

DISSERTATION

FOREST REGENERATION AND FUTURE STAND TRAJECTORIES FOLLOWING
MOUNTAIN PINE BEETLE-CAUSED LODGEPOLE PINE MORTALITY

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ABSTRACT

FOREST REGENERATION AND FUTURE STAND TRAJECTORIES FOLLOWING MOUNTAIN PINE BEETLE-CAUSED LODGEPOLE PINE MORTALITY

A mountain pine beetle (MPB) (*Dendroctonus ponderosae*) outbreak that began in the late 1990s has killed lodgepole pine (*Pinus contorta* var. *latifolia*) on up to 10 million hectares in western North America. Over one million hectares have been affected in northern Colorado and southern Wyoming. The large footprint of this disturbance has prompted widespread concern about the composition, structure, and function of forests as they develop following MPB. In this dissertation, I ask how variation in species composition and mortality level will affect the future forest in the Southern Rockies.

I used forest growth models to predict forest structure and fuel loads during the century after MPB outbreak. I compared three lodgepole pine-dominated forest types (all > 80 % lodgepole by basal area) and the simulated effects of no-action and fuel reduction treatments. Forest with Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*) became much more dominated by these species, resulting in highly hazardous canopy fuels. In contrast, stands of lodgepole and aspen (*Populus tremuloides*) did not shift composition and did not show a marked increase in fire hazard. The effects of management were also differed: hazardous fuels were best mitigated in the forest types with spruce and fir, but treatment had few positive effects in the stands of only lodgepole and aspen due to their lower hazard without treatment. The results show management of lodgepole-dominated forests must consider even subtle variation in composition to be effective.

I also examined post-outbreak regeneration in these forests. In mixed lodgepole pine and aspen stands, I asked if regeneration is sufficient to reforest areas affected by MPB. Both species excel in high light environments that are created by overstory mortality, but lodgepole pine is thought to require ground disturbance to regenerate. Aspen regeneration can be prevented by browsing. I found lodgepole regeneration is occurring in 85% of stands, and all stands had aspen sucker density above 1000 stems ha⁻¹. Many suckers are damaged by browsing, but my results suggest that sufficient quantities of down lodgepole pine may protect suckers and allow them to recruit to the overstory. Overall, I conclude aspen and lodgepole forests are regenerating successfully and that these areas will remain mixed forests of both species in the future.

Finally, I measured the effects of mortality level on regeneration. I compared regeneration density and growth of lodgepole, spruce, and fir in high (85% of basal area) and moderate (40% of basal area) mortality forest. Lodgepole pine regeneration density and growth was high where outbreak was most severe, though all species grew faster in high mortality than moderate mortality. All three species will likely be important to future forest in areas with high mortality, and lodgepole pine will play a substantial role. In contrast, in moderate mortality areas lodgepole pine regeneration is nearly absent and spruce and fir are growing fastest. Here the forest understory will be made up of shade tolerant species, and the forest will become progressively more dominated by these species as this stratum develops.

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CHAPTER 1

INTRODUCTION

Mountain pine beetle (MPB) (*Dendroctonus ponderosae*) is a bark beetle native to western North America that attacks *Pinus* spp., killing trees by disrupting nutrient and water flow through the phloem and sapwood (Hubbard et al., 2013). The insect has caused substantial mortality in lodgepole pine (*Pinus contorta* var. *latifolia*) forests in the past, but an outbreak that began in the late 1990s is unprecedented in its scale and severity (Raffa et al., 2008). Lodgepole pine has been killed on up to 10 million hectares continent wide (Meddens et al., 2012), with over one million hectares affected in northern Colorado and southern Wyoming (U.S.D.A. Forest Service, 2013). The large footprint of this disturbance has prompted widespread concern about future forest composition, structure, and function. Research in the past decade has allowed us to begin predicting future forest trajectories following MPB, but we do not fully understand the impact of variation in species composition and mortality.

We know the forest trajectory following MPB epidemic will in part be determined by initial forest species composition and the degree of mortality. Mountain pine beetle typically kills trees > 15 cm dbh, though the insect will attack smaller diameter trees when larger trees are scarce (Cole and Amman, 1969; Amman and Baker, 1972; Leatherman et al., 2010). Forest composition immediately following MPB mortality will be dominated by surviving (often small) lodgepole pine and non-host species present, such as shade-intolerant aspen (*Populus tremuloides*) and more shade-tolerant Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*). Long-term species dominance will be a combined result of

post-MPB forest composition, growth in the post-MPB forest environment, and any post-beetle regeneration that occurs.

Growth models based on studies of stand dynamics can be used to inform future forest predictions. In **Chapter 2**, I use Forest Vegetation Simulator (Dixon, 2002, 2008) to explore the effects of relatively small variation in composition on development. Variation in future forest structure and composition is important to a variety of social and ecological concerns, such as wildlife habitat, fire hazard, water yield, and recreation. I also ask if treatments must be tailored to each stand's unique composition to meet fire hazard reduction objectives. However, it is important to acknowledge that these forest development projections do not have tested models of post-beetle regeneration (Dixon, 2008).

Models do not reliably predict regeneration because we have little data about species composition or density of recruitment following MPB outbreaks. There is particular concern about future stocking of forest where lodgepole pine is the only conifer. MPB-caused mortality does not disturb the forest floor and lodgepole pine is thought to need mineral soil to regenerate (Lotan and Perry, 1983). Shade-intolerant aspen may regenerate prolifically due to the increase in understory light following MPB (Kaufmann et al., 2008). This may not occur, however, since aspen is vulnerable to damage by ungulates (e.g., Bartos and Campbell, 1998; Binkley, 2008) and has experienced widespread mortality in recent years that could reduce regeneration potential (Worrall et al., 2010). In **Chapter 3** I explore how these two species are regenerating in stands across the Southern Rockies.

In higher elevation lodgepole-dominated forests, the future mix of pine, spruce, and fir will determine forest structure. These species have different life history strategies and respond differently to various light levels (Lotan and Critchfield, 1990; Alexander et al., 1990; Alexander

and Shepperd, 1990). Research has not explicitly evaluated the effect of mortality level on future forest development, even though mortality varies from < 10 to 100% (Meddens and Hicke, 2014). In **Chapter 4**, I test the effect of mortality level on each species' regeneration density and growth. I expect these species to regenerate and grow differently depending on overstory mortality level. In areas with high mortality, MPB may change the regeneration environment enough to permit shade-intolerant lodgepole pine to establish and outgrow subalpine fir. In contrast, subalpine fir and spruce may outcompete lodgepole in lower-light understories. If evidence shows that the regeneration composition and growth varies with outbreak severity, it will be important to incorporate mortality level variation into predictions about future forest conditions.

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CHAPTER 2

SPECIES COMPOSITION INFLUENCES MANAGEMENT OUTCOMES FOLLOWING MOUNTAIN PINE BEETLE IN LODGEPOLE PINE-DOMINATED FORESTS

SUMMARY

Mountain pine beetle outbreaks have killed lodgepole pine on more than one million hectares of Colorado and southern Wyoming forest during the last decade and have prompted harvest operations throughout the region. In northern Colorado, lodgepole pine commonly occurs in mixed stands with subalpine fir, Engelmann spruce, and aspen. Variation in tree species composition will influence structure, fuel profiles and fire hazard as forests recover from bark beetle outbreaks, and this diversity has implications for design and implementation of fuel reduction treatments. I used stand inventory data to predict forest structure and fuel loads during the century after bark beetle infestation for three distinct lodgepole pine-dominated forest types (pine, pine with aspen, pine with fir and spruce), and compared simulated effects of no-action and fuel reduction treatments (thinning, broadcast burning). In pine stands mixed with significant density of fir and spruce, the high canopy bulk density and low canopy base height increases passive and active crown fire hazards. In contrast, stands of pine mixed with aspen had lower canopy bulk density and active crown fire hazard. All three forest types had high snag and coarse woody debris loads. Thinning and broadcast burning reduced canopy fuels in all forest types for several decades, but had the largest effect in forests with abundant fir. Burning temporarily reduced fine woody fuel, and caused a longer-term reduction in coarse wood and

duff. Overall, these simulations indicate that management aimed at reducing canopy fuels in beetle-killed lodgepole pine forests should prioritize stands with high densities of overstory and understory fir and spruce. Post-treatment forest growth requires frequent stand manipulation (i.e., every 20 years) to maintain acceptable fuel conditions and fire hazard, and as such activities are most appropriate where resource and infrastructure protection and human safety concerns are high.

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INTRODUCTION

Mountain pine beetle (MPB; *Dendroctonus ponderosae*) has killed trees on over one million hectares of lodgepole pine-dominated (*Pinus contorta* var. *latifolia*) forests in Colorado and southern Wyoming since the late 1990s (U.S.D.A. Forest Service, 2013). The severity of tree mortality elevated public concerns about crown fire hazard. Low foliar moisture content increases flammability of fine fuels during the ‘red needle phase’ (Jolly et al., 2012; Page et al., 2012), though this contributor to crown fire hazard is thought to decline with needle fall, typically 3-5 years after beetle infestation (Simard et al., 2012). The abundance of snags and subsequent accumulation of coarse woody debris generated by overstory mortality represent a longer-term fire hazard (Gray, 2013; Page et al., 2013). Loss of the relatively uniform lodgepole pine overstory (even age, single strata) has also been shown to increase dominance of shade-tolerant conifers in some stands (Collins et al., 2012; Pelz and Smith, 2012) and create more

continuous fuel profiles, and increase crown fire hazard starting 1 to 2 decades after beetle infestation (Gray, 2013; Page et al., 2013). These longer-term contributors to fire hazard have prompted fuels reduction treatments on hundreds of thousands of hectares throughout the region (Collins et al., 2010).

Post-outbreak changes in forest structure and fuel profiles depend on the size and species composition of the remaining live trees. Non-host tree species are unaffected and small diameter lodgepole are less susceptible to MPB attack (Cole and Amman, 1969; Klutsch et al., 2009; Diskin et al., 2011). Even the nearly pure lodgepole stands selected for post-outbreak treatments are well stocked with pine and non-host advance regeneration (Collins et al., 2012). Lodgepole pine-dominated forests of the Southern Rockies are commonly mixed with Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*) or quaking aspen (*Populus tremuloides*) (Peet, 1981; Diskin et al., 2011; Kayes and Tinker, 2012).

Fire hazard also varies with species composition in beetle-killed lodgepole pine forests (Klutsch et al., 2011; Hicke et al., 2012; Pelz and Smith, 2012). Lodgepole forests mixed with subalpine fir or Engelmann spruce typically have lower canopy base height (CBH) and higher canopy bulk density (CBD) than pure lodgepole stands (Muir, 1993; Scott and Reinhardt, 2001; Gray, 2013). Vertical continuity of branches and foliage from the forest floor to the overstory canopy create ladder fuels that permit surface fires to burn into the forest canopy and become active crown fires (Alexander et al., 2004). In these mixed pine, fir and spruce stands, the combination of ladder, canopy and coarse fuels, from the release of understory conifers and windthrow of beetle-killed overstory, may generate torching and high intensity surface fires with long residence time and increased potential for spotting (Hvenegaard, 2012; Albini et al., 2012; Page et al., 2013). In contrast, crown fire probability is expected to be lower where pine is

mixed with abundant aspen due the elevated CBH and greater foliage moisture of this forest type compared to pure lodgepole (Turner and Romme, 1994; Cumming, 2000).

Clearcut harvests are the most widely applied prescription in lodgepole pine-dominated forests, and land managers currently lack information needed to assign prescriptions to distinct forest types in beetle-affected forests. Little is known about the short and long term effects of fuel reduction treatments in distinct forest types or how they complement or conflict with other management objectives. For example, the increase in coarse wood and fir and spruce abundance will enhance Canada lynx (*Lynx canadensis*) habitat following MPB (Chan-McLeod, 2006), and protection of forest structure beneficial to lynx will conflict with fuel reduction priorities. Here I simulated forest structure and fuel dynamics in three distinct lodgepole-dominated forest types common to the Southern Rockies and examined changes following two potential fuel reduction treatments (thinning, broadcast burning) during the century after bark beetle infestation. In the absence of well-replicated, field-scale thinning and prescribed burning trials, these simulations provide a first approximation to help assess the consequences of these treatments on forest structure, fuel profiles and potential fire hazard in multiple forest types.

METHODS

Study area and data collection

I used stand inventory and fuels data collected in uncut stands within four bark beetle management areas in northern Colorado (105° 51' to 106° 38' W and 39° 53' to 40° 36' N; Collins et al., 2012) to initiate simulations of post-bark beetle stand development and to inform treatment comparisons. Significant beetle activity began in this area between 1998 and 2002 (U.S.D.A. Forest Service, 2013), peaked around 2008, and killed 60-92% of total basal area

(Chapman et al., 2012; Creeden et al., 2014; Meddens and Hicke, 2014). Forest and fuels were inventoried in 2008 after the majority of pine needles had fallen. Diameter, species, and condition (live or dead) were recorded along 100 x 5 m belt transects for trees ≥ 2.5 cm diameter at breast height (1.37 m high, dbh). I tallied regeneration (trees < 2.5 cm dbh and ≥ 0.15 m tall) by species in two, 3.6-m radius plots per transect. Surface fuel loads were measured along two, 15-m transects (Brown et al., 1982) per belt transect. Fuels ≥ 7.62 cm in diameter (coarse woody debris, CWD) were classified as rotten or sound, and litter and duff depths were measured at three points along each fuel transect (see Collins et al., 2012, for more details).

I partitioned the inventoried stands into: 1) lodgepole pine (LP) ($\geq 90\%$ of pre-outbreak basal area in lodgepole with fir-dominated regeneration); 2) lodgepole pine with aspen (LP-AS) (5 - 30% of pre-outbreak basal area in aspen with aspen-dominated regeneration); and, 3) lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) (10 - 30% of pre-outbreak basal area in spruce and fir with fir-dominated regeneration) (Table 1). The U.S. Forest Service Forest Inventory and Analysis program estimates that LP, LP-AS, and LP-SF types, similar to ours, represent 33%, 22% and 20% of Colorado's lodgepole pine-dominated forests, respectively. Pure lodgepole pine forests (e.g., no fir or spruce regeneration) comprise the remaining 25% (Woudenberg et al., 2010), but they were absent from our study areas.

Simulations of forest and fuel dynamics

I used the Central Rockies variant of the Forest Vegetation Simulator (FVS) (Dixon, 2002, 2008) and its Fire and Fuels Extension (FFE) (Rebain et al., 2012) to project forest and fuel changes for 100 years after mountain pine beetle outbreak. FVS is a density-dependent growth and yield model that projects forest structure and fuels based on initial forest and fuel data and site index. Self-thinning began when stands reached 60% relative density. Regional

maximum heights, basal areas, and densities were used to adjust the model's default levels of aspen growth (Shepperd, 1990; Shepperd, *unpublished data*; Smith et al., 2011). I used Regeneration Imputation Extractor (REPUTE) to add seedling cohorts based on inventory data from beetle-affected forests in Colorado and southern Wyoming (Vandendriesche, 2010).

FFE-FVS generates surface fuel loads and canopy characteristics based on initial fuels measurements and simulated stand development. It accounts for litter and woody fuel inputs, and biomass decomposition through time (Reinhardt and Crookston, 2003; Rebain et al., 2012). Canopy bulk density (CBD; kg dry foliage + branch [< 6 mm diameter] biomass m^{-3}) is estimated by averaging within 0.3 m-thick horizontal layers (Scott and Reinhardt, 2001). Stand CBD is defined as the maximum value of a 4 m-running mean from the 0.3-m layers. Stand canopy base height (CBH) is the height at which stand CBD exceeds 0.01 kg m^{-3} .

Treatment design and effectiveness criteria

Simulated fuel reduction treatments coincided with formation of dense ladder fuel strata commencing 10 years after the outbreak (Gray, 2013; Page et al., 2013). A thin-from-below treatment was designed to reduce canopy fuels in the short and long term. This treatment removed 95% of subalpine fir and Engelmann spruce trees < 15.2 cm dbh and immediately eliminated canopy biomass from the ladder fuel stratum. It also aimed to delay subsequent development of ladder fuels by removing small fir and spruce trees and to promote lodgepole pine and aspen. Resulting biomass from the thinning treatment was left on-site due to the high cost of removing sub-merchantable material. The second treatment, a broadcast burn, was modeled after a planned U.S. Forest Service project in beetle-killed forests of southern Wyoming. It was designed to reduce ladder fuels by killing small fir, to promote future lodgepole pine and aspen dominance, to encourage beetle-killed snag fall, and to consume heavy

surface fuels (M. Hood, U.S.D.A. Forest Service, 2012, *personal communication*). Fall season burning was simulated using the following moderate weather conditions: 13 km hr⁻¹ windspeed at 6.1 m above ground, 19.5°C air temperature, and 7, 8, and 9% moisture in 1-, 10-, and 100-hr lag fuel classes.

I selected regionally-established forest structure, fuel and habitat criteria to evaluate the treatment alternatives (Table 2). I chose CBH and CBD levels for which FVS-FFE would predict low likelihood of passive or active crown fire initiation with 1-minute wind gusts typical of 97 percentile weather conditions and 2-m surface fire flame lengths (Rebain et al., 2012). I used the following CWD levels stipulated by local fuels reduction projects (U.S.D.A. Forest Service, 2009b, 2012): < 67 Mg ha⁻¹ to allow firefighter access and reduce smoldering fires and spotting and > 22 Mg ha⁻¹ to provide sufficient structure for wildlife habitat (Brown et al., 2003). Biomass of MPB-killed snags was added to CWD loads to account for all coarse fuels that would eventually be contributed by MPB-caused mortality.

