexander, R.R., and W.D. Shepperd. 1990. *Picea engelmannii* Parry ex Engelm. Engelmann Spruce. *In*: Burns, R. M. and Honkala, B. H., tech. coords. *Silvics of North America. Volume 1, Conifers*. Washington, DC: USDA Forest Service. pp. 353-388.

Axelson, J.N., R.I. Alfaro and B.C. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia. *Forest Ecology and Management* 257:1874-1882.

Axelson, J.N., R.I. Alfaro, and B.C. Hawkes. 2010. Changes in stand structure in uneven-aged lodgepole pine stand impacted by mountain pine beetle epidemics and fires in central British Columbia. *Forestry Chronicle* 86:87-99.

Astrup, R., K.D. Coates and E. Hall. 2008. Recruitment limitation in forests: Lessons from an unprecedented mountain pine beetle epidemic. *Forest Ecology and Management* 256:1743-1750.

Bigler, C. and T.T. Veblen. 2011. Changes in litter and dead wood loads following tree death beneath subalpine conifer species in northern Colorado. *Can. J. For. Res.* 41:331-340.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report. INT-16. 24 p.

Coates, K.D., C. DeLong, P.J. Burton, D.L. Sachs. 2006. Abundance of secondary structure in lodgepole pine stands affected by the mountain pine beetle. Report for the Chief Forester, August, 2006. 17 p.

Cole, W.E., and G.D. Amman. 1969. Mountain pine beetle infestation in relation to lodgepole pine diameters. Research Note 95. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT. 7 p.

Collins, B.J., C.C. Rhoades, R.M. Hubbard, M.A. Battaglia. 2010. Post-harvest seedling recruitment following mountain pine beetle infestation of Colorado lodgepole pine stands: a comparison using historical survey records. *Canadian Journal of Forest Research* 40: 2452–2456.

Collins, B.J., C.C. Rhoades, R.M. Hubbard, M.A. Battaglia. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine forests. *Forest Ecology and Management* 261:2168-2745.

Diskin, M. 2010. Forest regeneration trajectories in mountain pine beetle-disturbed forests of Rocky Mountain National Park. M.Sc. thesis, Department of Forest, Rangeland and Watershed Stewardship, Colorado State University, Fort Collins, Colorado. 58 p.

Diskin, M., M.E. Rocca, K.N. Nelson, C.F. Aoki, and W.H. Romme. 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research* 41:782-792.

Forest Practices Board. 2007. Lodgepole pine stand structure 25 years after mountain pine beetle attack. Forest Practices Board, Victoria, BC. FBR/SR/32. 16 p.

Hawksworth, F.G. 1977. The 6-class dwarf mistletoe rating system. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report RM-48, 7 p.

Heath, R. and R. Alfaro. 1990. Growth response of a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle. *Journal of the Entomological Society of British Columbia* 87:16-21.

Jenkins, M.J., E. Herbertson, W. Page and C.A. Jorgensen. 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management* 254: 16-34.

Heinrichs, J. 1983. The lodgepole killer. *Journal of Forestry*: 290-292.

Knight, D.H., 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. *In*: Turner, M.G. (Ed.), *Landscape Heterogeneity and Disturbance*. Springer-Verlag, New York, NY, pp. 59–83.

Klutsch, J.G., J.F. Negrón, S.L. Costello, C.C. Rhoades, D.R. West, J. Popp and R. Caissie. 2009. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle outbreak in Colorado. *Forest Ecology and Management* 258:641-649.

Kueppers, L.M., J. Southon, P. Baer and J. Harte. 2004. Dead wood biomass turnover time, measured by radiocarbon, along a subalpine elevation gradient. *Oecologia* 141:641-651.

Kulakowski, D., and T.T. Veblen. 2007. Effect of prior disturbance on the extent and severity of wildfire in Colorado subalpine forests. *Ecology* 88:759-769.

Leatherman, D.A., I. Aguayo and T.M. Mehall. Mountain Pine Beetle. Colorado State University Extension. Fact Sheet no. 5.528. 4 p.

Lotan, J.E., and W.B. Critchfield. 1990. *Pinus contorta* Dougl. ex. Loud. Lodgepole Pine. *In*: Burns, R. M. and B.H. Honkala, tech. coords. *Silvics of North America. Volume 1, Conifers*. Washington, DC: USDA Forest Service. pp. 302-315.

Lotan, J.E. Brown, J.K., and L.F. Neuenschwander. 1985. Role of fire in lodgepole pine ecosystems. *In*: Baumgartner, D., Krebill, R., Arnott, J. and G. Weetman, Eds., *Lodgepole Pine: The Species and its Management*. Washington State University, Offices of Conferences and Institutes, Pullman, WA, pp. 133-152.

Lynch, H. J., R.A. Renkin, R.L. Crabtree, and P.R. Moorcroft. 2006. The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems* 9:1318-1327.

Amman, G.D. and M.D. McGregor. 1985. The beetle. *In*: McGregor, M.D. and D.M. Cole, eds. *Integrating Management Strategies for the Mountain Pine Beetle with Multiple-Resource Management of Lodgepole Pine Forests*. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT. General Technical Report INT-174. 68 p.

Mitchell, R.G., and H.K. Preisler. 1998. Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. *Western Journal of Applied Forestry* 13:23–26.

Muir, P.S., and J.E. Lotan. 1985. Disturbance history and serotiny of *Pinus contorta* in western Montana. *Ecology* 66:1658-1668.