Statistical analysis

I compared differences in forest composition and structure among the three forest types and the effects of treatments using a repeated-measures, generalized mixed linear model, with forest type and treatment as fixed effects and site as a random effect (GLIMMIX, SAS 9.3, SAS Institute Inc., Cary, NC). I used the model shown in Equation 1 to examine the difference among untreated stands of the three forest types (LP, LP-AS, and LP-SF).

$$\text{Equation 1: } y = \text{forest type} + \text{year} + \text{type} \times \text{year}$$

I examined the effect of treatments within each forest type separately with the model shown in Equation 2:

$$\text{Equation 2: } y = \text{treatment} + \text{year} + \text{treatment} \times \text{year}$$

Residual plots were used to select the appropriate response distributions for each variable. Basal area, surface litter, and surface duff were normally distributed; woody surface fuels, CBH, and CBD were lognormal. I used logistic regression to compare the proportion of total basal areas contributed by each species. I report significant differences at the $\alpha = 0.05$ level with a Bonferroni adjustment when comparing forest types or treatments at specific times.

RESULTS

Forest and fuel dynamics in untreated stands

Species composition, basal area, and canopy fuels changed over the century-long simulation, but the three forest types remained distinct. In both the LP and LP-SF types, fir became an increasing proportion of total basal area with time and pine decreased (Figure 1). Aspen was consistently about 40% of total basal area in the LP-AS type and < 10% of basal area in the others. Live basal area differed among forest types at the end of the outbreak, but these differences receded through time (Figure 2). Basal area of the LP-SF type was 8 - 12 m² ha⁻¹ greater than the other types during the first half of the simulation. Average CBH extended to within 1 m of the forest floor in the LP-SF type for more than 50 years after the outbreak (Figure 3a). In contrast, in the LP and LP-AS forest types CBH exceeded 6 m for two decades after the outbreak before it lowered with the increase in understory tree density and became similar to the LP-SF type. CBD was low after the outbreak in all forest types and increased steadily with time (Figure 3b). The LP-AS and LP-SF types consistently had the lowest and highest CBD throughout the simulation.

Simulated treefall removed 50% and 90% of snags within 10 and 20 years of the outbreak, respectively, in all forest types. Consequently, coarse wood loads increased rapidly

and peaked after 20 years. The LP-AS type had nearly 2 times more snag mass initially and subsequently 0.5 to 2 times more CWD than the other types during the first 50 years (Table 3). By the end of the simulation, CWD loads were similar among types. Fine woody debris (FWD), litter, and duff were also similar among forest types. Litter declined during the first decade, and then along with FWD doubled over the 100 year simulation.

Treatment effects: Species composition and stand basal area

The treatments altered the species composition of the LP and LP-SF, but had little effect in the LP-AS type. Thinning and burning both reduced the proportion of fir in the LP and LP-SF types, but had no effect on proportion of fir in the pine - aspen mix (Figure 1). Both treatments increased the proportion of aspen in LP-SF stands; aspen represented 8 and 13% in Thin and Burn stands, respectively, by year 100, compared to the untreated stands where it comprised < 0.1% of basal area (Figure 1). In the LP-AS mix, burning increased aspen by 7 - 17% relative to untreated stands.

The Thin and Burn treatments reduced live basal area by varying degrees in the three forest types (Figure 2). Thinning removed 1532 fir and 78 spruce ha⁻¹ from the LP type, 117 fir and 0 spruce ha⁻¹ from the LP-AS type, and 3951 fir and 410 spruce ha⁻¹ from the LP-SF type. Although the thinning removed < 10% of stand basal area in all types, basal area reductions persisted through much of the simulation in the LP-SF and LP types. Thinning had no effect on LP-AS basal area due to the scarcity of understory spruce and fir. The Burn treatment lowered average basal area 55 - 60% initially in all forest types, and the reductions remained significant until year 100. At that time, burning had eliminated 14, 5, and 11 m² ha⁻¹ of basal area (26, 6 and 16%) from the LP, LP-AS and LP-SF types relative to untreated stands.

Treatment effects: Canopy and surface fuels

The Thin treatment elevated CBH from years 20 through 30 in the LP and LP-AS forest types relative to untreated stands. Burning raised CBH in all three forest types, and similar to thinning, the effects were relatively short-lived and diminished by year 40 (Figure 4a, b, c). Thinning reduced CBD in the LP and LP-SF types; burning reduced it in all forest types (Figure 4d, e, f). The effect of thinning on CBD became evident in year 20 in the LP and LP-SF types and continued until the end of the simulation; the reduction from burning persisted throughout the simulation for these forest types. For the LP-AS type, the effect of burning on CBD was only evident during the first half of the simulation (Figure 4e).

Thinning did not increase surface fuels in any forest type, but rather reduced them in the LP and LP-SF types over the long term (Table 3). The only effect of the treatment on snag or CWD loads was a 26% reduction measured in year 100 in the LP-SF type relative to the Control. Thinning reduced FWD by 32% and 27% in the LP-SF and LP types in latter periods of the simulation, respectively. Thinning also reduced litter mass in the LP-SF type in year 20 and in later years for the LP and LP-SF types, respectively.

Burning reduced duff mass by roughly 50% in all forest types throughout the simulation, but its effects on other surface fuel loads varied through time and with forest type (Table 3). In all forest types, burning reduced standing snag mass by nearly 90% the year of treatment, but had little effect on snags in subsequent years. Burning decreased CWD loads throughout the simulation in the LP and LP-AS types; maximum CWD loads were reduced 27% relative to untreated stands. In the LP-SF type, burning reduced CWD by 45% the year of treatment, and by 42% at the end of the simulation, but not during the interim. Burning reduced FWD loads 43 - 72% in all the forest types initially, but responses differed among types later in the simulation.

For example, in the second half of the simulation, FWD loads were lower in burned LP and LP-SF stands compared to untreated stands, but the treatment increased FWD loads in the LP-AS type.

DISCUSSION

Approximately 75% of Colorado's lodgepole pine-dominated forests occur in mixed species stands (Woudenberg et al., 2010). In spite of distinct stand structure and species composition, the three forest types found within my study areas are typically treated with a prescription based on the dominant lodgepole pine overstory. However, I found that responses to the fuel reduction treatment alternatives differ between the forest types. My simulations of the post-outbreak dynamics in canopy structure, fuel conditions and fire hazard also indicated that stands of all three forest types will fail to meet fuel criteria without management intervention (Table 4). The LP-SF and LP forest types would be priorities for fuel reduction treatment.

In each forest type, growth of advanced regeneration and seedling recruits following MPB outbreaks will create fuel profiles that will require active management to meet designated fuel thresholds (Tables 2, 4). As has been widely documented (Page and Jenkins, 2007; Klutsch et al., 2011; Collins et al., 2012; Pelz and Smith, 2012; Gray, 2013), I project that subalpine fir will become a dominant component in stands such as my LP and LP-SF forest types that contained fir prior to the beetle outbreak. Development of post-outbreak fir creates vertical fuel continuity (low CBH) that promotes torching and a dense overstory canopy (high CBD) that favors active crown fire. All my LP-SF stands had sufficient ladder fuels to exceed CBH criteria during most of the simulation; similarly, growth of abundant ladder fuels lowered the CBH in all LP stands 20 years after the outbreak (Table 4). Forest structure that develops in these LP and

LP-SF stands also contains adequate canopy bulk density to create active crown fire hazards in most stands (Table 4). Similar processes also contribute ladder fuels in LP-AS stands and make torching likely in many of these stands by year 20. However, subsequent self-pruning lifts the canopy base height above the critical threshold in 88% of the simulated stands.

The loss of standing snags peaked in my simulated stands 10 – 20 years after the outbreak, as has been observed following bark beetle in lodgepole pine forests elsewhere (Mitchell and Preisler, 1998; Lewis and Thompson, 2011). This overstory loss generated surface CWD loads in excess of my criteria for many stands of all forest types (Table 4). The highest CWD loads occurred in the LP-AS type, where 75-100% of stands were above threshold levels during the first half of the simulation. The high CWD loads in the LP-AS stands are the combined result of high initial density of MPB-susceptible pine and unstable aspen snags. More than half the LP and LP-SF stands exceeded the CWD load initially, but due to wood decay 70 - 80% of stands met the desired levels the second half of the simulation.

Treatment effectiveness

The effectiveness of the Thin and Burn treatments at reducing fuel hazards varied among forest types in these recovering bark beetle infested forests. Thinning increased the proportion of LP and LP-SF stands that met canopy fuels criteria, but had little effect in LP-AS stands, as there were few understory spruce and fir trees to remove (Table 4). Thinning in LP stands, for example, resulted in 40% more stands that met the CBH and CBD criteria the decade after the treatment. Thinning also reduced the CBD of LP-SF stands and increased the proportion of that forest type below the hazard threshold. However, the Thin treatment did not remove sufficient large fir and spruce (> 15.3 cm dbh) to reduce the density of ladder fuels and raise CBH. My simulated Thin treatment did not significantly add to surface fuels as reported elsewhere (Agee

and Skinner, 2005; Reinhardt et al., 2008) owing to the very small size of the trees treated. The lower stand density actually reduced long-term surface fuel additions in the LP and LP-SF types and increased the proportion of stands that met the CWD criteria. This demonstrates an advantage of conducting treatments shortly after the outbreak, before understory trees have grown in response to overstory mortality.

In general, the simulated Burn was more effective than the Thin at reducing fuel hazards (Table 4). Burning scorched spruce and fir branches, killed many overstory trees, and increased the CBH immediately in many LP-SF stands. It also limited the number of small trees that developed into ladder fuels and had a delayed, positive effect on CBH in LP and LP-AS stands. Burning consumed about half of CWD, fine woody fuels, litter, and duff in all forest types and increased the number of stands that met the CWD criteria. In contrast to these simulated conditions, burning conducted at higher fuel moisture would not have much effect on surface fuels (e.g., Stephens and Moghaddas, 2005; Knapp et al., 2005; Battaglia et al., 2008).

Implications for management of recovering bark beetle forests

Site-specific prescriptions that account for the species composition and fuel profiles of individual stands would be more effective than these generic Thin or Burn treatments though my simulations suggested a number of modifications. For example, raising the diameter limit of spruce and fir removed in LP-SF stands would both elevate CBH and increase revenue generated by thinning. Similarly, removal of standing live or dead biomass and future surface fuels enhance both the fuel reduction aims of thinning and the possible economic rewards of the treatment. Pruning to directly increase CBH may be appropriate in specific, sensitive areas.

Like numerous other studies, my simulations showed that ladder fuel and residual overstory growth following management decreases treatment effectiveness to reducing torching

and active crown fire hazards within a few decades (Battaglia et al., 2008; Reinhardt et al., 2010; Collins et al., 2012; Stephens and Collins, 2012; Stephens et al., 2012; Chiono et al., 2012). I found that re-entry would be required every 20 years to maintain desired CBH, regardless of forest or treatment type. Further, additional manipulations are needed in year 20 and 40 to maintain CBD target levels after thinning in LP-SF and LP forest types, respectively.

The results indicate that LP and LP-SF forest types characterized by dense fir and spruce advance regeneration would be top priorities for fuel reduction treatments given regional fuel reduction criteria. However, intervention to remove ladder fuels, increase CBH, and reduce torching conflicts with requirements to maintain or enhance habitat of the federally-listed, threatened Canada lynx (U.S.D.A. Forest Service, 2009a). Treatments conducted in LP-AS and pure LP stands may avoid the conflicting management objectives but result in treating lower priority, lower hazard areas. Though simulations and field experimentation are needed, treatments that create or expand within-stand and landscape variation may help achieve a balance between fuels reduction and lynx habitat needs.

These projections of forest dynamics should be interpreted with appropriate care. My previous modelled predictions of general structural and compositional change following MPB derived from plot measurements (Collins et al. 2011, 2012) have been corroborated by resurvey of historical MPB outbreaks (Pelz and Smith, 2012). Nevertheless, the ability of current models to accurately predict tree regeneration and long-term forest change following MPB and associated management is uncertain. The FVS-FFE model, for example, generally underestimates CBD and canopy fuel hazard in conifer forests (Keyser and Smith, 2010). Further, the simulation does not account for factors that could alter future tree growth and mortality, such as extreme weather events and climate change, insect, disease, and animal

damage (Worrall et al., 2013). Well-replicated, long-term measurement of forest development in distinct forest types and management treatments is the best way to make certain estimates of post MPB forest recovery. In the absence of appropriate operational trials, my simulations demonstrate important relative differences among forest types and treatments.

CONCLUSION

Differences in species composition can help prioritize fuels reduction treatments following mountain pine beetle. Post-outbreak canopy structure poses an immediate canopy fire hazard in pine-dominated stands mixed with fir and spruce in the overstory and understory (LP-SF). Within two decades of the outbreak, LP stands containing fir and spruce advance regeneration develop low canopy base heights and high canopy bulk densities that create similar hazards. In contrast, in lodgepole forest mixed with aspen (LP-AS), the hazard of active crown fire is relatively low for many decades after outbreak. Fuel reduction treatments are therefore likely to have the greatest effect on canopy fire hazard in forests where subalpine fir is abundant. Burning and to a lesser extent thinning have potential to reduce canopy fire hazard and resistance to control, though there is a need for repeated interventions to account for growth and formation of the ladder fuel strata. Although decade-scale treatment intervals are not consistent with the century-scale return interval of natural disturbances in high elevation forests (e.g., Romme and Despain, 1989; Kipfmueller and Baker, 2000; Schoennagel et al., 2004), intensive hazardous fuel management is increasingly justified by expanding wildland urban interface areas and escalating wildfire suppression costs (U.S.D.A. Office of Inspector General, 2006; Aronson and Kulakowski, 2012; Gorte, 2013).

TABLES AND FIGURES

Table 2. Canopy and surface fuel criteria based on fuels reduction objectives for mountain pine beetle management in the U.S. Forest Service, Rocky Mountain Region (R2).

Attribute	Criteria	Rationale
Canopy Fuels	Canopy Base Height (CBH) > 3.5 m	At CBH > 3.5 m, passive crown fire initiation ("torching") likelihood is low below <97%ile windspeeds, 110% live fuel moisture, and 2 m surface fire flame lengths (VanWagner, 1977).
	Canopy Bulk Density (CBD) < 0.086 kg m ⁻³	At CBD < 0.086 kg m ⁻³ , active crown fire spread likelihood is low below < 97%ile windspeeds, constant slope, 0.05 kg m ⁻² critical horizontal mass flow rate (Scott and Reinhardt 2001; after VanWagner, 1977).
Coarse Woody Debris	Coarse Woody Debris (CWD) 22 to 67 Mg ha ⁻¹	CWD is limited to reduce smoldering, improve fire fighter mobility and reduce wildfire resistance to control while leaving woody biomass for wildlife (U.S.D.A. Forest Service, 2009; Brown et al., 2003; Page et al., 2013). Biomass from MPB-killed snags was added to surface CWD loads to account for all coarse fuels contributed by the MPB outbreak.

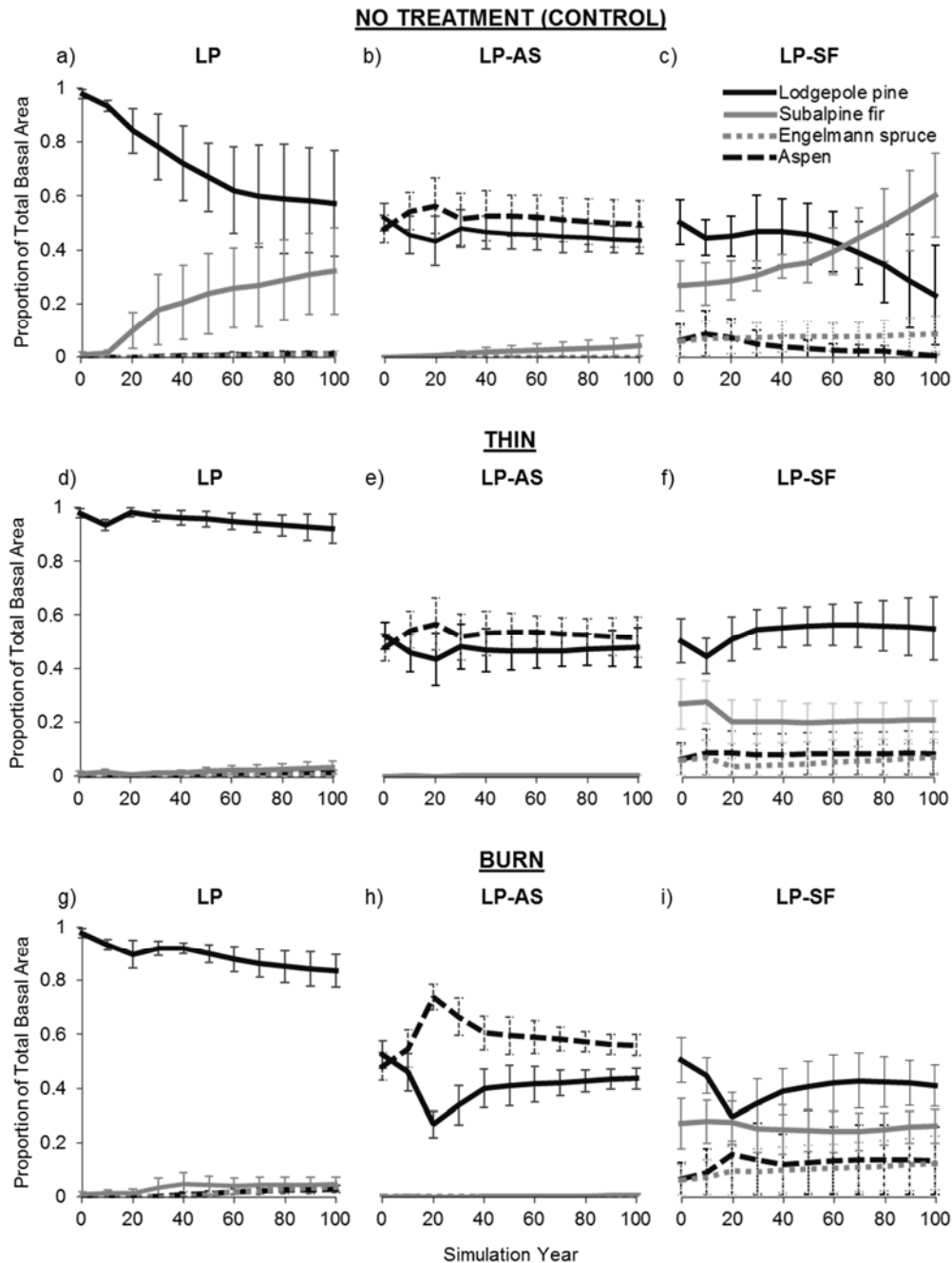


Figure 1. Species composition in lodgepole pine (LP), lodgepole pine with aspen (LP-AS) and the lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) stands after MPB infestation and simulated Thin, Burn and Control treatments. Data are median proportion of total basal area type (\pm absolute deviation) by species and forest type. Simulated treatments were implemented 10 years after the outbreak.

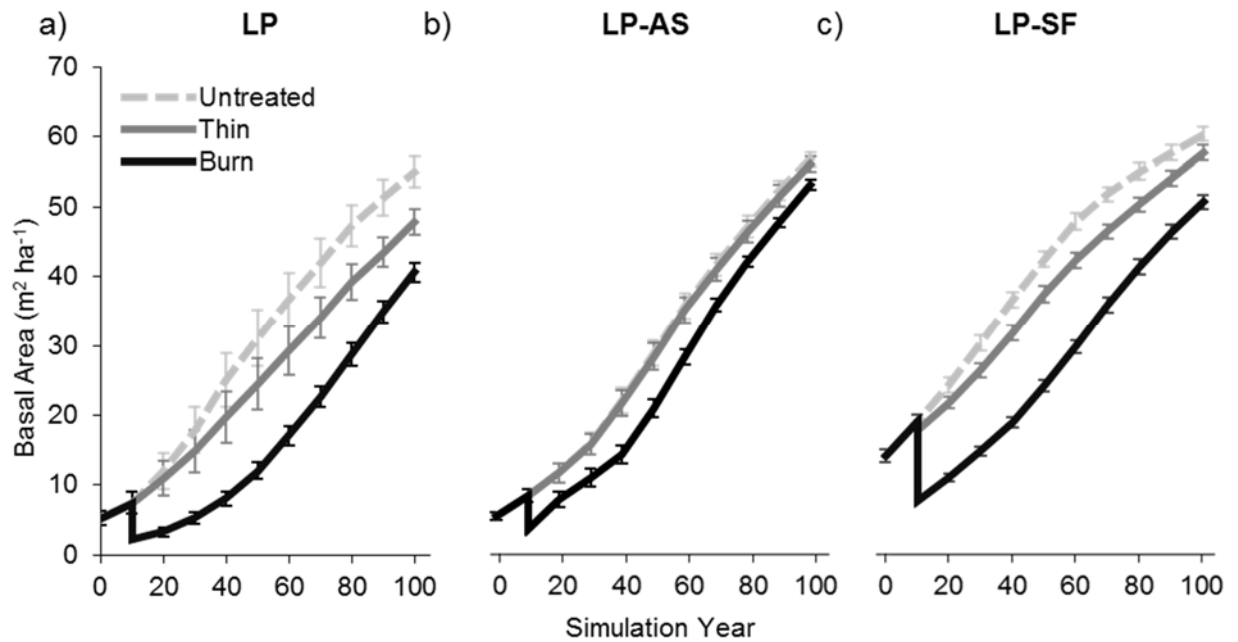


Figure 2. Live basal area (Mean \pm SE) after MPB in lodgepole pine (LP), lodgepole pine with aspen (LP-AS), and lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) forest types after Thin, Burn and Control treatments. Simulated treatments were implemented 10 years after the outbreak.

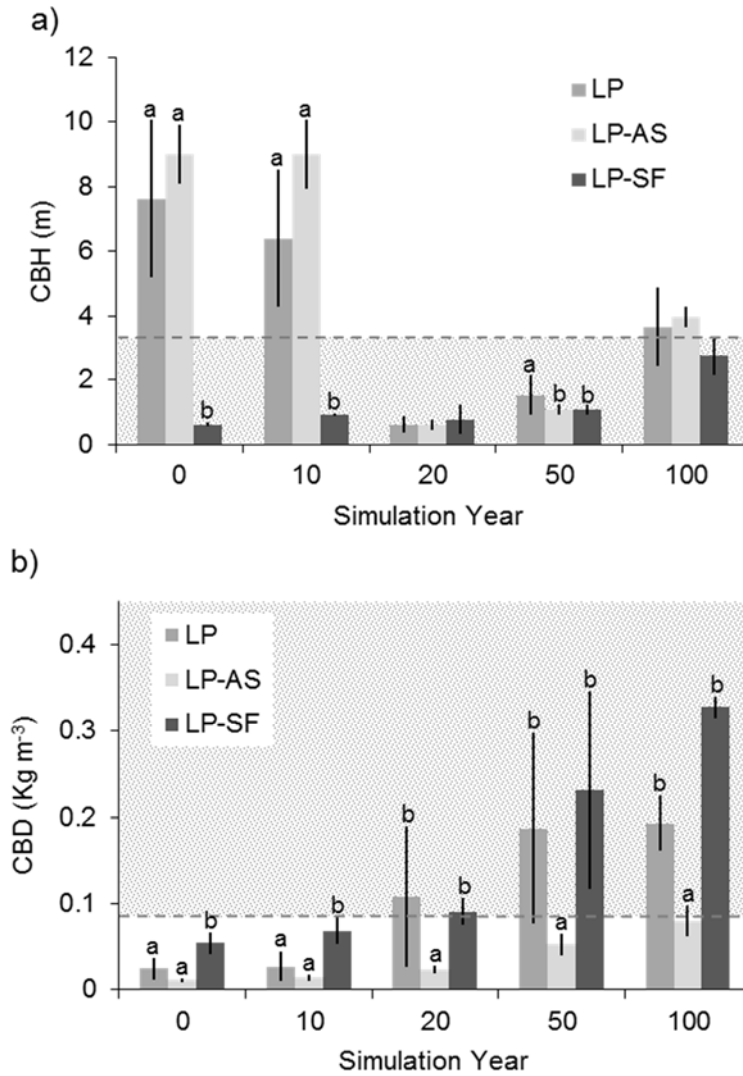


Figure 3. Canopy base height (CBH) and canopy bulk density (CBD) for lodgepole pine (LP), lodgepole pine with aspen (LP-AS) and lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) forest types 0, 10, 20, 50 and 100 years after MPB (medians \pm absolute deviations). Shaded areas denote where CBH and CBD violated hazardous fuel criteria. Letters indicate significant differences among forest types within a time period ($\alpha = 0.05$; Bonferroni adjusted).

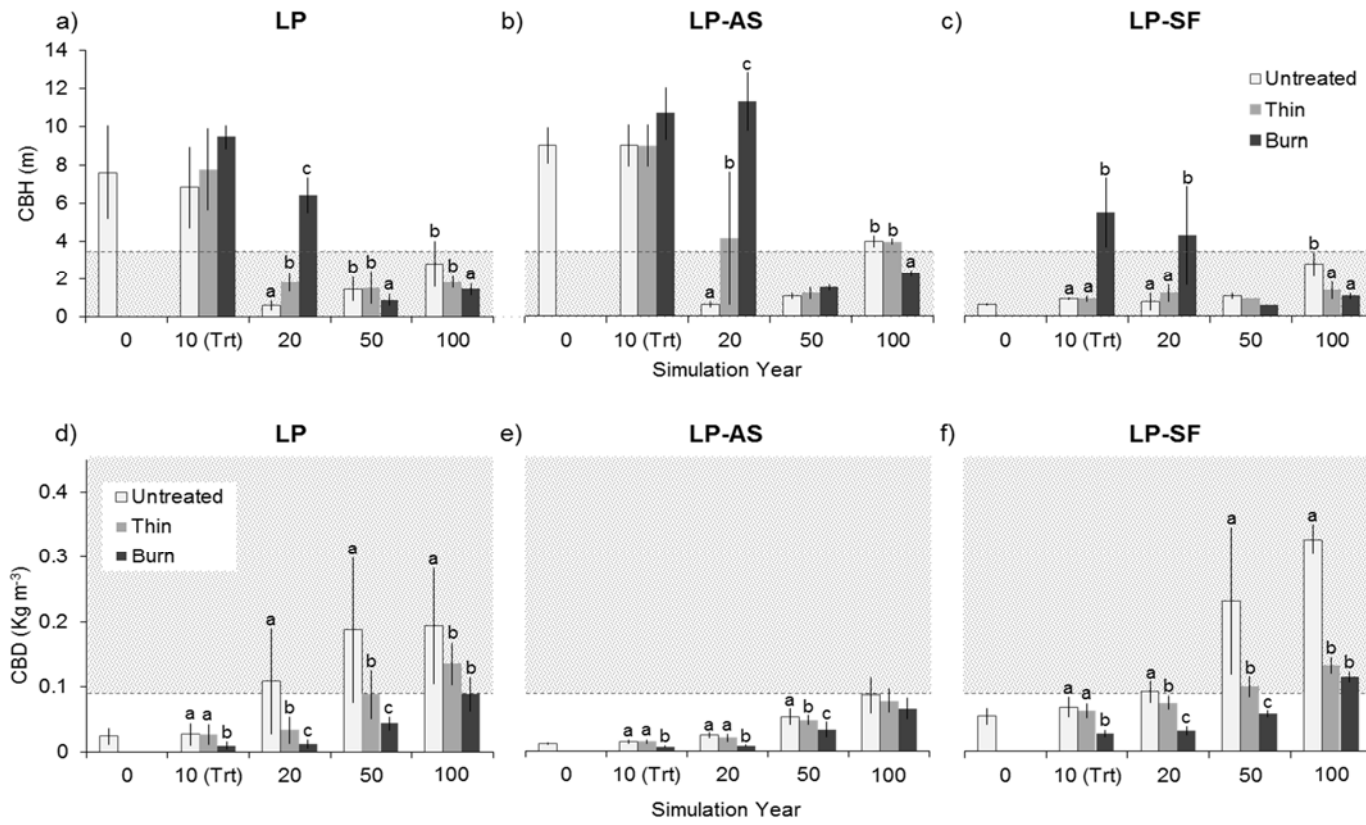


Figure 4. Canopy base height (CBH) and canopy bulk density (CBD) for lodgepole pine (LP), lodgepole pine with aspen (LP-AS) and lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) forest types after simulated Thin, Burn and Control treatments (medians \pm absolute deviations). Shaded areas denote where CBH and CBD violated hazardous fuel criteria. Letters indicate significant differences among forest types within a time period ($\alpha = 0.05$; Bonferroni adjusted). Simulated treatments were implemented 10 years after the outbreak.

Table 3. Surface fuel and snag loads (Mg ha⁻¹) with and without fuels reduction treatments for lodgepole pine (LP), lodgepole pine with aspen (LP-AS) and lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) forest types. For Untreated stands the ⁺ symbol indicates loads were significantly different among forest types within a time period. Subscript letters indicate significant differences among forest types within a time period ($\alpha = 0.05$; Bonferroni adjusted). Simulated treatments were implemented 10 years after the outbreak.

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Var.	Trt. Type	Simulation Year												
		0	10 (Treatment Year)			20			50			100		
		Untreated	Untreated	Thin	Burn	Untreated	Thin	Burn	Untreated	Thin	Burn	Untreated	Thin	Burn
Snag ⁺	LP	22.4 (5.8)	11.1 (3.0) ^a	11.1 (3.0) ^a	0.7 (0.5) ^b	0.9 (0.4)	0.7 (0.5)	0.7 (0.5)	0.22 (0.19)	0.13 (0.09)	0.04 (0.03)	3.8 (2.3) ^a	1.7 (0.5) ^b	0.8 (0.6) ^c
	LP-AS	39.3 (6.3) ⁺	19.9 (2.8) ^{+a}	19.9 (2.8) ^a	2.7 (1.1) ^b	2.8 (1.1) ⁺	2.8 (1.1)	2.7 (1.1)	0.19 (0.11)	0.17 (0.11)	0.05 (0.02)	1.6 (0.2) ^{+a}	1.6 (0.2) ^a	1.3 (0.2) ^b
	LP-SF	22.7 (7.8)	11.0 (5.3) ^a	11.0 (5.3) ^a	1.2 (0.9) ^b	0.9 (0.5)	0.5 (0.3)	1.1 (0.9)	2.05 (0.79) ⁺	0.25 (0.09)	0.13 (0.05)	5.9 (2.6) ^a	2.4 (0.7) ^b	1.3 (0.4) ^b
CWD ⁺	LP	10.5 (3.7)	41.5 (12.4) ^a	41.5 (12.4) ^a	19.1 (5.8) ^b	55.7 (12.7) ^a	55.7 (12.7) ^a	37.9 (11.4) ^b	46.8 (10.4) ^a	46.8 (11.1) ^a	32.7 (9.5) ^b	47.7 (8.5) ^a	44.2 (10.8) ^a	24.9 (6.2) ^b
	LP-AS	24.9 (6.1) ⁺	69.3 (10.1) ^{+a}	69.3 (10.1) ^a	35.0 (7.8) ^b	98.6 (20.6) ^{+a}	98.6 (12.6) ^a	69.5 (14.0) ^b	86.1 (18.4) ^{+a}	86.1 (18.3) ^a	60.8 (11.4) ^b	69.3 (11.3) ^a	69.2 (11.5) ^a	48.1 (6.5) ^b
	LP-SF	14.7 (3.6)	35.5 (11.4) ^a	35.5 (11.4) ^a	19.5 (6.5) ^b	52.4 (20.5)	52.4 (20.5)	44.6 (16.1)	44.9 (16.9)	44.7 (18.1)	38.7 (14.2)	52.5 (14.9) ^a	38.6 (9.3) ^b	30.6 (8.1) ^b
FWD ⁺	LP	6.4 (3.3)	6.1 (2.0) ^a	6.2 (2.0) ^a	3.5 (0.6) ^b	6.7 (1.3)	6.8 (1.4)	6.9 (2.2)	6.8 (2.8) ^a	4.7 (1.2) ^a	2.8 (1.2) ^b	13.0 (4.0) ^a	9.5 (1.4) ^b	6.6 (0.7) ^c
	LP-AS	5.9 (2.2)	8.2 (0.3) ^a	8.2 (0.3) ^a	2.3 (0.2) ^b	8.4 (1.3)	8.4 (1.3)	9.2 (1.9)	6.8 (2.1) ^a	6.7 (2.1) ^a	8.5 (2.2) ^b	18.7 (0.9) ^a	18.6 (0.7) ^a	21.6 (0.2) ^a
	LP-SF	8.1 (4.4)	8.9 (4.2) ^a	9.9 (4.2) ^a	3.9 (0.4) ^b	9.8 (3.4) ^a	10.0 (3.5) ^{ab}	11.9 (1.5) ^b	10.5 (2.7) ^a	7.7 (0.4) ^b	7.1 (1.4) ^b	21.2 (6.5) ^a	12.8 (0.9) ^b	11.6 (1.8) ^b
Litter ^{**}	LP	6.4 (2.8)	2.6 (1.5) ^a	2.8 (1.7) ^a	1.1 (0.8) ^b	3.6 (2.4) ^a	3.0 (2.3) ^a	0.9 (0.5) ^b	9.4 (4.7) ^a	7.2 (3.9) ^b	3.5 (1.0) ^c	15.6 (3.7) ^a	12.5 (1.5) ^b	11.3 (1.1) ^b
	LP-AS	7.1 (1.8)	3.2 (0.8) ^a	3.2 (0.8) ^a	1.2 (0.2) ^b	4.0 (1.4) ^a	3.9 (1.4) ^a	2.2 (0.7) ^b	9.9 (1.7) ^a	9.8 (1.8) ^a	7.8 (1.4) ^b	19.5 (1.5)	19.5 (1.5)	19.5 (1.1)
	LP-SF	9.0 (3.3)	5.9 (1.1) ^a	6.5 (1.2) ^a	2.5 (0.7) ^b	7.6 (1.3) ^a	6.1 (1.0) ^b	2.9 (0.4) ^c	13.3 (2.6) ^a	9.6 (1.2) ^b	7.0 (0.7) ^c	18.1 (2.3) ^a	14.3 (1.7) ^b	14.3 (1.5) ^b
Duff ^{**}	LP	20.7 (9.3)	20.8 (9.3) ^a	20.8 (9.3) ^a	9.1 (4.1) ^b	20.9 (9.2) ^a	20.9 (9.2) ^a	9.2 (4.0) ^b	21.6 (9.0) ^a	21.4 (9.0) ^a	9.5 (4.0) ^b	24.3 (8.8) ^a	23.4 (8.6) ^a	11.2 (4.0) ^b
	LP-AS	26.2 (11.8)	26.3 (11.7) ^a	26.3 (11.7) ^a	11.5 (5.1) ^b	26.4 (11.6) ^a	26.4 (11.6) ^a	11.6 (5.1) ^b	27.1 (11.2) ^a	27.1 (11.2) ^a	12.5 (4.9) ^b	30.5 (10.7) ^a	30.5 (10.7) ^a	16.2 (4.8) ^b
	LP-SF	27.4 (9.9)	27.6 (9.8) ^a	27.6 (9.8) ^a	12.1 (4.3) ^b	27.8 (9.8) ^a	27.8 (9.8) ^a	12.3 (4.3) ^b	29.0 (9.7) ^a	28.6 (9.6) ^a	13.0 (4.2) ^b	32.4 (9.7) ^a	30.9 (9.3) ^a	15.6 (4.0) ^b

⁺Medians (median absolute deviation) shown for coarse woody debris (CWD), snag, and fine woody debris (FWD) loads, which were analyzed with a lognormal distribution.