Muir, P. S. 1993. Disturbance effects on structure and tree species composition of *Pinus contorta* forests in western Montana. *Canadian Journal of Forest Research* 23:1617-1625.

Nelson, K.N. 2009. The effect of mountain pine beetle caused mortality on subalpine forest stand and landscape structure in Rocky Mountain National Park. M. Sc. thesis, Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, Colorado. 62 p.

Page, W. and M.J. Jenkins. 2007a. Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the Intermountain region. *Forest Sci.* 53:507–518.

Page, W., and M.J. Jenkins. 2007b. Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. *Forest Sci.* 53:662–674.

Perala, D.A. 1990. *Populus tremuloides* Michx. Quaking Aspen. *In: Burns, R. M. and Honkala, B. H., tech. coords. Silvics of North America. Volume 2, Hardwoods.* Washington, DC: USDA Forest Service. pp. 302-315.

PRISM Climate Group, 2006. United State Average Annual Precipitation, 1971-2000. Oregon State University, Corvallis, Oregon, USA.

Roe, A. and G. Amman. 1970. The mountain pine beetle in lodgepole pine forests. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT. Research Paper INT-71. 23 p.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* 52:199-221.

Romme, W.H., D.H. Knight, and J.B. Yavitt. 1986. Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *The American Naturalist* 127:484-494.

Rothermel, R.C. 1972. A mathematical model for predicting fire spread in Wildland fuels. U.S. Forest Service Research Paper INT-115.

SAS Institute. 2002-2008. SAS 9.2 TS level 2M3 XP\_Pro Platform. Cary, NC, USA.

Schmid, J.M. and Amman, G.D. 1992. *Dendroctonus* beetles and old-growth forests in the Rockies. In: Kaufmann, M.R., W.H. Moir, and R.L. Bassett, Tech. cords., *Old-growth forest in the Southwest and Rocky Mountain Regions, Proceedings of a Workshop*. USDA Forest Service, Gen. Tech. Rep. RM-GTR-213. pp. 51-59.

Scott, J.H., and E.D. Reinhardt. 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. Rocky Mountain Research Station Research Paper RMRS-RP-29. 59 p.



Sibold, J.S., T.T. Veblen, K. Chipko, L. Lawson, E. Mathis and J. Scott. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. *Ecological Applications* 17:1638-1655.

Simard, M., W.H. Romme, J.M. Griffin, and M.G. Turner. 2011. Do mountain pine beetle outbreaks changes the probability of active crown fire in lodgepole pine forests? *Ecological Monographs* 81:3-24.

Stone, W.E. and M.L. Wolfe. 1996. Response of understory vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio* 122:1-12.

Smith, A.E. and F.W. Smith. 2005. Twenty-year change in aspen dominance in pure aspen and mixed aspen/conifer stands on the Uncompahgre Plateau, Colorado, USA. *Forest Ecology and Management* 213:338-348.

Teste, F.P., V.J. Lieffers, and S.M. Landhäusser. 2011. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. *Ecological Applications*, 21:150-162.

Tinker, D.B., and D.H. Knight. 2000. Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. *Ecosystems* 3: 472-483.

Turner, M. G., W.H. Romme, and R.H. Gardner. 1999. Prefire heterogeneity, fire severity, and early post fire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 9:21-36.

Turner, M. G., and W.H. Romme. 1994. Landscape dynamics in crownfire ecosystems. *Landscape Ecology* 9:59-77.

USDA Forest Service. 1997. 1997 revision of the land resource management plan. Arapaho and Roosevelt National Forests and Pawnee National Grassland, Fort Collins, Colo. Available from [www.fs.fed.us/r2/arnf/projects/forest-planning/management-plan/index.shtml](http://www.fs.fed.us/r2/arnf/projects/forest-planning/management-plan/index.shtml) [accessed 30 May 2011].

USDA Forest Service. 2007. Natural Resource Information System: Field Sampled Vegetation Common Stand Exam Field Guide, Region 2. USDA Forest Service Natural Resource Conservation Service, Washington, DC. 107 p.