^{**}Means (standard error) shown for litter and duff loads, which were analyzed with a normal distribution.

Table 4. Percent of post-MPB stands that met canopy base height (CBH), canopy bulk density (CBD), and coarse woody debris (CWD) hazardous fuel criteria (see Table 2) with and without fuels reduction treatments (Unshaded = 75 – 100%; Light Grey = 50 – 75%; Dark Grey = < 50% of stands met criteria). Percents are underlined when Thin or Burn treatment changed the proportion of stands to meet the hazardous fuel criteria.

<i>Trt</i>	<i>Criteria:</i> <i>Type</i>	Treatment Year														
		0			10 (Trt year)			20			50			100		
		<i>CBH</i>	<i>CBD</i>	<i>CWD</i>	<i>CBH</i>	<i>CBD</i>	<i>CWD</i>	<i>CBH</i>	<i>CBD</i>	<i>CWD</i>	<i>CBH</i>	<i>CBD</i>	<i>CWD</i>	<i>CBH</i>	<i>CBD</i>	<i>CWD</i>
		----- % -----														
Untreated (Control)	LP	64	100	45	100	100	55	0	45	64	0	36	82	55	0	82
	LP-AS	100	100	0	100	100	0	38	100	13	0	100	25	88	50	38
	LP-SF	0	100	40	0	80	50	0	30	60	0	0	70	10	0	60
Thin	LP	-	-	-	100	100	55	<u>36</u>	<u>82</u>	64	0	<u>45</u>	82	<u>27</u>	<u>18</u>	<u>91</u>
	LP-AS	-	-	-	100	100	0	<u>50</u>	100	13	0	100	25	88	<u>63</u>	38
	LP-SF	-	-	-	0	<u>100</u>	50	0	<u>80</u>	<u>50</u>	0	<u>30</u>	70	<u>20</u>	0	<u>100</u>
Burn	LP	-	-	-	100	100	<u>82</u>	<u>82</u>	<u>100</u>	<u>91</u>	0	<u>91</u>	<u>91</u>	0	<u>45</u>	<u>73*</u>
	LP-AS	-	-	-	100	100	<u>25</u>	<u>100</u>	100	<u>38</u>	<u>13</u>	100	<u>75</u>	<u>25</u>	<u>75</u>	<u>87</u>
	LP-SF	-	-	-	<u>90</u>	<u>100</u>	<u>60</u>	<u>60</u>	<u>100</u>	<u>80</u>	<u>10</u>	<u>100</u>	<u>90</u>	10	<u>10</u>	<u>100</u>

*In the LP stands in year 100, criteria was not met in 100% of stands only because loads were too low (below 22 Mg ha⁻¹).

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CHAPTER 3

EFFECTS OF STAND STRUCTURE, BROWSING AND SITE VARIABLES ON REGENERATION OF LODGEPOLE PINE AND ASPEN ACROSS MOUNTAIN PINE BEETLE-AFFECTED FORESTS OF NORTH-CENTRAL COLORADO

SUMMARY

Aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta* var. *latifolia*) co-occur in the Southern Rockies, where mountain pine beetle (*Dendroctonus ponderosae*) has caused extensive lodgepole pine mortality since the late 1990s. Both species excel in post-disturbance high light environments, but it is uncertain how these stands will develop following overstory loss that does not disturb the forest floor or overstory aspen. I ask whether lodgepole pine and aspen will regenerate in sufficient quantity to revegetate these forest stands. I visited a random sample of aspen and lodgepole stands ($n = 33$) across northern Colorado and southern Wyoming to measure regeneration and overstory mortality. Lodgepole regeneration is occurring in 85% of stands, and most stands have > 550 stems ha^{-1} . All but one stand had aspen sucker densities above 1250 stems ha^{-1} . Surprisingly, neither lodgepole nor aspen regeneration density was related to overstory mortality level. Animal damage is currently affecting aspen in these forests. Over 50% of stands had damage to 60% or more of suckers, but 30% of stands had $< 20\%$ of stems damaged. Browsed stems were significantly shorter for their ages, and were all shorter than the 2.5 m height threshold for elk browsing. However, the results suggest that sufficient quantities of down lodgepole pine may protect aspen from damage and allow it to successfully

recruit to the overstory. Multiple regression analysis showed that down lodgepole basal area, followed by browsing pressure, were the most important predictors of sucker height (mean and maximum) and proportion of suckers browsed. Overall, I conclude these forests are regenerating successfully despite animal browsing and that they will remain mixed forests of both species in future decades.

INTRODUCTION

Both lodgepole pine (*Pinus contorta* var. *latifolia*) and aspen (*Populus tremuloides*) are known to regenerate and dominate stands following disturbances such as wildfire and clearcut logging (Lotan and Perry, 1983; Crouch, 1983; Perala, 1990). Both species are extremely shade-intolerant and grow quickly in open environments. Where high mountain pine beetle-caused (MPB) (*Dendroctonus ponderosae*) mortality of lodgepole pine has occurred overstory density is substantially reduced, which may provide enough light for successful regeneration of both species. However, since lodgepole pine is thought to need bare mineral soil for seedling establishment (Lotan and Perry, 1983), its regeneration may be limited because of lack of ground disturbance. Aspen regeneration may also require more than just light: suckering is often triggered hormonally by death of overstory aspen, while MPB only kills pine (Frey et al., 2003). It is uncertain how these species will respond to post-outbreak conditions in northern Colorado, where mixed lodgepole and aspen stands cover over 250,000 acres (Woudenberg et al., 2010). I ask whether lodgepole pine and/or aspen will regenerate in sufficient quantity to revegetate these forest stands.

Following MPB, seed availability and or lack of mineral soil substrate may limit lodgepole pine regeneration despite high light availability. Lack of seed could limit regeneration,

though research indicates this is unlikely (Teste et al., 2011). Although lodgepole may have serotinous cones that remain closed until opened by heat (keeping seed from the forest floor until fire), non-serotinous cones are usually present in stands (Tinker et al., 1994), and even closed cones open following tree mortality. Viable seed from dead trees falls for > 9 years after outbreak (Teste et al., 2011). Lack of mineral soil seedbed is a more likely limit to lodgepole regeneration (Lotan and Perry, 1983; Astrup et al. 2008; Teste et al., 2011). It is also possible that evidence of lodgepole recruitment may not be apparent due to the short time since outbreak. Lodgepole recruitment may not begin until understory light increases following needle fall, as long as 10 years after initial mortality (Amoroso et al., 2013).

Aspen suckers prolifically following stand-replacing disturbances, but may not following MPB-caused mortality. Aspen sucker densities often exceed 10,000 stems ha⁻¹, and can exceed 1,000,000 stems ha⁻¹, following clearfell harvests and stand-replacing fires (Crouch, 1983; Shepperd, 1993; Smith et al., 2011). However, suckering response is strongly related to mortality of overstory aspen due to loss of aboveground sucker-suppressing auxin production and subsequent transport to roots (Farmer, 1962; Frey et al., 2003). It is not clear if mortality of lodgepole pine will trigger a large increase in sucker density. In many intact stands, however, sucker densities are often around 2,500 ha⁻¹ (Crouch, 1983) which may be sufficient to regenerate the stand. Although this density is much lower than is common after stand-replacing disturbances, Bartos and Campbell (1998) suggest 1250 stems ha⁻¹ are adequate to regenerate an aspen forest.

Regardless of MPB effect on sucker density, decline in aspen health could reduce aspen regeneration capacity. Widespread aspen mortality in the Southern Rockies, first observed in 2004, coincided with the recent MPB epidemic and drought. Early signs of this dieback,

sometimes called “sudden aspen decline”, were partial canopy mortality and small, chlorotic leaves, eventually leading to tree mortality across > 200,000 ha in Colorado. This overstory loss was accompanied by root mortality and lack of new regeneration (Worrall et al., 2010). Onset of dieback was largely caused by drought and site factors associated with moisture stress, such as slope position, and low annual precipitation and high temperatures (Rehfeldt et al., 2009; Worrall et al. 2013). Reduced vigor and regeneration capacity of aspen due to drought-related decline may reduce clones ability to respond to overstory loss due to mountain pine beetle.

Where suckering does occur, factors that limit growth of aspen and recruitment to the overstory will determine if aspen becomes a major part of the future forest. Light is a major determinant of growth; even minor shading has substantial effects on growth rates and aspen often die under > 50% canopy cover (Huffman et al., 1999). Where high MPB-caused mortality occurs and few live trees remain, large canopy gaps may provide high light conditions favoring fast aspen growth (e.g., Groot et al., 2009; Calder et al., 2011). Regardless, browsing could preclude aspen recruitment. Aspen stems are often damaged by wild ungulates, such as elk (*Cervus canadensis*) and deer (*Odocoileus* spp.), and by domestic livestock. Studies have shown that aspen recruitment is unlikely when animals remove $\geq 40\%$ of each stem’s annual growth (Ripple and Beshta 2007; Zeigenfuss et al., 2008). There is evidence that this may be occurring in forests affected by the recent MPB outbreak. In Rocky Mountain National Park where ungulate densities are extremely high, approximately 75% of suckers under MPB-affected canopies were browsed in 2007 (Nelson, 2009). Suckers were fewer, if not gone entirely, when plots were re-surveyed three years later (Renwick, 2012). Variation in animal numbers and management across the landscape, or stand conditions that reduce animal use, may result in lowered browsing pressure and better recruitment in some areas. For example, following a 1970s

spruce beetle outbreak in Utah, aspen only successfully recruited in areas with rocky lava substrate that were not used by domestic cattle (DeRose and Long, 2010).

Forests of mixed lodgepole and aspen cover a large portion of the area affected by recent MPB-mortality. But, we are not certain that lodgepole pine will regenerate at sufficient densities to regenerate forests without ground disturbance. It has been assumed that aspen will increase in abundance (e.g., Kaufmann et al., 2008; Diskin et al., 2011), but it may not sucker prolifically while aspen overstories remain intact. Poor aspen health and/or browsing could also reduce aspen response. So, how will mixed aspen and lodgepole pine forests develop following mountain pine beetle? In this study I ask if lodgepole pine and aspen are regenerating at sufficient densities to restock these forests across northern Colorado and central Wyoming. I measured regeneration and overstory mortality in stands across this area. I expected that with increased MPB-caused mortality, there would be higher aspen and lodgepole density due to the greater light reaching the forest floor. I also ask if ungulate browsing will reduce aspen sucker density and height growth. I measured sucker density, damage, and height, compared these values to cattle grazing and wild animal densities to assess animals effects on recruitment.

METHODS

Study area

The study area included north-central Colorado and southern Wyoming (between 39.6 and 41.0°N and 106.0 and 106.7°W). Lodgepole pine and aspen dominate forested areas at lower elevations and on southern aspects, with increasing Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*) at higher elevations and northern aspects. The area has a continental climate and the majority of precipitation falls as winter snow, with much

of the remainder in falling during thunderstorms beginning in mid-summer (Doesken et al., 2003).

Site selections

Forest stands with > 5 and $< 40 \text{ m}^2 \text{ ha}^{-1}$ aspen and lodgepole pine basal area ($n = 691$) were identified from inventory data from the Medicine Bow-Routt, Arapaho, Roosevelt, and White River National Forests. From these stands, I chose those with $10 - 15 \text{ m}^2 \text{ ha}^{-1}$ aspen basal area and $< 5 \text{ m}^2 \text{ ha}^{-1}$ basal area of non-lodgepole conifers. These stands were stratified into 3 groups based on pre-MPB lodgepole pine basal area: stands with $10 - 20$, $20 - 30$ and $30 - 40 \text{ m}^2 \text{ ha}^{-1}$. I randomly chose a set of stands from each group for sampling. They were visited in the field to ensure that no harvest had occurred and that inventory data was correct. Thirty-three stands were selected for sampling. Average precipitation at the study stands was approximately 560 mm annually, with a range from 400 to 730 mm (PRISM Climate Group).

Field data collection

Four to six plot centers, 50 m apart, were installed on a grid in each stand at the end of the growing season. Basal area of overstory trees ($> 2.5 \text{ cm dbh}$) by species was recorded at each plot using a $4.6 \text{ m}^2 \text{ ha}^{-1}$ prism in a variable-radius plot. Tree status (live, dead, and beetle-killed) was recorded for each overstory tree. Tree seedlings/suckers ($< 2.5 \text{ cm dbh}$) were tallied by height class in 3.6 m radius plots. Damage to aspen suckers was recorded. Two aspen suckers in each size class were measured for height and aged to establish an age-height relationship. Aspect and slope, and GPS location were recorded at each plot. I identified the approximate year of onset of epidemic MPB activity in each stand using Forest Service aerial detection survey data from 1996 – 2012 (U.S.D.A. Forest Service 2013). Widespread MPB-caused mortality began between 2001 and 2006 in all stands.

Animal use information

Many public lands in the study area are leased for cattle grazing, and all areas are used by wild ungulates. I obtained information about the grazing activity (Yes or No) in the year of sampling at all sites (2012 for 9 stands, 2013 for 24 stands) from Forest Service range management staff. I calculated wild animal density from Colorado Department of Wildlife data. I obtained elk and deer population estimates at the finest scale possible, either at the Data Analysis Unit (DAU) or Game Management Unit (GMU). Elk and mule deer densities were converted to animal unit equivalents (AUE), using a factor of 0.2 for mule deer and 0.6 for elk (U.S.D.A. Natural Resources Conservation Service, 2003). I standardized animal numbers by the hectares of summer habitat in each GMU or DAU.

Topographic and landform data

Aspect and slope were recorded at each plot, and averaged to the stand level. I obtained elevation values for each plot from a digital elevation model (DEM) from the National Elevation Dataset (U.S. Geological Survey, 2009). I also derived a Topographic Wetness Index (*TWI*) from the DEM with the equation $TWI = \ln (As / \tan \beta)$, where *As* is the cumulative upslope area that drains through the cell, divided by the contour width, and β is the slope (Bevin and Kirkby, 1979). *TWI* has a long record of use in hydrology and has been used extensively in studies of vegetation occurrence and density in the past decade (e.g., Franklin, 2002; Parolo et al., 2008; Evans and Cushman, 2009; Dirnbock et al., 2002; Bader and Ruijten, 2008).

Statistical analysis

Tree basal area ($\text{m}^2 \text{ha}^{-1}$), regeneration density (stems ha^{-1}), mean sucker height (cm), plot maximum sucker height (cm), and proportion of suckers browsed were summarized at the stand level. I first did a Spearman's rank correlation test to determine if relationships existed between

regeneration density or height (aspen sucker density, lodgepole pine density, sucker mean height, sucker maximum height) and independent variables (pre-MPB live basal area [$\text{m}^2 \text{ha}^{-1}$], basal area killed by MPB [$\text{m}^2 \text{ha}^{-1}$], live aspen basal area [$\text{m}^2 \text{ha}^{-1}$], dead and down aspen basal area [$\text{m}^2 \text{ha}^{-1}$], down lodgepole pine basal area [$\text{m}^2 \text{ha}^{-1}$], time since onset of MPB epidemic [years], slope [percent], aspect, average annual precipitation [cm], average annual maximum temperature [$^{\circ}\text{C}$], Topographic Wetness Index, grazing status [Yes or No], and wild animal density [AUE ha^{-1} summer habitat]; all averaged to stand level). I also used a Spearman's rank correlation to assess the relationship between proportion of suckers browsed with the independent variables I hypothesized would affect animal activity (basal area killed by MPB, live aspen basal area, down lodgepole pine basal area, slope, domestic grazing status, and wild ungulate density). Where significant ($\alpha = 0.1$) correlations were identified, I performed a more conservative univariate linear regression analysis for continuous variables. Dependent and independent variables were transformed, if necessary, to meet the assumptions of normality. Observations with high leverage (Cook's $D > 0.5$) were removed. I tested the effect of grazing status, a categorical variable (Grazed in year of sampling: Yes or No), on aspen sucker mean height, maximum height, and proportion of suckers browsed with an ANOVA.

I then used Akaike's Information Criterion adjusted for small sample size (AIC_c) to select the most parsimonious multivariate model to explain each of the four dependent variables (Burnham and Anderson, 1998). I built models stepwise, with $\alpha = 0.1$ threshold for leaving or entering the model, by adding all independent variables with significant univariate regression relationships or ANOVAs, starting from greatest to least adjusted R^2 . When stepwise selection kept multiple variables in the model, I added terms for the interactions among independent

variables. Models were assessed for colinearity of predictor variables; no violations were found (Burnham and Anderson, 1998).

RESULTS

Live and dead basal area was highly variable in sampled stands (Table 1). All stands had dead lodgepole pine and some amount of live aspen. There was a median of $7.6 \text{ m}^2 \text{ ha}^{-1}$ live basal area (median values reported unless indicated otherwise), approximately half in aspen and half in lodgepole pine. Standing dead MPB-killed lodgepole basal area ranged from 3.3 to $34.8 \text{ m}^2 \text{ ha}^{-1}$, with a median of $21.8 \text{ m}^2 \text{ ha}^{-1}$. Seventy percent of stands had fallen MPB-killed trees. Dead aspen was present in all but 4 stands, with $2.2 \text{ m}^2 \text{ ha}^{-1}$ standing and $2.2 \text{ m}^2 \text{ ha}^{-1}$ down. Fir and/or spruce overstory was present in only 6 of the 33 stands, with no more than $2.2 \text{ m}^2 \text{ ha}^{-1}$ in any stand.

Understory (trees $< 2.5 \text{ cm dbh}$) density of aspen and lodgepole pine was high in most stands, with median stem densities of 556 ha^{-1} pine and $> 6000 \text{ ha}^{-1}$ aspen (Table 1). Aspen and lodgepole understory density was highly variable among stands and size classes. Aspen understory density ranged from $1,167$ to over $27,000 \text{ ha}^{-1}$ (Table 1). Two-thirds of stands had sucker densities between $3,000$ - $10,000 \text{ stems ha}^{-1}$; five stands had densities $< 3,000 \text{ stems ha}^{-1}$ and six had $> 10,000 \text{ stems ha}^{-1}$. Unbrowsed aspen stem densities were relatively evenly distributed across the size classes, while browsed aspen stems were mostly 0.25 to 1 m tall (Figure 1). Five stands had no lodgepole pine understory, three stands had $< 250 \text{ stems ha}^{-1}$, but 21 stands had $250 - 2,000 \text{ stems ha}^{-1}$ and 4 stands had $> 2000 \text{ stems ha}^{-1}$ (Table 1). Lodgepole pine understory was mostly $\leq 1 \text{ m}$ tall (Figure 1). Fir and spruce understory densities were below $100 \text{ stems ha}^{-1}$ in the majority of stands, but 6 stands had $1,000 - 3,600 \text{ ha}^{-1}$.

Proportion of aspen suckers browsed in each stand varied widely. Less than 20% of suckers were browsed in 30% of sampled stands (Figure 2). However, browse rates were between 60 – 100% in the majority (60%) of stands. The age-height relationship of sampled aspen shows that browsing damage had an effect on height of aspen stems (Figure 3). Unbrowsed stems were significantly taller for their age than browsed aspen stems.

Spearman's rank correlation tests identified several potential predictor variables for regression analysis. There were significant ($\alpha = 0.1$) correlations among regeneration variables (regeneration density [mean aspen density, lodgepole density] and aspen height [mean sucker height, maximum sucker height]) and all variables listed in Table 2. Proportion of suckers browsed was related to all variables shown in Table 3. MPB-killed basal area was not related to aspen sucker density ($r_s = -0.17, P = 0.36$) or lodgepole regeneration density ($r_s = 0.25, P = 0.16$). MPB-killed basal area had mixed relationships with sucker heights and proportions of suckers browsed. It had no relationship to aspen sucker mean height ($r_s = -0.22, P = 0.21$), but was negatively related to maximum height ($r_s = -0.31, P = 0.07$), and more strongly related to proportion of suckers browsed ($r_s = 0.36, P = 0.04$).

Down lodgepole pine basal area, maximum temperature, precipitation, and wild animal density had the strongest correlations with aspen regeneration density and height variables. Regression analysis showed that down lodgepole pine basal area had a substantial positive relationship with mean (*Adj. R*² = 0.49) and maximum sucker height (*Adj. R*² = 0.39) (Table 2). Mean and maximum aspen heights were also related to maximum temperature, wild animal density, and precipitation, which all had adjusted *R*² > 0.15. The relationship between aspen height and temperature was positive, while the relationship with wild animal density and precipitation was negative (Table 2). Down basal area was the strongest predictor of aspen

density, but had a weaker positive relationship ($R^2 = 0.23$) with aspen density than with aspen height. Aspen density was negatively related to maximum temperature ($Adj. R^2 = 0.20$). Lodgepole pine density was somewhat positively related to live lodgepole pine density ($Adj. R^2 = 0.23$), and weakly positively related to *TWI* ($Adj. R^2 = 0.11$) (Table 2).

In the initial Spearman's rank correlation test to screen for potential predictor variables, proportion of suckers browsed was negatively correlated with down lodgepole pine and live aspen basal area, and positively correlated with wild animal density and MPB-killed basal area ($P < 0.05$ for all). Regression analysis showed that down lodgepole pine basal area had a strong negative relationship with proportion of suckers browsed ($Adj. R^2 = 0.46$, $P < 0.01$), a moderate positive relationship with MPB-killed basal area ($Adj. R^2 = 0.25$, $P < 0.01$), and a relatively weak relationship with wild animal density ($Adj. R^2 = 0.16$, $P = 0.01$). Live aspen basal area had no effect on browsing rate ($Adj. R^2 = -0.03$, $P = 0.94$) (Table 3).

Cattle grazing had significant effects on mean height, maximum height, and proportion of suckers browsed (Table 4). The effect of grazing was clearest on maximum sucker height, with average maximum heights around 230 cm in ungrazed stands but only 150 cm in grazed stands. Effects of grazing on mean height and proportion of suckers browsed were smaller, and the significance of effects less certain (P values were < 0.1 but > 0.05).

Multivariate model selection showed that one to three variables were the most important predictors of regeneration density, height, or proportion of suckers browsed (Table 5). The model predicting mean aspen sucker density included down lodgepole basal area and live aspen basal area, but was only moderate in strength, with an adjusted R^2 of 0.29. Lodgepole regeneration density was explained best by live lodgepole pine basal area alone, and this relationship was only moderately strong ($Adj. R^2 = 0.23$). Mean and maximum sucker height, and proportion of suckers

browsed, were best predicted by models that included down lodgepole pine basal area and wild animal density. Of the three, mean height had the strongest model (greatest *Adj. R*² [0.54] and lowest *AIC*_C [9.27]). Proportion of suckers browsed also had a strong model, with an adjusted *R*² of 0.50. Maximum sucker height had two models with nearly equivalent *AIC*_C values. Both included down lodgepole and wild animal density, and one included *TWI*.

DISCUSSION

Mixed lodgepole and aspen forests affected by MPB are regenerating successfully and will remain mixed forests of both species in the future. Lodgepole regeneration is occurring in 85% of stands, with densities above 550 stems ha⁻¹ in the majority. Lodgepole densities will increase further if recruitment continues for the next few years which is likely (e.g., Amoroso et al., 2013). Aspen regeneration is occurring, and, like lodgepole regeneration, was not related to overstory mortality level. All but one stand had sucker densities above the 1250 stems ha⁻¹ threshold for aspen stand regeneration suggested by Bartos and Campbell (1998). Sucker densities were not as high as would be expected following stand replacing disturbances (fire, clearcut), and not much above sucker densities reported from intact aspen stands (e.g., Crouch, 1983; Binkley, 2008). The moderate suckering response and lack of relationship between density and MPB-caused mortality level suggests that MPB may facilitate recruitment primarily through increase in light that can enhance sucker survival and growth rather than increasing suckering rates.

Forest mortality and basal area had little effect on regeneration. Contrary to my expectations, neither lodgepole pine nor aspen regeneration density was related to MPB-killed basal area. Time since onset of outbreak-level MPB mortality was also not related to

regeneration density or height. Down lodgepole pine basal area was the only forest structure variable with a major influence on aspen density or height. This relationship was strongest (*Adj. R*² = 0.49) for mean aspen sucker height and proportion of aspen suckers browsed (*Adj. R*² = 0.46).

Damage by ungulates is affecting aspen. Wild animal density was the second most important factor affecting aspen height and proportion of suckers browsed, as shown by its inclusion in the final multivariate models. Browsed suckers were not taller than 2.6 m, suggesting that elk were limiting their maximum height. Elk are thought to be able to browse stems up to 2.5 m tall (Romme et al., 1995). In stands grazed by cattle, stems were much shorter: maximum sucker heights were on average 152 cm, near the maximum height of cattle browse. However, the results suggest wild browsing had a more important effect overall since grazing was not included as a term in the final models (Table 5).

My results indicate there is more aspen browsing in areas with greater MPB-caused mortality, but less browsing after trees fall. Proportion of suckers browsed increased somewhat with mortality level, but decreased strongly with down lodgepole pine. Other studies show animal use intensifies with forest mortality level (Relva et al., 2009), perhaps due to increased understory production and nutrition of forage (Griffin and Turner, 2012; Stone and Wolfe, 1996). However, the importance of down lodgepole pine basal area in the height and proportion browsed models suggests that beetle-killed trees, once fallen, are providing protection to aspen suckers. Protection by down logs has also been reported elsewhere (Ripple and Larson, 2001; de Chantal and Granstrom, 2007; Seager, 2010). Some studies suggest that this protection may not be enough to allow stem recruitment to the overstory in very high browsing intensity situations or where aspen is rare on the landscape (Forester et al., 2007; Romme et al., 1995). However, the

extensiveness of MPB disturbance, and of aspen presence, in north-central Colorado may be enough to reduce overall browsing pressure on suckers (e.g., Smith et al., 2011). Although browsing affected aspen regeneration height, it may be unlikely to limit recruitment across the MPB-affected landscape.

Aspen density and height did have relationships with climate and site variables, though these were much less important secondary to the effects of stand structure and browsing. Climate variables were not a factor in the final multivariate regression models. In the univariate models, maximum temperature was negatively related to aspen density but positively related to height, while precipitation was positively related to aspen density but negatively related to height. The different directions of the relationships of these variables to density and height were surprising but not entirely unsupported. The increase in aspen height with temperature makes sense since growth is strongly related to temperature (Frey et al., 2003; Heineman et al. 2010). Lower sucker density with higher temperatures could be due to climate-related aspen decline, root mortality, and reduced regeneration capacity (Rehfeldt et al., 2009; Worrall et al. 2013). Similarly, it is possible aspen density may have declined with moisture since drought is tied to aspen decline (Rehfeldt et al., 2009; Worrall et al. 2013). Although I expected aspen growth to increase with average precipitation, in fact it declined. A plausible reason could be that waterlogged soils can reduce growth and make aspen more susceptible to pathogens (Perala, 1990; Bates et al., 1990; Dudley, 2010). However, the reduced growth with soil moisture could be due to the negative correlation between precipitation and temperature along an elevation gradient in the Southern Rockies, and decreasing temperatures were related to decreased height. Overall, I suggest these relationships between climate variables and regeneration be interpreted cautiously since they were not included in the final models.

Despite the abundance of new recruits of both aspen and lodgepole in most areas, regeneration may be a problem in a small portion of forest surveyed. Five (15%) of the stands had no lodgepole regeneration present though aspen suckers were sufficiently high to regenerate an aspen stand. Understories in these sites were dominated by dense grass and sedge cover, which has been tied to low lodgepole pine seedling recruitment (Stahelin 1943; Schmautz and Williams, 1967; Lotan and Perry, 1983). I did not rigorously measure forest floor cover so further work is necessary to confirm its effect on lodgepole regeneration in post-beetle forests. Heavy browsing damage in many areas is also cause for concern. Twelve percent of the stands had browsing damage to > 80% of aspen stems, and 39% had damage to 60 – 80% of aspen stems. These areas may have little aspen recruitment in these areas if trees do not fall before sucker mortality occurs, or if fallen tree density is insufficient to provide a barrier to animal use.

CONCLUSION

Throughout the area most affected by MPB in the Southern Rockies, lodgepole and aspen are regenerating. Although 15% of the stands had no lodgepole regeneration, in most stands suitable lodgepole pine stocking is already present, and regeneration densities are likely to increase for a decade or more following MPB (Amaroso et al., 2013). Ninety-seven percent of sampled stands had regeneration exceeding the suggested 1250 suckers ha⁻¹ threshold for successful aspen stand recruitment (Bartos and Campbell, 1998), and most had 6000 or greater stems ha⁻¹. Although browsing is currently reducing aspen height, the results suggest ongoing fall of MPB-killed snags will protect many suckers and allow successful overstory recruitment. This study is the first to present a regional perspective on regeneration in MPB-affected

lodgepole pine and aspen forests, and overall, intervention does not seem necessary to ensure a mix of both species in the future.

TABLES AND FIGURES

Table 1. Summary of basal area and understory tree density in sampled stands (n = 33).

		Median	Minimum	Maximum
		----- <i>Basal area m² ha⁻¹</i> -----		
LIVE		7.6	1.1	37.0
	Pine	3.3	0.0	22.9
	Aspen	2.2	1.1	14.2
	Fir + Spruce	0.0	0.0	2.2
DEAD		21.8	4.4	34.8
	Pine <i>Standing</i>	20.7	3.3	34.8
	<i>Down</i>	3.3	0.0	24.0
	Aspen <i>Standing</i>	2.2	0.0	10.5
	<i>Down</i>	2.2	0.0	13.1
	Fir + Spruce <i>Standing</i>	0.0	0.0	0.9
	<i>Down</i>	0.0	0.0	0.0
		----- <i>Density ha⁻¹</i> -----		
UNDERSTORY (Stems < 2.5 cm dbh)				
	Pine	556	0	7040
	Aspen	6175	1167	26861
	Fir + Spruce	62	0	3520

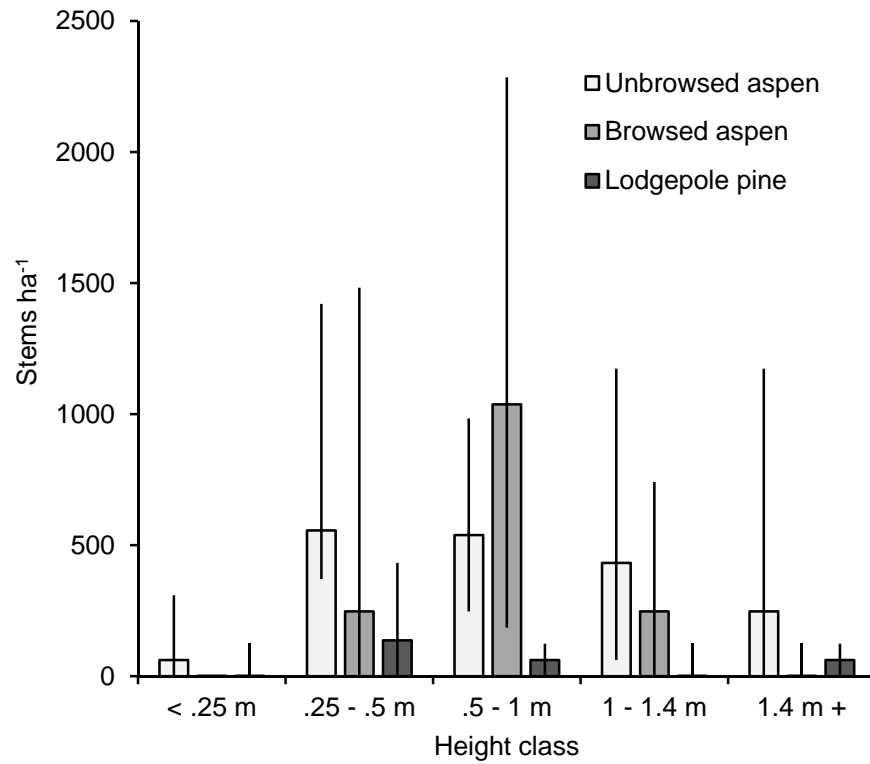


Figure 1. Understory stem density for unbrowsed aspen, browsed aspen, and lodgepole pine in sampled stands. Bars show medians; whiskers show 1st to 3rd quartile range. Data include all stems up to 2.5 cm diameter at breast height.

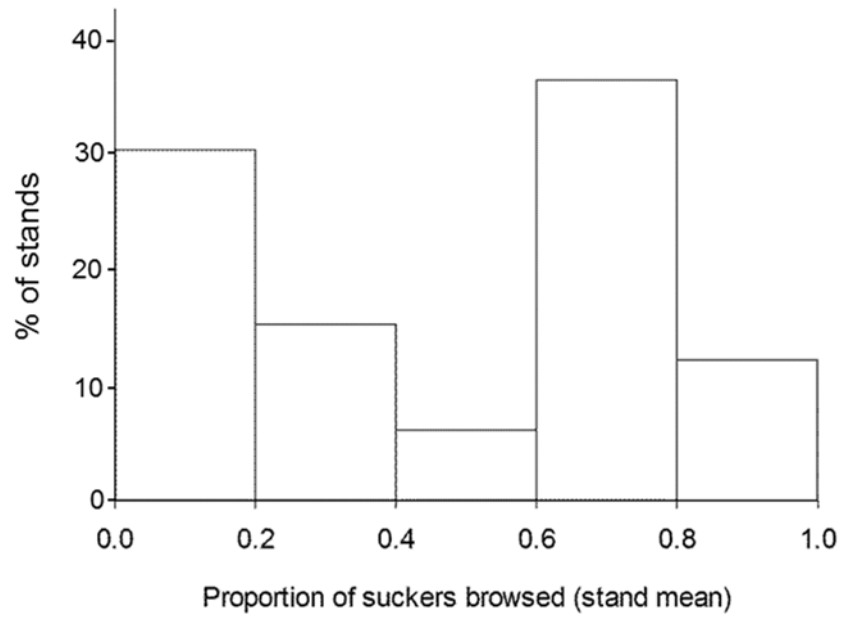


Figure 2. Distribution of proportion of suckers browsed across stands (n = 33).