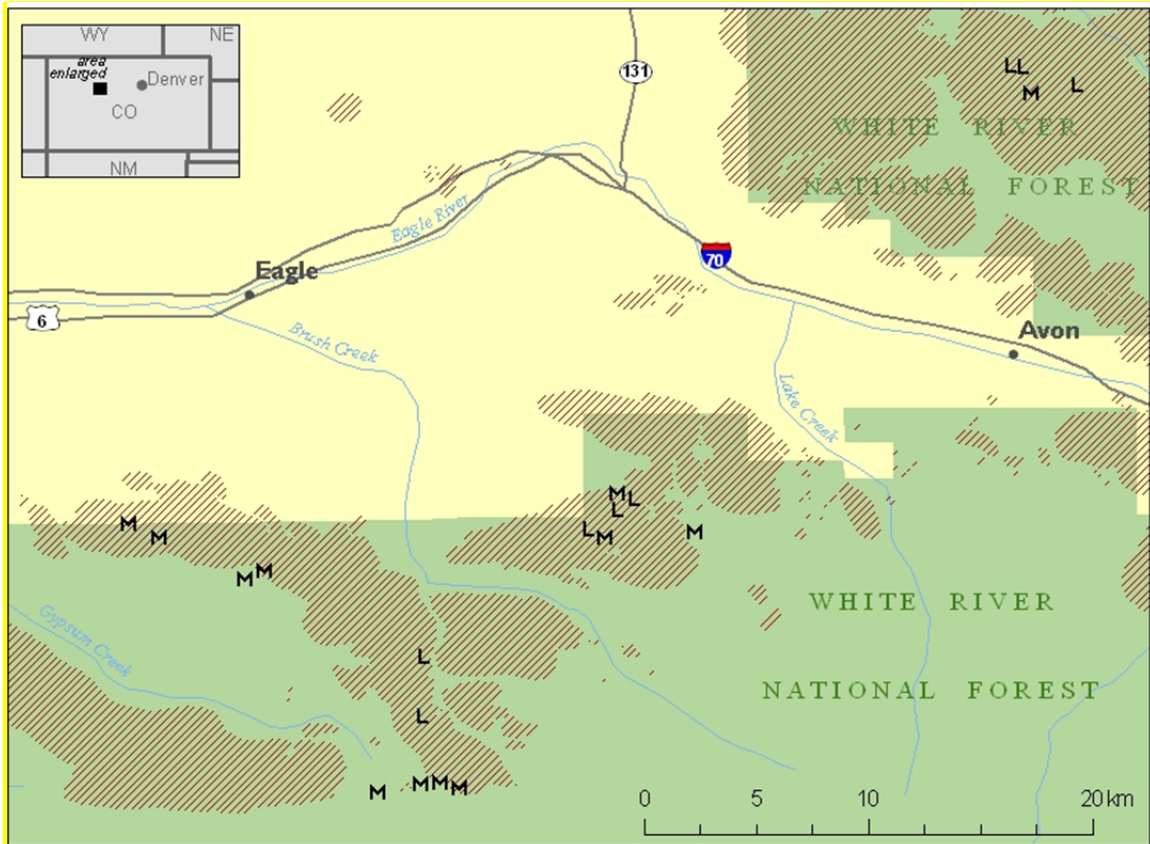
USDA Forest Service and Colorado State Forest Service. 2011. Forest Health Annual Aerial Survey data, Rocky Mountain Region. Available from <http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/download> [accessed 21 January 2011]

Van Wagner, C.E. 1977. Conditions for the start and spread of a crown fire. *Canadian Journal of Forest Research* 7:23-24.

Vyse, A., C. Ferguson, D.J. Huggard, J. Roach and B. Zimonick. 2009. Regeneration beneath lodgepole pine dominated stands attacked or threatened by the mountain pine beetle in the south central Interior, British Columbia. *Forest Ecology and Management* 258S:S36-S43.

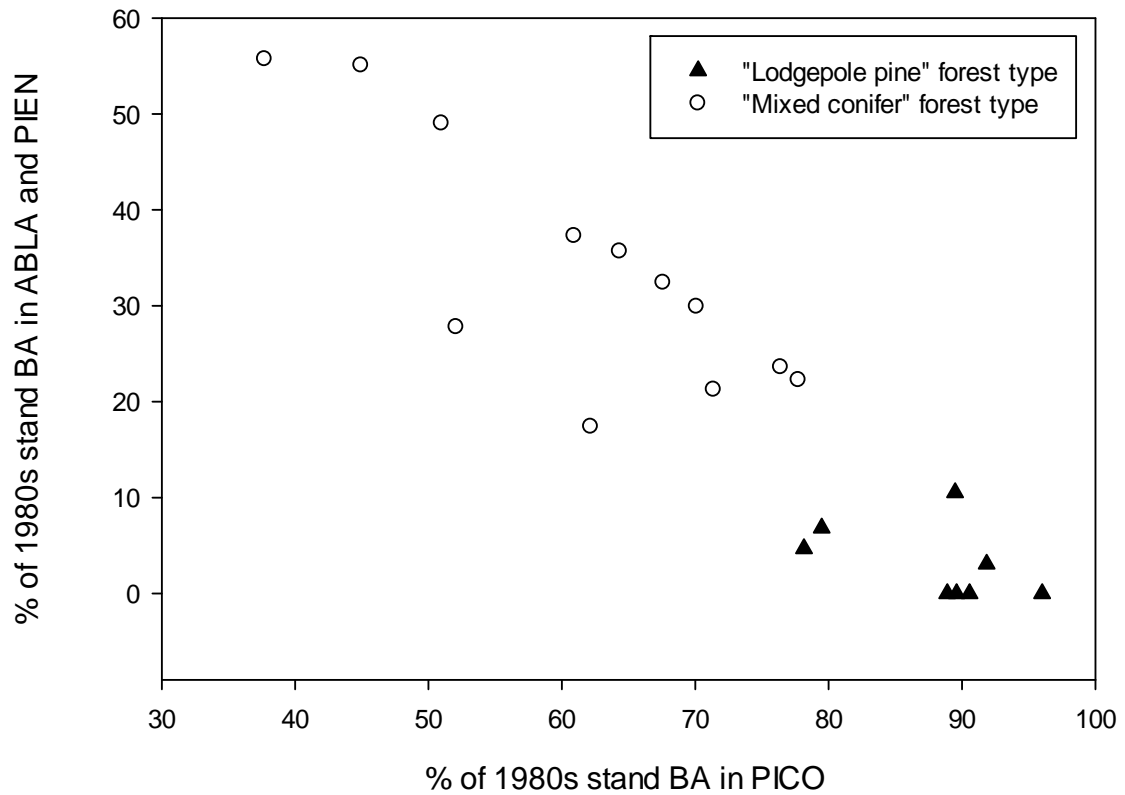
## **TABLES AND FIGURES**

**Figure 1.**



**Figure 1.** Map showing locations study area in Colorado, USA. Sampled stands are marked by 1980s forest type: “M” denotes mixed conifer stands, “L” denotes lodgepole pine stands (as defined in Methods and Figure 2). Hatch-marking indicates areas of mountain pine beetle mortality according to 1980s aerial forest health survey maps.