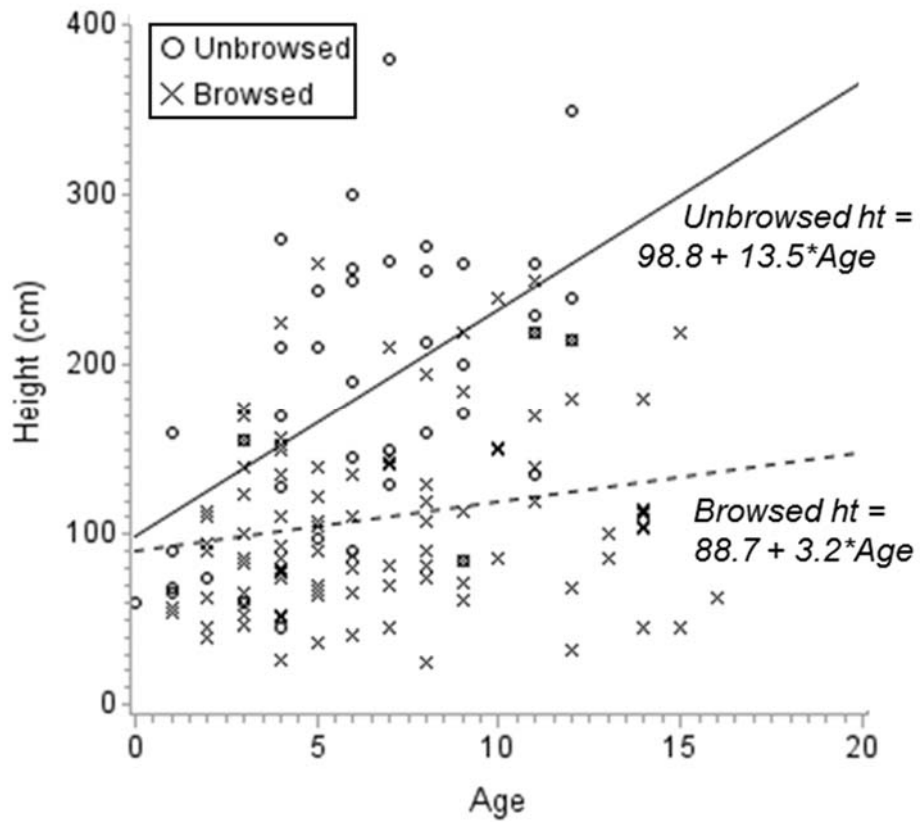


Figure 3. Height and age relationship for unbrowsed (solid line) and browsed (dotted line) aspen suckers < 2.5 cm dbh. Data include 41 unbrowsed and 109 browsed stems.

Table 2. Results of univariate regression analysis among regeneration density (aspen and lodgepole) and height (aspen) and independent variables. Independent variables are listed in order of the strength of their relationship with the response variable (as measured by the adjusted R^2). All independent variables shown had a significant ($\alpha < 0.1$) Spearman's rank correlation with the response variable. Signs (+ or -) indicate if regression relationship is positive or negative. All variables met assumptions of normality; all variables were log-transformed except for mean annual precipitation and the wild animal density.

Response variable	Independent variable	+ / -	Adjusted R^2	P
Mean aspen density	Down lodgepole pine	-	0.22	0.0038
	Mean annual maximum temperature	-	0.20	0.0051
	Live aspen	-	0.11	0.0323
	Dead and down aspen	-	0.11	0.0351
	Mean annual precipitation	+	0.07	0.0791
Mean lodgepole density	Live lodgepole pine basal area	+	0.23	0.0027
	Topographic Wetness Index	+	0.11	0.0349
	Time since onset of MPB epidemic	-	0.02	0.2206
	Down lodgepole pine	-	-0.02	0.5497
Mean aspen sucker height	Down lodgepole pine	+	0.49	<.0001
	Maximum temperature	+	0.38	<.0001
	Wild animal density	-	0.27	0.0012
	Mean annual precipitation	-	0.23	0.0027
	Time since onset of MPB epidemic	+	0.06	0.0970
Maximum aspen sucker height	Down lodgepole pine	+	0.39	<.0001
	Mean annual precipitation	-	0.28	0.0012
	Mean annual maximum temperature	+	0.27	0.0010
	Wild animal density	-	0.17	0.0109
	Topographic Wetness Index	-	0.12	0.0287
	Live aspen basal area	-	0.09	0.0483
	MPB-killed basal area	-	0.06	0.0882

Table 3. Results of univariate regression analysis between proportion of suckers browsed (in each stand) and independent variables. All independent variables shown had a significant ($\alpha < 0.1$) Spearman's rank correlation with the proportion of suckers browsed. Signs (+ or -) indicate if regression relationship is positive or negative. All variables met assumptions of normality. Proportion of suckers browsed was transformed with an arcsine square-root transformation. All independent variables were log-transformed except for the wild animal density.

Response variable	Independent variable	+ / -	Adjusted R^2	P
Proportion of suckers browsed	Down lodgepole pine basal area	-	0.46	<.0001
	MPB-killed basal area	+	0.25	0.0027
	Wild animal density	+	0.16	0.0111
	Live aspen basal area	-	-0.03	0.9437

Table 4. Effect of cattle grazing status (Grazed or Ungrazed in year of sampling) on mean aspen sucker height, maximum aspen sucker height, and proportion of aspen browsed in each stand. Effect was tested with an ANOVA.

Response	Grazed	Ungrazed	F	P
	Estimated mean			
Mean sucker height (cm)	90	115	3.66	0.0649
Maximum sucker height (cm)	152	234	8.64	0.0062
Proportion of suckers browsed	0.55	0.27	3.07	0.0895

Note: All response variables were log transformed to meet assumptions of normality. Estimated means were back-transformed to scale of measurement.

Table 5. Most parsimonious multivariate models explaining mean sucker density, mean sucker height, maximum sucker height, and proportion of stems browsed, as evaluated with AIC_c. Two models to explain maximum sucker height had nearly equivalent AIC_c values; I report them both below.

<i>Response</i>	<i>Lowest AIC_c Model(s)</i>	<i>Adjusted R²</i>	<i>AIC_c</i>	
Mean aspen sucker density	Down Lodgepole BA + Live aspen basal area	0.29	80.67	
	β -0.25 (0.086)			β -0.27 (0.13)
	<i>P</i> 0.0063			<i>P</i> 0.0522
Mean lodgepole understory density	Live Lodgepole Pine BA	0.23	157.68	
	β 1.49 (0.46)			
	<i>P</i> 0.0027			
Mean sucker height	Down Lodgepole BA + Wild Animal Density	0.54	9.27	
	β 0.14 (0.03)			β -49.8 (17.3)
	<i>P</i> <0.0001			<i>P</i> 0.0072
Maximum sucker height	Down Lodgepole BA + Wild Animal Density	0.36	29.56	
	β 0.15 (0.05)			β -46.7 (24.2)
	<i>P</i> 0.0028	<i>P</i> 0.0636		
	Down Lodgepole BA + Wild Animal Density + Topographic Wetness Index	0.43	29.19	
	β 0.13 (0.04)			β -47.2 (22.8)
<i>P</i> 0.0049	<i>P</i> 0.0479	<i>P</i> 0.0376		
Proportion of suckers browsed	Down Lodgepole BA + Wild Animal Density	0.50	17.47	
	β -0.18 (0.04)			β 36.8 (19.8)
	<i>P</i> <0.0001			<i>P</i> 0.0732

Note: Values in parentheses next to parameter estimates (β) are standard errors. All response and predictor variables were transformed with a natural log transformation, except Proportion of suckers browsed which was transformed with an arcsine-square root transformation, and the Topographic Wetness Index, which was not transformed.

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CHAPTER 4

SPECIES-SPECIFIC EFFECTS OF MOUNTAIN PINE BEETLE-CAUSED OVERSTORY MORTALITY LEVEL ON LODGEPOLE PINE, SUBALPINE FIR, AND ENGELMANN SPRUCE REGENERATION

SUMMARY

Mortality in forest affected by the recent mountain pine beetle outbreak varies and is likely to lead to differences in future forest development trajectories. At the Fraser Experimental Forest in Colorado, USA, I studied the effects of high (85% of basal area) and moderate (40% of basal area) mortality on the regeneration of three conifers that commonly co-occur in mountain pine beetle-affected forests: shade-intolerant lodgepole pine, and more shade-tolerant subalpine fir and Engelmann spruce. Forests of both mortality levels were > 90% lodgepole pine with mature spruce and fir present at all sites. I found high densities of post-beetle recruitment in both mortality levels, but there were significantly more lodgepole in high than moderate mortality sites and significantly more subalpine fir in moderate than high mortality sites. Regeneration growth was 5 times greater for lodgepole pine and about 2 times greater for fir and spruce in high mortality than the moderate mortality sites. Lodgepole pine growth was 4 times greater in the high mortality sites than moderate mortality sites, while Engelmann spruce and subalpine fir growth was only 2 times greater. Lodgepole pine had the fastest growth rate in high mortality areas, but in moderate mortality areas Engelmann spruce and subalpine fir growth rates were fastest. Differences in regeneration density and growth suggest substantially different future

forest trajectories for the areas with high versus moderate mortality despite similar pre-outbreak basal area and species composition. Lodgepole pine will likely be a prominent part of future forest in high mortality areas, while spruce and fir will likely dominate regeneration in areas with more moderate mortality. My results indicate that post-disturbance recruitment, not just advance regeneration, will be important to post-beetle forest development in Colorado. Projections of future forest composition and structure should account for effects of mortality level and residual canopy cover on regeneration.

INTRODUCTION

Bark beetle-caused mortality level varies across outbreak-affected areas (e.g., Meddens and Hicke, 2014), and create a range of understory conditions that will affect tree regeneration. Recent mountain pine beetle (MPB) (*Dendroctonus ponderosae*) outbreaks have killed lodgepole pine (*Pinus contorta* var. *latifolia*) on 10 million hectares in North America (Meddens et al., 2012) spurring research about MPB-affected forest development (e.g., Astrup et al., 2008; Vyse et al., 2009; Klutsch et al., 2009; Collins et al., 2011; Diskin et al., 2011; Pelz and Smith 2012; Kayes and Tinker 2013). However, this work has not explicitly tested how levels of forest mortality influence seedling recruitment and growth. It is well established that forest canopy cover affects understory light, temperature, and other factors that can determine tree recruitment and growth patterns (Chen et al., 1993; Knapp and Smith, 1982; Dai, 1996; Feller, 1998). In this study I explore the relationships between forest mortality level, canopy cover, and regeneration composition/growth rates in order to better understand the future forest following beetle mortality.

Lodgepole pine forests have been the primary type affected by MPB in the southern Rocky Mountains; over one million hectares in Colorado and southern Wyoming have been impacted (U.S.D.A. Forest Service, 2013). Although lodgepole is predominant, approximately 55% of these forests in Colorado are mixed with some amount of shade-tolerant Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*) (Woudenberg et al., 2010). Shade-intolerant lodgepole establishes well on mineral soil seedbeds left following stand-replacing fire or harvest, and grows quickly in high light to dominate developing forests (Lotan and Critchfield, 1990). Shade-tolerant spruce and fir establish and grow more slowly in high light, but can establish under partially shaded (for spruce) and deep shade (for subalpine fir) conditions (Noble and Alexander, 1977; Alexander and Shepperd, 1990; Alexander et al., 1990). They can also persist and grow in low light where lodgepole pine will die (Lotan and Critchfield, 1990).

The role of post-disturbance tree recruitment in post-beetle stand development is uncertain. Trees that remain alive are able to take advantage of increased resource availability (Amman and Baker, 1972; Axelson et al., 2010). Advance regeneration is able to grow quickly following overstory mortality, which is composed primarily of the shade-tolerant species that survived low-light conditions beneath an intact canopy. Together with lodgepole's preference for disturbed seedbeds (Lotan and Critchfield, 1990), this has led many to conclude that primarily shade-tolerant advance regeneration will become more dominant after extensive lodgepole pine mortality (Amman, 1977; Astrup et al., 2008; Vyse et al., 2009; Kayes and Tinker, 2013). However, lodgepole recruitment have been documented in beetle-killed areas (Collins et al., 2011) and historic reconstructions of beetle outbreaks have suggested lodgepole

pine recruitment may begin pulses 5-10 years after overstory mortality despite the lack of surface disturbance (Sibold et al., 2007; Axelson et al., 2009).

The limited post-beetle pine regeneration may be due to timing. Most studies of MPB-effects on stand dynamics have collected data relatively soon after overstory mortality (within 3 - 7 years) (e.g., Astrup et al., 2008; Vyse et al., 2009; Klutsch et al., 2009; Diskin et al., 2011; Collins et al., 2011). Trees retain needles for several years following death, so understory light conditions are likely to increase with time since mortality. Pugh and Small (2011) found there was no difference between light beneath canopies with and without mortality while red needles remained on dead trees. Following needle loss, however, light levels will be elevated, particularly where overstory mortality is high (e.g., Pugh and Gordon, 2013). This may provide adequate light for shade-intolerant lodgepole pine seedling establishment provided it is not limited by lack of mineral soil exposure.

Mortality ranges from about 10 – 100% in areas affected by MPB, with mortality between 45 and 75% in half of affected forest (Meddens and Hicke, 2014). Variation in mortality level will result in canopy cover and light variation that will affect tree regeneration and growth (e.g., Knapp and Smith, 1982; Chen et al., 1993; Dai, 1996; Feller, 1998). Canopy cover and light will also impact regeneration indirectly through effects on soil temperature and evaporation. Maximum soil temperatures increase with decreasing canopy cover due to increased solar radiation, while minimum soil temperature is often lower under reduced canopy cover (Chen et al., 1993). Increased radiation (Winkler et al., 2014) may also increase evaporation (Adams et al., 1991) and lead to decreased soil surface moisture. Differential effects of mortality level on species' recruitment and growth may therefore lead to different stand development trajectories

(e.g., Oliver and Larson, 1996). Regardless, few studies have explicitly addressed the mortality level variation in research designs or questions.

Understanding the future forest in MPB-affected areas is important to a variety of ecological and social concerns. Forest composition differences will affect forest structure, changing wildlife habitat (Chan-McLeod, 2006), fire hazard (Page and Jenkins, 2007; Chapter 2, *This Dissertation*), and water yield (Pugh and Gordon, 2013). Research on the recent outbreak has increased our understanding of post-MPB forest dynamics (e.g., Astrup et al., 2008; Klutsch et al., 2009; Vyse et al., 2009; Collins et al., 2011; Diskin et al., 2011; Kayes and Tinker, 2012; Pelz and Smith, 2012), but has not explicitly studies the fact that mortality level varies across the landscape. I designed this study to see how regeneration density, composition and species-specific growth vary with MPB-caused mortality level. I also sought to understand how canopy cover, soil surface temperature, soil moisture, and forest floor substrate cover vary between mortality levels. I measured forest overstory, recruitment density, regeneration (recruitment and advance regeneration) leader growth and abiotic conditions in stands that experienced high and moderate mortality. I controlled for forest composition and site factors to isolate the effect of mortality level as much as possible.

METHODS

Study area

The study area is 3 x 2 km within Fraser Experimental Forest in north-central Colorado, USA. Elevation ranges between 2780 and 2930 m, slopes are between 4 to 30%, and aspects are generally north-west. Uplands are dominated by lodgepole pine mixed with scattered Engelmann spruce and subalpine fir. Lowlands are dominated by Engelmann spruce and blue spruce (*Picea*

pungens). Aspen (*Populus tremuloides*) dominated areas are also present, but lowlands and aspen were excluded from sampling. The study area receives an average of 640 mm of water from precipitation annually (PRISM Climate Group, Oregon State University, Corvallis, OR), about half of which falls as snow. Growing seasons are short, generally from late May until mid-October. Widespread lodgepole pine mortality caused by MPB began in the area around 2002 (Tishmack et al., 2004).

Study design

High and moderate mortality level area pairs (≤ 0.3 km of another) were defined using 0.3 m resolution satellite images (Google, Mountain View, CA). In each pair (replicate), a cluster of plots was randomly located using ArcGIS 10.0 (ESRI, Redlands, CA). Clusters had one central plot, with three plots located 30 m from the central plot at 120° angle intervals. Potential plot centers were visited in the field to ensure correct mortality level assessment from imagery, that forests were dominated by lodgepole pine but that Engelmann spruce and subalpine fir were present, that plots were on planar slopes, and that slope and aspect were similar between paired plots. In some cases, plot centers were moved up to 30 m to avoid concave or convex landforms or achieve similarity of slope and aspect between high and moderate plots of each replicate. Average slopes of high and moderate mortality pairs' plots differed by 1 - 12%, and pairs' aspects were within 8 – 47° of each other. Ten replicates of high and moderate mortality areas were deemed suitable for the study.

Tree data collection and analysis

At each plot, I collected overstory basal area (by species and status) using a 4.6 m² ha⁻¹ basal area factor prism. Tree dbh (diameter at breast height [1.37 m]), and tree status (live or dead), and mortality agent (if applicable) were recorded. MPB-killed trees were recorded by the

following categories: 1 = current attack, no fading needles; 2 = faded, some needles still green; 3 = all needles red; 4 = ~ 66% + needles still on; 5 = 33-66% needles on; 6 = 5 - 33% needles on; 7 = < 5% needles on, fine branches still present; 8 = fine branches gone; 9 = old attack. Dwarf mistletoe Hawksworth rating was recorded for live and dead (if possible) lodgepole pine trees. Post-beetle tree recruitment density (<2.5 cm dbh) was collected at each plot by species and size class on 40 m² circular plots. Post-beetle recruits were identified as trees that had less than 8 growth whorls and if they had < 3 cm along the stem above the ground without needles attached. Forest overstory basal area and understory density were summarized to per hectare values.

Leader growth was measured on four trees < 1.4 m tall (advance regeneration or recruits) of each species (lodgepole pine, subalpine fir, and Engelmann spruce) closest to plot center. This sometimes required going a substantial distance from plot center (up to 37.5 m), meaning the growth conditions of the tree had little relationship to forest characteristics measured at plot center. I therefore limited my analysis to trees ≤ 7.5 m from plot center. Trees with leader damage were also excluded. I used 154 lodgepole pine (96 in high, 58 in medium), 111 Engelmann spruce (41 in high, 70 in medium), and 175 subalpine fir (81 in high, 94 in medium) in analysis.

I tested effect of mortality level on basal area, regeneration density, and each species' 2012 leader growth using PROC GLIMMIX (SAS, Version 9.3, Cary, NC). I used a normal distribution for basal area and growth, and a Poisson distribution for regeneration analysis and accounted for random effects of replicate and plot within mortality level. I tested effect of mortality level on each species' growth with PROC GLIMMIX (SAS, Version 9.3, Cary, NC) and accounted for random effects of replicate, and plot within mortality level. I also analyzed the

effect of canopy cover on species' regeneration densities and leader growth with a linear regression model (PROC REG, SAS, Version 9.3, Cary, NC).

Forest floor

Percent cover of forest floor substrates were recorded in each plot by 1/8 plot segments. Substrate categories were: 1) duff/litter, 2) forb/grass, 3) mineral soil, 4) wood debris, 5) shrub, and 6) *Vaccinium* spp., 7) lichen/moss, and, 8) rock. There were very few places (only a small portion of two plots) where needles formed a layer and were not decomposing, so we classified duff and needles together. I compared plot substrates between high and moderate mortality levels using GLIMMIX and accounting for random effects of replicate and plot within mortality level. For each species, I compared the proportion of observed trees on each substrate and the average substrate occurrence on all plots using the chi-square test of PROC FREQ (SAS, Version 9.3, Cary, NC). To account for portion of plots that was not suitable growing space, I removed rock and down wood cover from this analysis.

Canopy cover data collection and processing

Hemispherical photographs were used to estimate canopy cover. Photos were taken as recommended by Chianucci and Cutini (2012) from plot center. I used a Canon EOS 50D 15.1 Megapixel Digital SLR camera (Canon U.S.A., Inc., Melville, NY) with a Sigma 4.5 mm F2.8 EX DC HSM Circular Fisheye Lens (Sigma Corporation of America, Ronkonkoma, NY). Photos were taken pre-dawn or post-dusk with the camera leveled on a tripod at 1.4 m above the forest floor. Sutter speed was set to 1/125th second, and exposure levels were manually set so that sky patches near the zenith was overexposed by 1 – 2 exposure stops. A built-in light meter was used to determine over-exposure.

Photo analysis was done with HemiView 2.1 SR4 Canopy Analysis Software (1998, 2009 Delta-T Devices Ltd., Cambridge, UK). Because setting the threshold for canopy versus open sky is subjective, photos were analyzed repeatedly until the proportion of visible sky was within 0.1 of the previous estimate (Chianucci and Cutini, 2012). I also used a visual standard for the threshold: the threshold was set so that areas of grouped cones on fine branches of dead lodgepole pine were classified as canopy, while uncrossed branches surrounding them were classified as sky. To minimize the effect of topography on canopy cover estimates, I applied a mask to the hemispherical field of view equal to the greatest slope (17 degrees) of all plots (Schleppi et al., 2007). I determined visible sky ('Canopy gap fraction') from a 146 degrees field of view rather than the full 180 degrees captured by the photos. Canopy gap fraction is simply the portion of the sky that is visible from beneath the canopy.

Soil temperature and moisture

Soil temperatures were recorded hourly from July 1, 2013 until first snowfall (September 21, 2013) with ThermoChron® iButtons (Maxim Integrated™, San Jose, CA) buried below 1 cm of litter/duff at each plot center. Data from 64 of the 80 plots was recorded due to disturbance by animals. For analysis, I determined maximum, minimum, and mean temperatures for each day of sampling. I then calculated the average daily maximum, minimum, and mean temperature across all days recorded. I tested effect of mortality level on temperatures with PROC GLIMMIX (SAS, Version 9.3, Cary, NC) and accounted for random effects of replicate and plot within mortality level. I analyzed the relationship between canopy cover and soil surface temperatures with PROC REG (SAS, Version 9.3, Cary, NC).

I measured volumetric water content of the top 12 cm of soil every two weeks using the HydroSense II that had 12 cm rods and a $\pm 3\%$ accuracy (Campbell Scientific, Logan, UT). I

measured soil moisture of all plots on the same day, and only if there had been no previous precipitation that day. Plots in high and moderate mortality areas of each replicate were measured within 30 minutes of each other. At each plot four measurements were taken 0.3 m from plot center in the cardinal directions. Moisture was averaged to the plot, and then across all four plots in each high and low mortality level replicate.

RESULTS

Forest overstory and understory

Total pre-MPB basal area was not significantly different between high ($33 \text{ m}^2 \text{ ha}^{-1}$) and moderate ($32 \text{ m}^2 \text{ ha}^{-1}$) mortality areas, though there were about $5 \text{ m}^2 \text{ ha}^{-1}$ more lodgepole pine in high mortality stands, and about $2 \text{ m}^2 \text{ ha}^{-1}$ more subalpine fir in moderate mortality stands (Figure 1a). High mortality areas lost 85% of their basal area, while moderate areas experienced 40% mortality (Figure 1b). Live post-MPB basal area was $19 \text{ m}^2 \text{ ha}^{-1}$ in moderate mortality stands, almost 4 x greater than in high mortality stands. High mortality stands had $24 \text{ m}^2 \text{ ha}^{-1}$ dead basal area, nearly twice that of moderate mortality stands. Distance to nearest mature Engelmann spruce or subalpine fir was not significantly different between mortality levels (about 15 m for spruce and 11 m for fir), and nearest lodgepole pine was only ~ 1 m further from plot center in high mortality (3 m) than moderate mortality (2 m) forest. Canopy cover was much lower in high mortality stands; canopy gap fraction was 0.47 in high mortality stands, 0.22 greater than in moderate mortality stands (Figure 1c). Live basal area was a significant predictor of canopy gap fraction ($R^2 = 0.3823$, $P < 0.0001$).

Regeneration density and leader growth

There was more lodgepole pine and Engelmann spruce regeneration, and less subalpine fir regeneration, in the high mortality than moderate mortality stands (P values all < 0.0001) (Figure 2). Regression analysis showed lodgepole pine increased with canopy gap fraction ($R^2 = 0.22$) (Figure 3a), while subalpine fir density decreased ($R^2 = 0.16$) (Figure 3c). Engelmann spruce showed no relationship to canopy cover (Figure 3b).

Leader growth (of trees < 1.4 m tall) was greater in high mortality than moderate mortality areas for all species (P values all < 0.0001) (Figure 4). At high mortality levels, lodgepole pine growth was 3 cm (about 0.3 x) more than spruce and fir growth. In moderate mortality, Engelmann spruce and subalpine fir growth was about 2 cm (2 to 3 x) greater than lodgepole pine growth. Regression analysis reflected the different responses of growth among species to mortality level (Figure 5). Growth was significantly related to canopy gap fraction for all species. The slope of the lodgepole pine regression was significantly (< 0.0001) greater than that of both Engelmann spruce and subalpine fir, which were not different. The relationship between growth and canopy gap fraction was quite strong for lodgepole pine ($R^2 = 0.48$), moderate for Engelmann spruce ($R^2 = 0.23$) and weak for subalpine fir ($R^2 = 0.06$).

Soil moisture and temperature

Soil temperature varied between mortality levels while moisture did not. The differences in average soil moisture between high and moderate mortality pairs were within the $\pm 3\%$ sensor accuracy margin of error. Daily mean, maximum, and minimum soil temperatures were different between mortality levels ($P < 0.02$). High mortality plots were on average warmer, and had much warmer maximum temperatures, than the moderate mortality plots (Figure 6a). Minimum temperatures were slightly lower in the high than moderate mortality plots (Figure 6b). The

overall mean temperature was 1.5°C greater in the high (13.7°C) than moderate (12.2°C) mortality ($P = 0.0004$). The overall daily maximum temperature was 7.0°C warmer in high (29.9°C) than moderate (22.9°C) mortality ($P = 0.0002$), and average minimum temperature was 0.7°C cooler in the high (6.4°C) versus moderate (7.1°C) mortality plots ($P = 0.0119$). Canopy cover explained 0.38 and 0.46 of the variation in mean (intercept: 11.0, $P < 0.0001$; slope: 5.4, $P < 0.0001$) and maximum (intercept: 16.8, $P < 0.0001$; slope: 25.7, $P < 0.0001$) soil temperatures, respectively, but a much smaller amount of the variation ($R^2 = 0.16$) in minimum temperatures (intercept: 7.7, $P < 0.0001$; slope: -2.4, $P = 0.0019$).

Forest floor and seedling distribution

Forest floor was primarily covered by duff/needles, *Vaccinium* spp., and wood (Table 1). There were no significant differences in cover between the high and moderate mortality groups for all but two forest floor substrates. Down wood cover was 15% in the high mortality, about 6% more than in moderate mortality ($P < 0.0001$). Duff/needles covered 57% of plots in the moderate mortality areas, 16% more than in high mortality ($P = 0.0001$) (Table 1). Chi-square tests showed that the distribution of seedlings across substrates was different than the observed distribution of substrates covering all plots ($P = 0.0260$ for lodgepole pine, $P = 0.0007$ for Engelmann spruce, and $P = 0.0308$ for subalpine fir). All species seedlings were on duff/needles more than expected. Seventy-one percent of lodgepole pine, 64% of Engelmann spruce, and 69% of subalpine fir seedlings were on duff/needles, though this covered 50% of forest floor (Table 1). Eight percent of Engelmann spruce seedlings were on moss/lichen, although this substrate covered only 3% of plots. Very few seedlings of all species (0.7%, 0%, and 1% for lodgepole pine, Engelmann spruce, and subalpine fir) established on wood despite its coverage of 12% of the plots.

DISCUSSION

The future forest composition following mountain pine beetle will depend on the level of mortality. Where mortality was high, lodgepole pine will be more abundant than in moderate mortality areas, and will be the fastest growing conifer. Subalpine fir was most abundant and spruce and fir grew faster than lodgepole in moderate mortality areas. The differences in regeneration were related to the variation in canopy cover between mortality levels. These differences in seedling composition and species' growth rates will lead to a divergence in forest composition between mortality levels, despite the stands' similar composition before MPB outbreak.

Regeneration composition, density, and growth vary between mortality level and in relation to canopy cover. Canopy cover and its effects on abiotic conditions, rather than seed availability, seem to be behind this difference between regeneration density in mortality levels since mature trees of each species were present at similar distances from plots in high and moderate mortality areas. Over 1000 lodgepole seedlings ha⁻¹ were present in high mortality areas, where soil surface temperatures and light were high, but they were almost absent in moderate mortality areas. This density trend and the high growth in high mortality stands are consistent with our knowledge that lodgepole seedlings thrive in high light and can withstand soil surface temperatures above 60°C (Lotan, 1964; Lotan and Critchfield, 1990), but dies beneath closed canopies (Coates, 2000; Coates, 2002). Likewise, lower fir regeneration density in high mortality, and the fact that spruce and fir grew faster than lodgepole where outbreak was less severe, is consistent with our expectations. Subalpine fir is susceptible to heat girdling (Alexander et al., 1990), and initial seedling survival is low in canopy gaps compared to shaded understory (5% vs 40%) (Cui and Smith, 1991). Spruce and fir have lower light compensation

points than lodgepole so can grow under lower light conditions (Ekwebelam and Reid, 1983; Knapp and Smith, 1982). It was surprising that spruce seedlings were slightly denser in high mortality than moderate mortality areas because seedling death due to heat girdling is common at temperatures above 30°C (Noble and Alexander, 1977), which was often exceeded in high mortality plots. However, spruce recruitment showed no regression relationship to canopy cover, and it is likely that microsites with adequate shade to provide protection from high temperatures were present in most plots.

Unexpectedly, all species, including lodgepole pine, regenerated primarily on undisturbed forest floor. Subalpine fir is known to regenerate well on organic seedbeds (Alexander et al., 1990), but thought that lodgepole pine needs mineral soil for substantial regeneration (Lotan and Critchfield, 1990). However, upon closer examination many studies show that lodgepole pine germinates and survives on undisturbed duff and litter, provided it is thin (< 3 cm) (Tackle, 1956; Ackerman, 1957). I did not observe duff or litter > 3 cm on any plots when installing temperature sensors (which is similar with other work in the region; Klutsch et al., 2009; Collins et al., 2012). The work often cited as evidence for lodgepole's affinity for mineral soil but actually found seedling survival was no better on burned, disked, or scalped seedbeds than undisturbed forest floor (Lotan, 1964). (Only intensive treatments which created small trenches significantly increased lodgepole survival, which the author attributes to microtopography more than soil exposure.) It does not seem that seedbed is limiting lodgepole regeneration where mortality levels are high enough to meet its light requirements due to thin organic horizons typical in the Southern Rockies. The success of lodgepole regeneration observed in my study is in contrast to the common assumption that lodgepole pine's adaptation to stand-replacing disturbance will

limit its future presence and that shade-tolerant advance regeneration will dominate MPB-affected forests (Astrup et al., 2008; Vyse et al., 2009; Kayes and Tinker, 2013).

Composition of future forests will vary by mortality level because of the differences in species regeneration density and growth rates. The variation in responses to MPB-caused mortality level is not surprising given each species' silvical characteristics (Alexander et al., 1990; Alexander and Shepperd, 1990; Lotan and Critchfield, 1990), but has not been previously documented. All three species have relatively high growth in areas with severe mortality. This will likely lead to a mixed species forest stratum where species dominance is determined by composition of regeneration rather than subsequent survivorship. Lodgepole pine will be a prominent part of this stratum due to its high establishment and its fast growth under high light conditions. In moderate mortality, density of lodgepole regeneration is low, and its growth is suppressed which may limit its short-term survivorship. The more shade-tolerant subalpine fir and Engelmann spruce are more abundant and growing more rapidly. Species composition will likely shift progressively to these more shade-tolerant species as this stratum develops over time. These results will be useful to improve future forest projections beyond their current focus on residual stand structure by incorporating post-beetle regeneration composition and growth.

CONCLUSION

Acknowledging the variation in pathways of development in MPB-affected stands of different mortality levels is important to predicting forest composition across vast landscapes. Many studies have concluded that subalpine fir will become the most dominant component in these lodgepole-dominated forests following MPB (Astrup et al., 2008; Vyse et al., 2008; Klutsch et al., 2009; Collins et al., 2011; Diskin et al., 2011; Pelz and Smith, 2012; Kayes and

Tinker, 2013), but this transition may be limited in areas with very high outbreak intensity due to substantial lodgepole pine regeneration and fast growth rates. Although this study was conducted on a small portion of the MPB-affected landscape, my results clearly show mortality level will have a substantial effect on post-MPB recovery and future forest conditions.

TABLES AND FIGURES

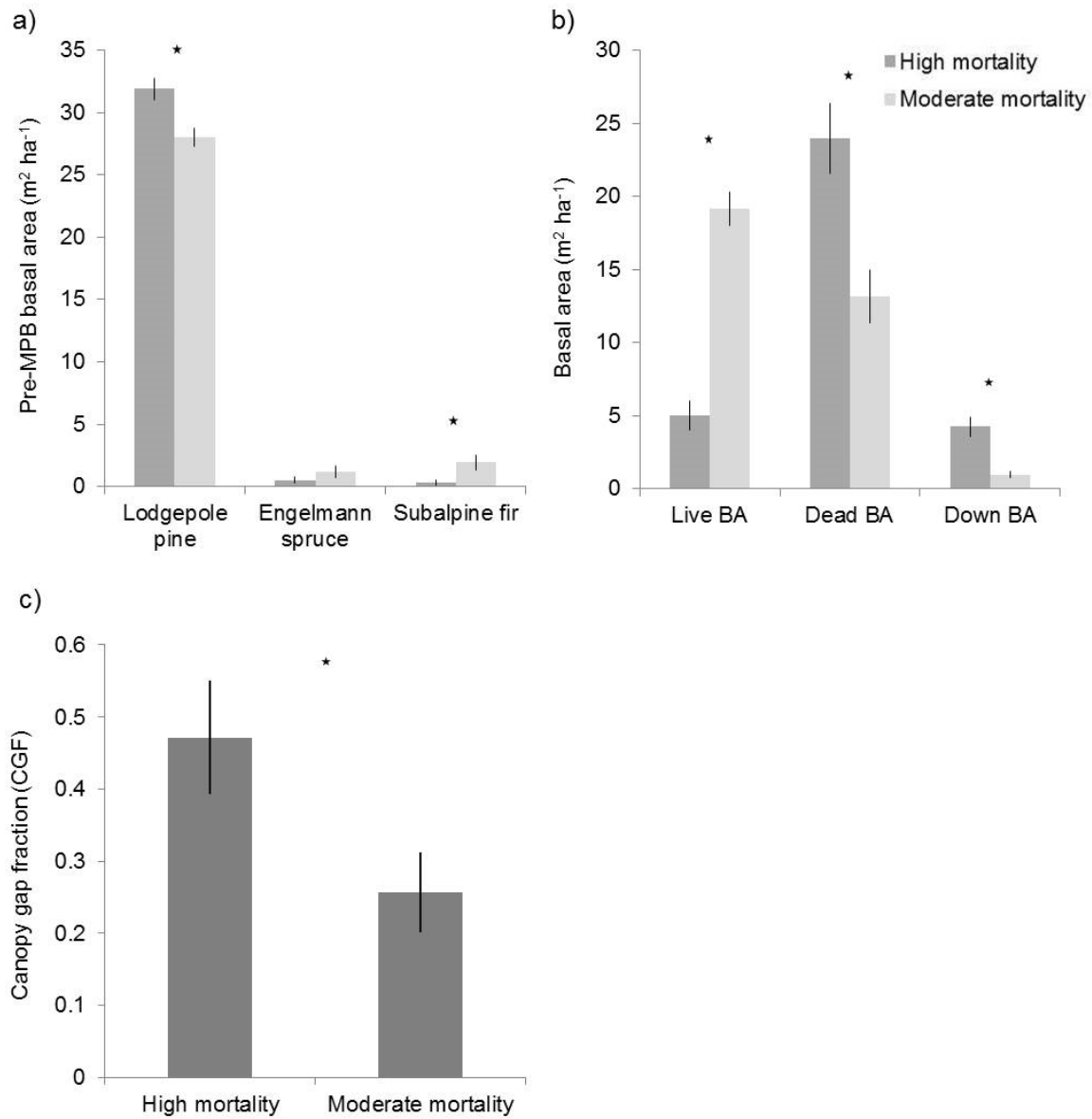


Figure 1. Overstory characteristics of high and moderate mortality areas: live basal area by species before MPB-caused mortality (a); live, dead, and down basal area following MPB (b); and canopy gap fraction (c). Stars indicate significant differences between the two mortality levels ($\alpha = 0.05$). Bars show means and lines are standard errors.