**Figure 2.**

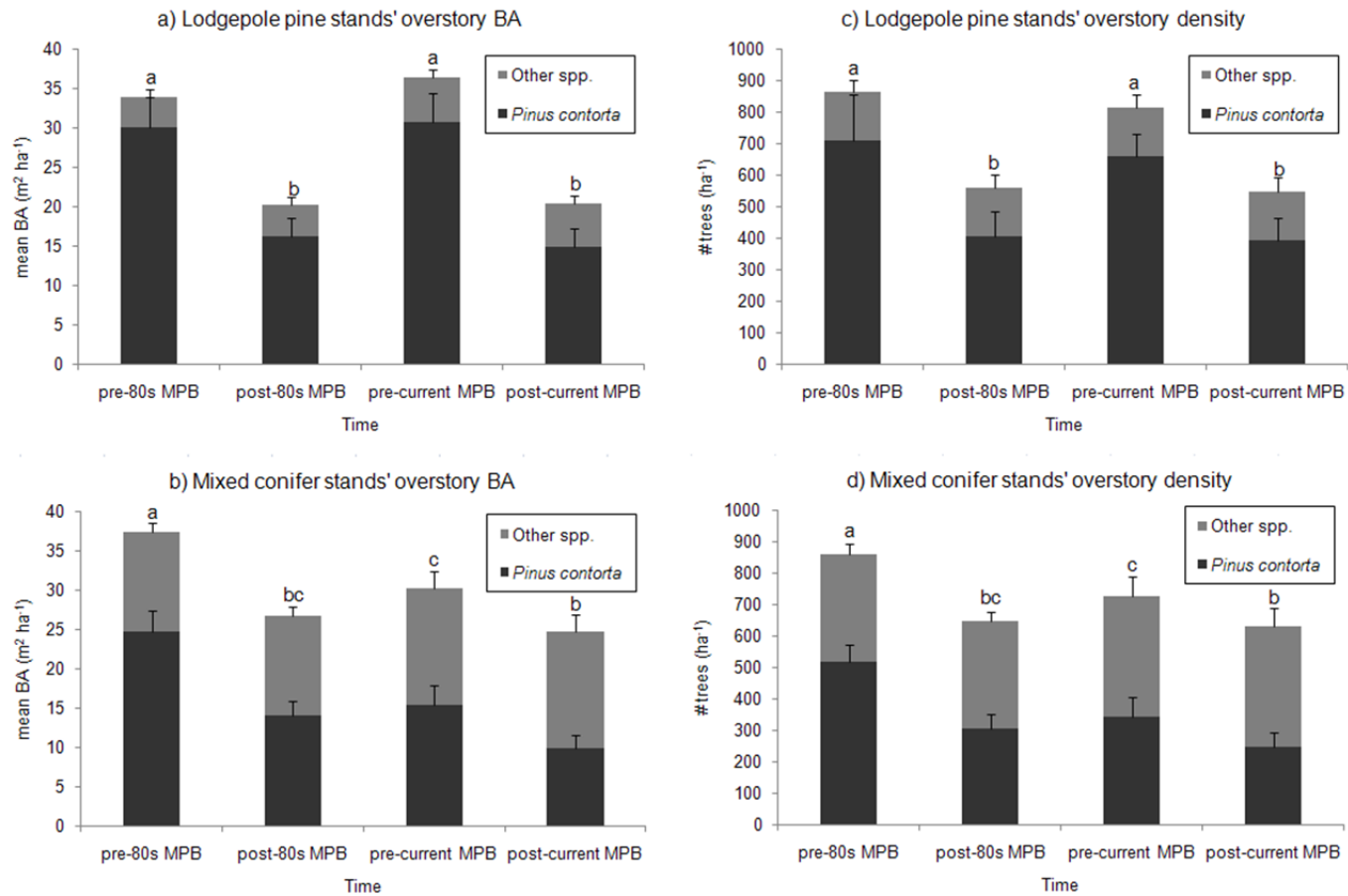


**Figure 2.** Sampled stands' Pre-1980s MPB species' percentages of total stand basal area. Axis abbreviations: PICO=*Pinus contorta*, ABLA=*Abies lasiocarpa*, PIEN=*Picea engelmannii*.