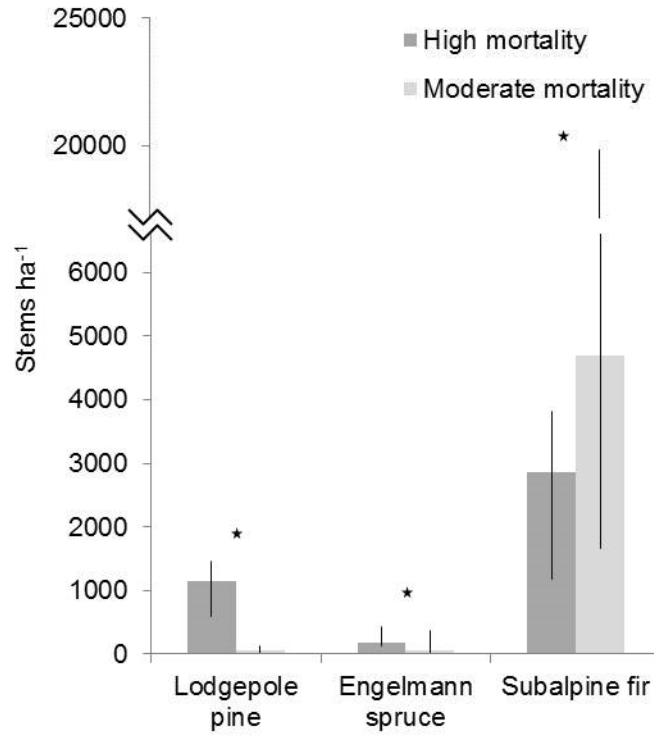


Figure 2. Median density of lodgepole pine, Engelmann spruce, and subalpine fir recruitment (< 1.4 m tall) in the high and moderate mortality areas. Stars indicate a significant difference between the two mortality levels ($\alpha = 0.05$). Lines show the 25th and 75th percentile densities.

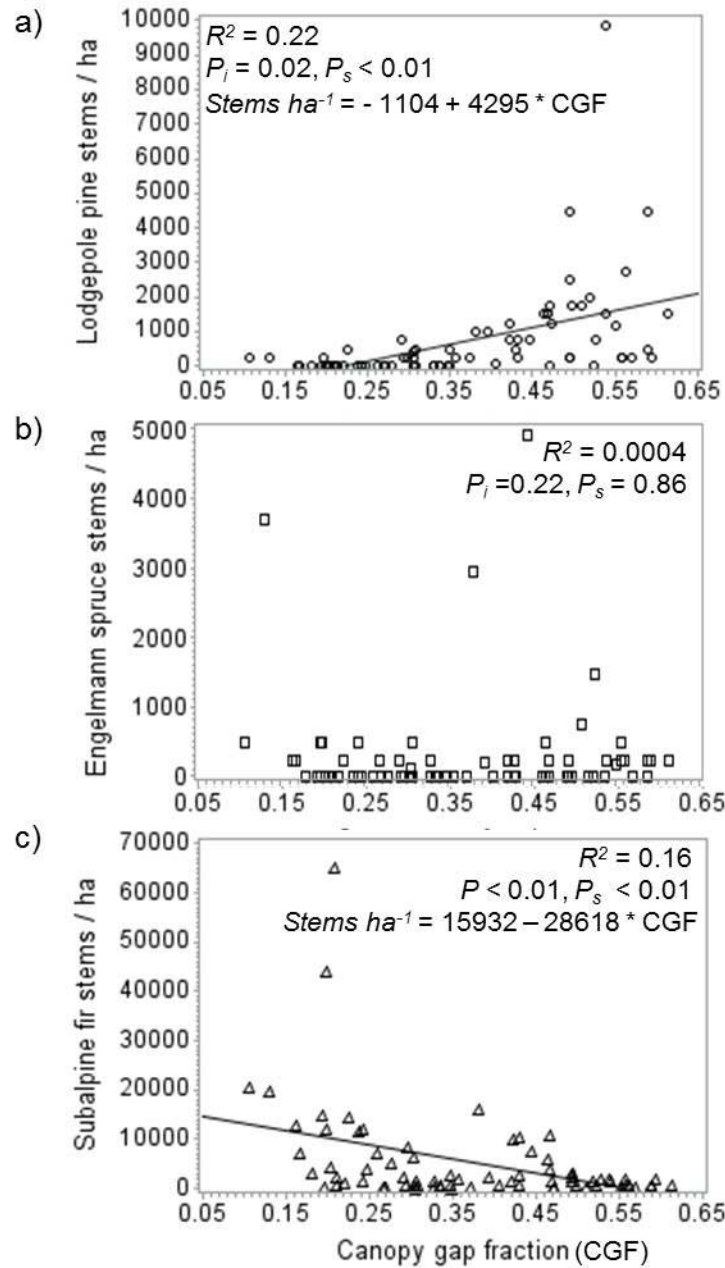


Figure 3. Regression relationships of lodgepole pine, Engelmann spruce, and subalpine fir recruitment density (at the plot scale, $n = 80$) to canopy gap fraction (CGF). R^2 , P -values (for intercept [P_i] and slope [P_s]), and regression equations (if parameters were significant) are given.

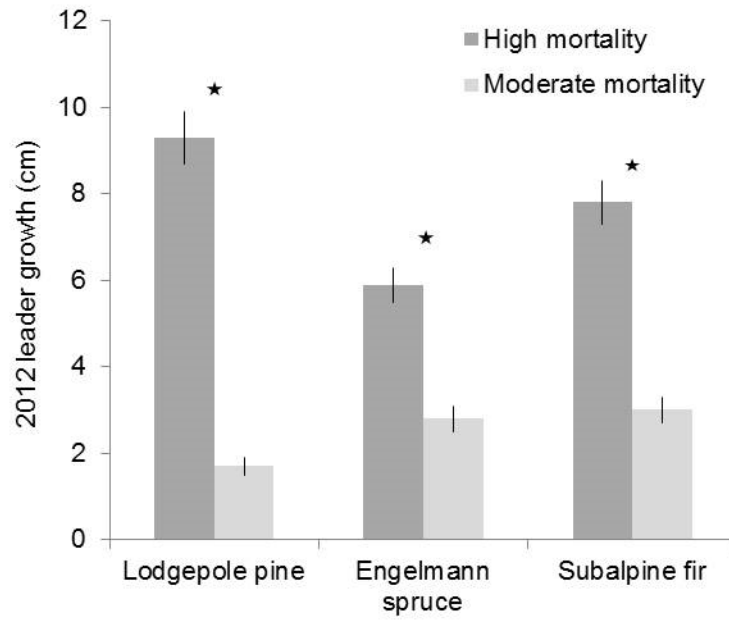


Figure 4. Average 2012 leader growth of lodgepole pine, Engelmann spruce, and subalpine fir (trees < 1.4 m tall) in high and moderate mortality forest. Stars indicate a significant difference between growth at the two mortality levels ($\alpha = 0.05$). Lines show standard error of the mean.

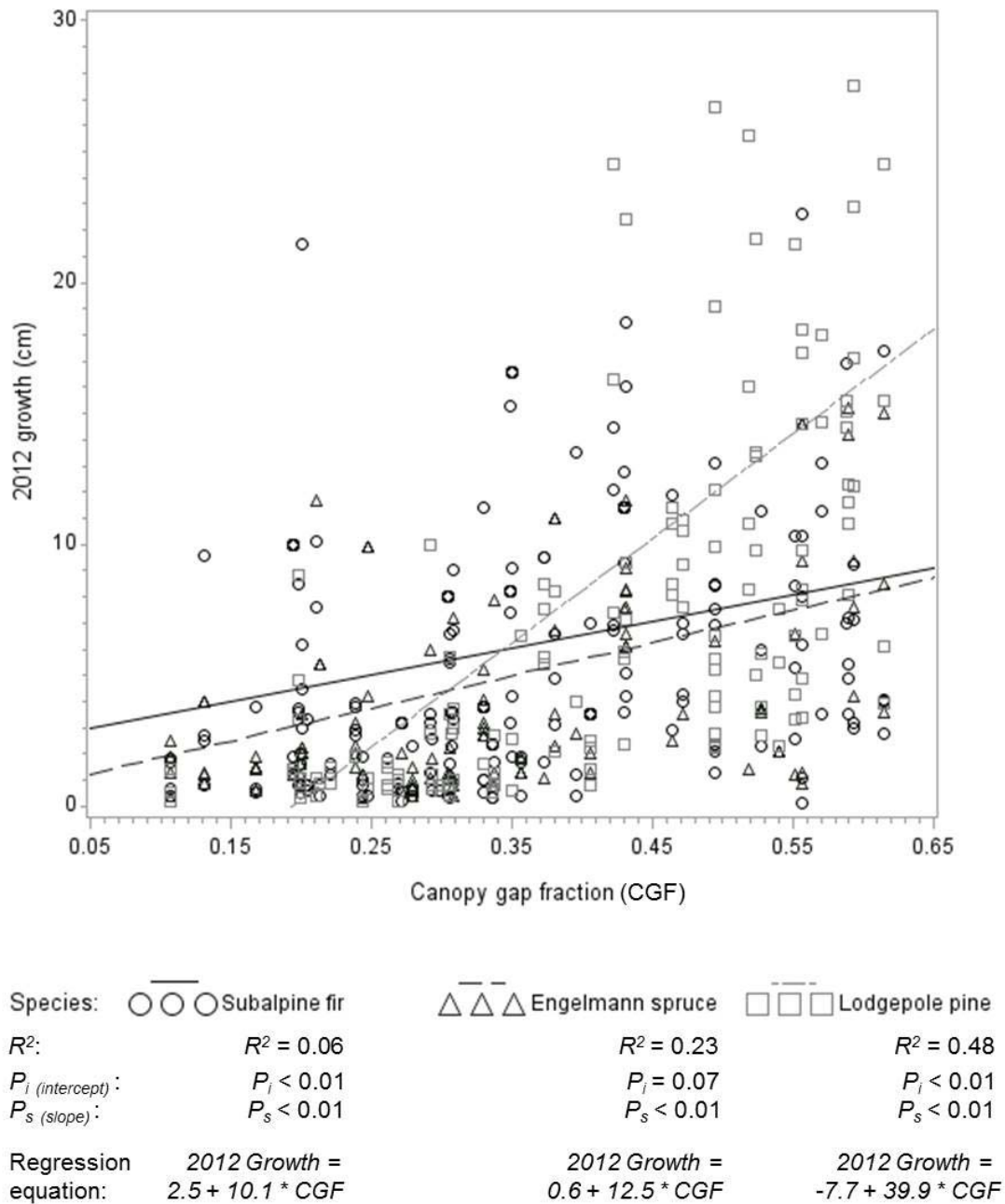
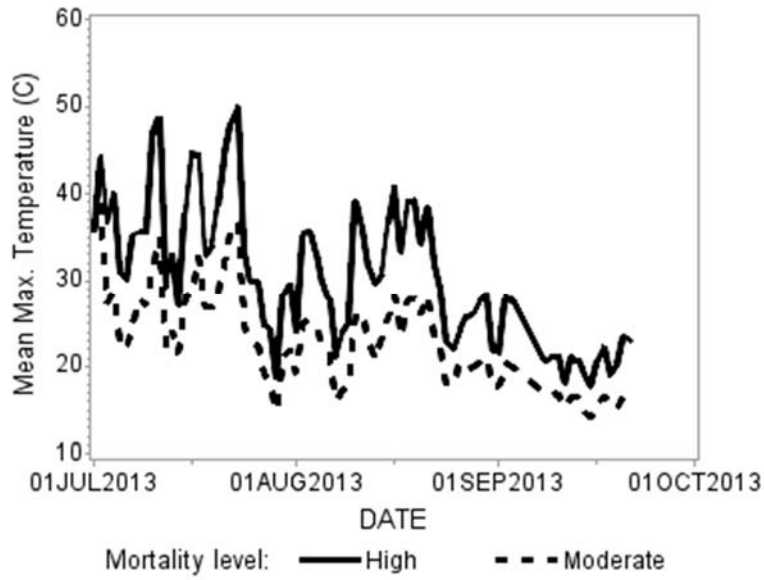


Figure 5. Regression relationships of lodgepole pine (n = 154), Engelmann spruce (n = 111), and subalpine fir (n = 175) 2012 leader growth to canopy gap fraction (CGF). The slope of the lodgepole pine regression line is significantly greater than that of both other species.

a)



b)

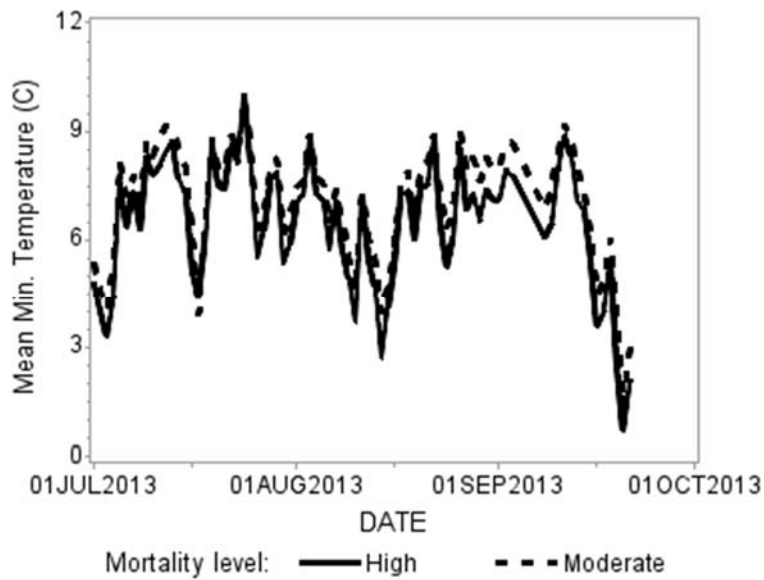


Figure 6. Mean daily maximum (a) and minimum (b) soil temperatures ($^{\circ}\text{C}$) in the high ($n = 32$) and moderate ($n = 32$) mortality areas. Temperatures were measured at the soil surface, below 1 cm of duff.

Table 1. Forest floor substrate for high and moderate mortality areas, and all plots (high and moderate mortality) combined. Asterisks indicate significant differences in substrate between mortality levels ($\alpha = 0.05$).

Substrate	Observed substrate cover (%)		
	<i>Mortality level</i>		
	<i>High</i>	<i>Moderate</i>	<i>Combined</i>
Duff/needles	*44.2	*56.8	50.5
Grass/herbaceous plants	0.7	0.3	0.5
Mineral soil	0.1	0.4	0.3
Wood	*15.5	*8.9	12.2
Vaccinium spp.	25.3	23.2	24.3
Shrubs/conifer branches	9.1	5.7	7.4
Moss/lichen	3.3	3.5	3.4
Rock	1.8	1.1	1.5

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CHAPTER 5

CONCLUSIONS

This dissertation advances our understanding of how forests in the Southern Rockies will develop following the recent mountain pine beetle (MPB) (*Dendroctonus ponderosae*) outbreak. In the previous chapters, I show the importance of explicitly considering forest variation when projecting recovery and planning effective management of the outbreak's effects.

Forest development modeling in **Chapter 2** shows the importance of even small variation in species composition to forest recovery. All stands were > 80% lodgepole pine prior to mortality, but had very different trajectories according to my simulation of future stand conditions. Forest with spruce and fir became much more dominated by these species, resulting in highly hazardous canopy fuels. In contrast, stands of lodgepole and aspen did not shift composition and did not show a marked increase in fire hazard. The effects of management were also differed: hazardous fuels were best mitigated in the forest types with spruce and fir, but treatment had few positive effects in the stands of only lodgepole and aspen due to their lower hazard without treatment. Forest management of lodgepole-dominated forests could be more effective if it considers even small variation in composition.

Chapter 3 establishes that lower-elevation lodgepole pine and aspen forests are regenerating successfully. In nearly all stands, density of lodgepole pine and aspen are both above minimum stocking levels. Damage by ungulates is negatively affecting aspen height. However, my results give strong evidence that as killed lodgepole pine fall they will protect suckers. Overall, management to regenerate these forests does not seem necessary.

Chapter 4 shows that overstory mortality level will be important to future forest development. It challenges the assumption that where shade-tolerant species are present in the overstory, they will necessarily dominate the forest understory. Lodgepole pine regeneration density and growth was high in the most severe mortality areas. I conclude that this species will be a substantial part of the future forest here, since it is regenerating at high densities (555 – 3600 stems ha⁻¹) and growing faster than other conifers. In contrast, in moderate mortality areas the forest understory will be dominated by shade tolerant species. Lodgepole pine regeneration is nearly absent where MPB-caused mortality was more moderate, and spruce and fir are growing fastest.

My results can be used to make more informed decisions about management of MPB-affected forests. I solidify the importance of considering the specific composition of each stand in order to achieve management objectives. I also show that the prevailing wisdom that forest will regenerate primarily from advance regeneration is likely false in the Southern Rockies. Before this work, there were not published studies that provided information about tree regeneration following mortality. Regeneration, of both shade-intolerant and tolerant species, is certainly occurring, and species composition in mixed conifer forests will vary with mortality level. This work, in conjunction with other research, could be used to develop more robust models of forest development and improve the accuracy of projections of future forest composition and structure.