**Table 1.**

	Overstory BA (m <sup>2</sup> ha <sup>-1</sup> )					Overstory tree density (trees ha <sup>-1</sup> )				
	Lodgepole pine		Mixed conifer		<i>P</i>	Lodgepole pine		Mixed conifer		<i>P</i>
	<i>Mean</i>	<i>Std. Err.</i>	<i>Mean</i>	<i>Std. Err.</i>		<i>Mean</i>	<i>Std. Err.</i>	<i>Mean</i>	<i>Std. Err.</i>	
Pre-1980s MPB total	34.0	4.3	37.3	2.4	0.4735	863	4	861	50	0.9905
Total 80s live	20.2	3.0	26.7	1.8	<b>0.0311</b>	560	181	646	45	0.4920
1980 live PICO	16.3	2.3	14.1	1.9	0.4534	407	78	304	47	0.3242
1980 dead PICO	13.8	2.8	10.7	1.5	0.2952	303	81	214	27	0.2952
1980 total non-PICO	3.9	1.1	12.6	1.2	<b>&lt;.0001</b>	153	40	342	31	<b>0.0014</b>
1980 ABLA	0.4	0.4	7.2	1.2	<b>0.0001</b>	24	24	191	30	<b>0.0001</b>
1980 PIEN	0.8	0.6	4.0	0.6	<b>0.0013</b>	23	17	119	17	<b>0.0013</b>
1980 POTR	1.6	0.5	0.5	0.5	0.1262	80	27	11	11	0.1262
1980 PSME	1.1	0.8	1.0	2.1	0.8847	24	22	20	16	0.8847
Pre-current MPB total	36.5	3.1	30.2	1.9	0.0859	812	69	687	67	0.0859
Total 2010 live	20.5	3.0	24.8	2.4	0.2750	547	77	590	61	0.2750
2010 live PICO	14.8	2.4	9.9	1.7	0.1010	393	71	248	44	0.1010
2010 dead PICO	16.0	3.5	5.5	1.7	<b>0.0075</b>	266	55	98	29	<b>0.0075</b>
2010 total non-PICO	5.7	1.8	14.9	2.2	<b>0.0079</b>	155	44	382	61	<b>0.0079</b>
2010 ABLA	1.5	0.9	7.3	1.3	<b>0.0046</b>	43	30	226	46	<b>0.0009</b>
2010 PIEN	0.3	0.1	6.2	1.6	<b>0.0034</b>	8	4	121	32	<b>0.0011</b>
2010 POTR	1.9	1.2	0.8	0.3	0.3647	70	38	29	12	<b>0.0404</b>
2010 PSME	1.9	1.7	0.6	0.5	<b>0.0487</b>	32	32	6	6	0.8654

**Table 1.** Lodgepole pine and mixed conifer stands overstory ( $\geq 12.7$  cm dbh) mean basal area (m<sup>2</sup> ha<sup>-1</sup>) and tree density (ha<sup>-1</sup>) values in the 1980s and 2010. Pre-1980s and current MPB totals include basal area and trees ha<sup>-1</sup> killed in the indicated outbreak. P-values are two-sided results of t-tests.

**Figure 3.**

**Figure 3.** Changes in overstory ( $\geq 12.7$  cm dbh) basal area and density through time. Mean overstory basal area (a, b) and density (c, d) of *Pinus contorta* and all other species in lodgepole pine (a, c) and mixed conifer (b, d) stands through time. Differences in letters above bars indicate significant differences in total and *Pinus contorta* basal area or density in stands through time. There was no significant difference in overstory of other (non-MPB host) species from the 1980s to 2010.



**Table 2.**

<i>Species and time period</i>	BA (m <sup>2</sup> ha <sup>-1</sup> )				Density (trees ha <sup>-1</sup> )			
	Lodgepole pine		Mixed conifer		Lodgepole pine		Mixed conifer	
	<i>Mean change</i>	<i>P</i>	<i>Mean change</i>	<i>P</i>	<i>Mean change</i>	<i>P</i>	<i>Mean change</i>	<i>P</i>
Before to after 80s outbreak <i>P. contorta</i>	<b>-13.8±2.8</b>	<b>0.0008</b>	<b>-10.7±1.5</b>	<b>&lt;.0001</b>	<b>-303±81</b>	<b>0.0036</b>	<b>-214±27</b>	<b>&lt;.0001</b>
Before 80s to before 2000s outbreak <i>P. contorta</i>	<u>+0.7±4.61</u>	<u>0.441</u>	<u>-9.4±2.8</u>	<u>0.0032</u>	<u>-51±174</u>	<u>0.3890</u>	<u>-173±75</u>	<u>0.0206</u>
Before 80s to after 2010 <i>P. contorta</i>	<b>-15.3±5.1</b>	<b>0.0104</b>	<b>-14.8±3.1</b>	<b>0.0003</b>	<b>-316±158</b>	<b>0.0422</b>	<b>-271±73</b>	<b>0.0017</b>
After 80s to before 2000s outbreak <i>P. contorta</i>	<u><b>+14.5±4.0</b></u>	<u><b>0.0041</b></u>	<u>+1.3±2.4</u>	<u>0.3007</u>	<u><b>+252±117</b></u>	<u><b>0.0337</b></u>	<u>+40 ± 72</u>	<u>0.2937</u>
After 80s to after 2010 <i>P. contorta</i>	-1.5±3.5	0.3381	-4.2±2.5	0.0667	-13±96	0.4461	-57±67	0.2065
Before to after current outbreak <i>P. contorta</i>	<b>-16.0±3.5</b>	<b>0.0013</b>	<b>-5.5±1.7</b>	<b>0.0039</b>	<b>-265±55</b>	<b>0.0009</b>	<b>-97±29</b>	<b>0.0031</b>
All other species from 1980s to 2010	+1.7±1.5	0.1481	+2.3±2.2	0.1667	+2±53	0.4852	+41±58	0.2507

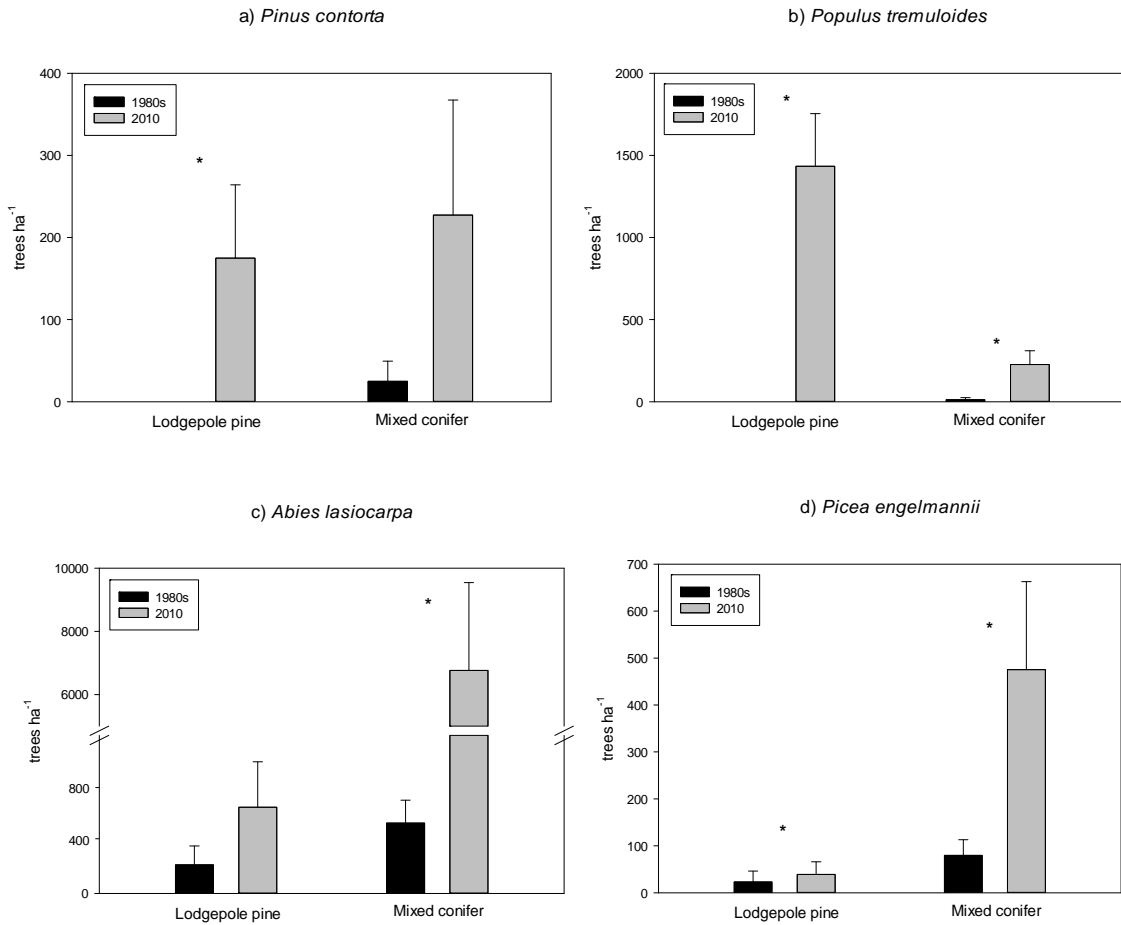
**Table 2.** Changes in overstory ( $\geq 12.7$  cm dbh) basal area and density through time. Bold indicates significant changes, underlines indicate a difference between lodgepole pine and mixed conifer stands. P-values are one-sided, where the null hypothesis is that 1980s density and basal area was  $\geq 2010$  density and basal area.

**Table 3.**

tree size:	<.61 m tall		≥.61 m tall - 3.8 cm dbh			3.8 - 12.7 cm dbh		
	1980s	2010	1980s	2010	<i>P</i>	1980s	2010	<i>P</i>
<b>Pure lodgepole</b>								
All spp.	-	7013 (2601)	239 (140)	2374 (373)	<b>0.0001</b>	207 (120)	150 (32)	0.4832
PICO	-	77 (37)	0	175 (89)	<b>0.0453</b>	77 (33)	88 (14)	0.3702
ABLA	-	5525 (2362)	216 (143)	655 (345)	0.0550	93 (93)	44 (17)	0.6965
PIEN	-	303 (283)	23 (23)	39 (27)	<b>0.0201</b>	0	6 (4)	0.0853
POTR	-	1108 (499)	0	1474 (308)	<b>0.0010</b>	37 (24)	12 (12)	0.7848
<b>Mixed conifer</b>								
All spp.	-	25023 (7372)	651 (178)	7713 (2792)	<b>0.0144</b>	654 (110)	844 (148)	0.1470
PICO	-	101 (74)	25 (25)	227 (84)	0.0886	66 (28)	145 (43)	0.0533
ABLA	-	22821 (7118)	534 (173)	6762 (2780)	<b>0.0245</b>	406 (102)	521 (126)	0.1913
PIEN	-	1894 (647)	78 (33)	475 (187)	<b>0.0255</b>	120 (27)	149 (41)	0.2805
POTR	-	207 (118)	12 (12)	227 (84)	<b>0.0164</b>	62 (39)	23 (10)	0.8471

**Table 3.** Understory trees per hectare density in 1980s and 2010. Mean trees per hectare (standard error) are shown. P-values are one-sided, where the null hypothesis is that 1980s tree densities are ≥2010 tree densities.

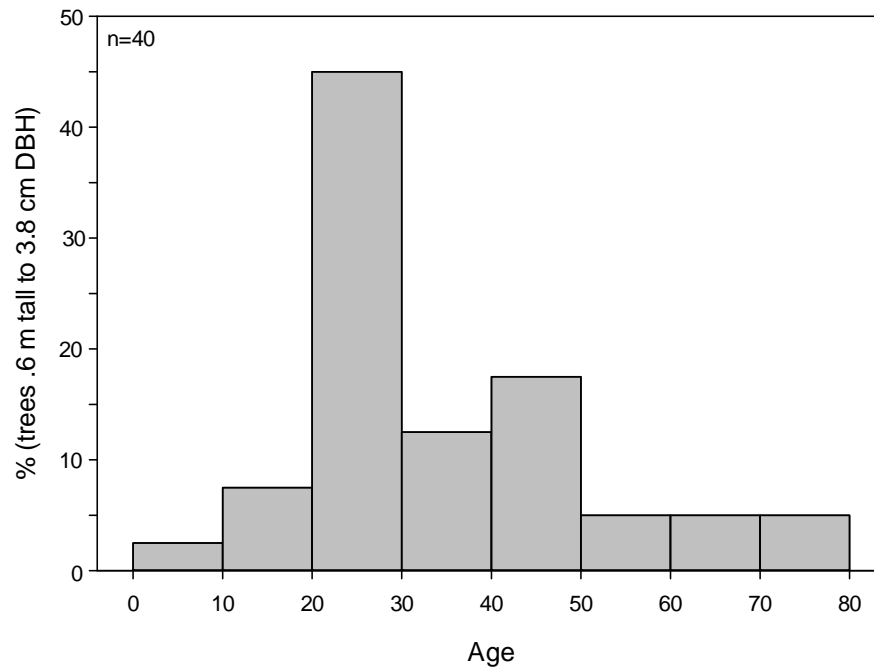
**Figure 4.**



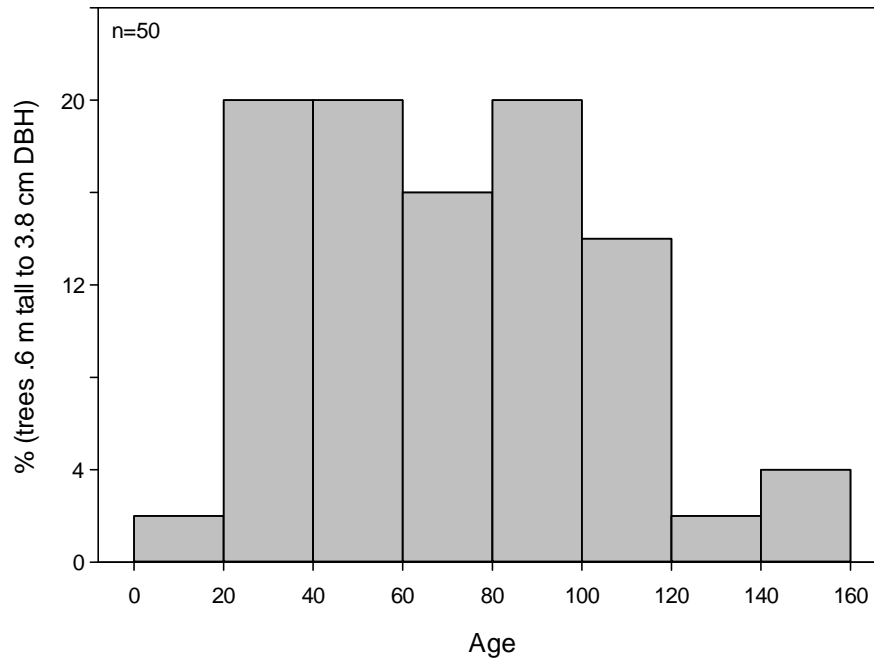
**Figure 4.** Post-outbreak change in seedling/sapling (trees >.6 m tall and >3.8 cm dbh) per hectare in lodgepole pine and mixed conifer stands. *Pinus contorta* (a) seedlings/saplings increased significantly in lodgepole pine stands from the 1980s to 2010, but still had a relatively low density in all stands. *Populus tremuloides* (b) seedlings/saplings increased significantly in all stands, but this increase was largest in lodgepole pine stands. *Abies lasiocarpa* (c) increased significantly in mixed conifer stands, but the increase was not quite significant in lodgepole pine ( $P=0.0550$ ). *Picea engelmannii* (d) trees per hectare increased significantly in all stands. Asterisks indicate a difference between 1980s and 2010 tree numbers at the  $P=0.05$  level, error bar is +1 standard error.

**Figure 5.**

a) *Abies lasiocarpa* in lodgepole pine stands



b) *Abies lasiocarpa* in mixed conifer stands



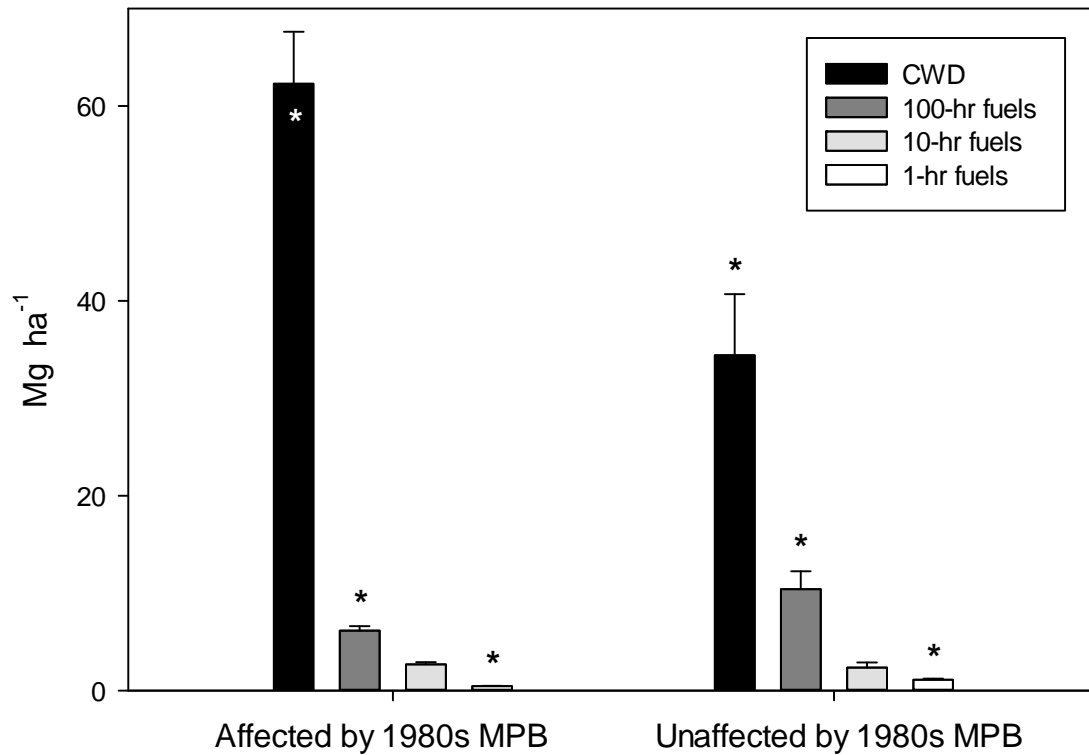
**Figure 5.** Ages of seedling/sapling (>.6 m tall and >3.8 cm dbh) *Abies lasiocarpa* in lodgepole pine (a) and mixed conifer (b) stands. Median age was significantly higher in mixed conifer (74) stands than in lodgepole pine stands (29,  $P < .0001$ ).

**Table 4.**

	Lodgepole pine	Mixed conifer	<i>P</i>	Affected by 1980s MPB	Unaffected by 1980s MPB	<i>P</i>
	<i>Mg ha<sup>-1</sup></i>			<i>Mg ha<sup>-1</sup></i>		
Total fuel load	62.58 (5.62)	78.35 (7.89)	7.89	71.59 (5.29)	48.17 (7.98)	<b>0.0220</b>
Coarse woody debris (CWD) total	52.69 (5.61)	69.48 (7.88)	7.88	62.28 (5.33)	34.41 (6.29)	<b>0.0023</b>
Sound CWD	44.85 (5.3)	36.75 (3.35)	3.35	40.22 (3.03)	-	-
Rotten CWD	7.83 (1.74)	32.73 (6.22)	6.22	22.03 (4.5)	-	-
Fine woody debris (FWD) total	9.89 (0.85)	8.87 (0.82)	0.82	9.31 (0.59)	13.87 (2.44)	0.144
100-hr fuels	6.36 (0.57)	5.99 (0.73)	0.73	6.15 (0.47)	10.41 (1.84)	<b>0.022</b>
10-hr fuels	3.04 (0.41)	2.44 (0.21)	0.21	2.7 (0.22)	2.35 (0.55)	0.1115
1-hr fuels	0.49 (0.07)	0.43 (0.03)	0.03	0.46 (0.03)	1.11 (0.13)	<b>0.0001</b>
		<i>cm</i>			<i>cm</i>	
Fuel bed depth	5.7 (2.2)	8.3 (1.8)	1.77	7.2 (1.1)	7.0 (0.7)	0.3419
Max. fuel bed depth	84.4 (6.7)	65.4 (8.8)	8.83	73.5 (6.1)	-	-
Duff depth	6.1 (0.7)	6.1 (.6)	0.5547	6.1 (0.4)	5.1 (0.5)	0.2381

**Table 4.** Mean down surface fuel loads and depths (standard error). The right side of the table shows comparisons between lodgepole pine (n=8) and mixed conifer (n=12) stands affected by the 1980s MPB outbreak. There was no significant difference between lodgepole pine and mixed conifer stands, except rotten coarse woody debris was greater in mixed conifer than in lodgepole pine stands. The left side shows down surface fuel load totals for stands affected (n=20) and unaffected (n=11) by the 1980s MPB outbreak. Stands affected by the 1980s outbreak had significantly higher total fuel loads than stands unaffected by the 1980s outbreak, though unaffected stands did have high and variable fuel loads. Stands affected by the 1980s MPB had significantly more CWD and 1-hr fuels, but significantly less 100-hr fuels than unaffected stands (Figure 3). P-values are two-sided results of Wilcoxon Rank Sum tests.

**Figure 6.**



**Figure 6.** Down surface fuel loads in stands affected by the 1980s outbreak vs. unaffected stands. There was significantly more CWD in stands affected by 1980s MPB, but significantly more 1- and 100-hour fuels in unaffected stands (Table 4b). Asterisks indicate a difference between affected and unaffected stands at the  $P=0.05$  level, error bar is +1 standard error.