THESIS

INITIAL AND FUTURE STAND DEVELOPMENT FOLLOWING MOUNTAIN PINE BEETLE IN HARVESTED AND UNCUT LODGEPOLE PINE FORESTS

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY BYRON COLLINS ENTITLED INITIAL AND FUTURE STAND DEVELOPMENT FOLLOWING MOUNTAIN PINE BEETLE IN HARVESTED AND UNCUT LODGEPOLE PINE FORESTS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

INITIAL AND FUTURE STAND DEVELOPMENT FOLLOWING MOUNTAIN PINE BEETLE IN HARVESTED AND UNCUT LODGEPOLE PINE FORESTS

The extent and severity of overstory lodgepole pine (*Pinus contorta* Dougl.) mortality from mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has created management concerns associated with forest regeneration, wildfire risk, human safety, and scenic, wildlife and watershed resources in western North America. In northern Colorado and southern Wyoming the long-term ecological and socioeconomic consequences of the outbreak hinge upon the response of tree regeneration in both harvested and untreated forests. To characterize initial and future forest development following mountain pine beetle mortality I conducted two studies. First, I used historic U.S. Forest Service stand and seedling survey records to compare the density and species composition of advance regeneration in uncut stands and post-harvest recruits in clearcut harvest units during pre-outbreak (1980-1996) and outbreak (2002-2007) periods. Second, I compared the effects of various intensities of forest management on site conditions, seedling establishment and growth of advance regeneration to uncut areas in beetle-infested lodgepole pine stands. Advance regeneration averaged 3,953 stems ha^{-1} and was at least as high in beetle-infested stands compared to the pre-outbreak period. Lodgepole pine advance regeneration showed increased leader growth from 2008 to 2009 in harvested and untreated stands in response to canopy removal and decreased canopy foliage following overstory mortality. The density of seedling recruitment was three times higher in harvested than untreated stands (6,487 versus 2,021 seedlings ha^{-1}), and did not differ between outbreak and pre-outbreak stands. Growth simulations showed uncut and partial cut stands will be dominated by subalpine fir (*Abies lasiocarpa*), while clearcut stands will be dominated by lodgepole pine and have attributes similar to pre-outbreak stands within a century.

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Chapter One

Introduction

Coniferous forests are one of the world's largest terrestrial habitat types, covering approximately 15% of the Earth's land surface (NRCS, 2003). In the United States, forests cover 304 million hectares, 87% of which are found west of the Mississippi River (USDA, 2009). National Forests encompass 78 million hectares in the U.S. and provide critical ecosystem services such as drinking water to 123 million people, wood products from 1.5 billion harvested trees and 200 million tons of carbon sequestration annually (USDA, 2009). Forests provide essential services and biodiversity unique from other habitats yet they are a shifting mosaic of disturbance and recovery (Schoennagel et al., 2006; Sibold et al., 2007; Veblen et al., 1991).

Coniferous forests are characterized not only by the services they provide but the forces that shape them. Disturbances are a critical component in maintaining the diversity that is essential to the integrity of forest ecosystems (Hessburg et al., 2000; Parker et al., 2006). Although varying greatly in frequency and severity, disturbances such as wildfire, windfall, and insect infestation routinely alter coniferous forests. Disturbances range from windthrow affecting a single hillside to wildfire events spanning 400,000 hectares (Despain et al., 1989). Although individual events are unpredictable, historic data and climatic patterns offer insights into the frequency and severity of various forest disturbances (Sibold & Veblen, 2006; Westerling et al., 2006).

Natural disturbances rarely remove all structural elements of the previous forest stand, and the many living organisms that survive begin the process of stand development in the footprint of the previous disturbance (Franklin et al., 2002). The persisting living and dead remnant materials following a natural disturbance are described as biological legacies, and these serve as the starting point for the development of a new stand (Franklin et al., 2000). Biological legacies vary greatly depending on the disturbance that created them. Following catastrophic windthrow, overstory trees are converted to logs and forest floor debris, however advance regeneration and some overstory trees typically survive and little organic material is lost (Cooper-Ellis et al., 1999). On the other hand, wildfire events may consume large amounts of organic matter including branches, portions of tree boles and soil organic layers, leaving behind standing dead snags, downed material and varying amounts of living trees (Franklin et al., 2002; Turner et al., 2004).

In the central and southern Rocky Mountains, the structure and development of lodgepole pine forests has historically been primarily a legacy of large, infrequent, stand-replacing fires (Romme, 1982; Sibold et al., 2007). However, in recent years an outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in western North America has surpassed historic precedents in scale, synchrony and severity (Raffa et al., 2008). In Colorado, pine beetles have routinely reduced lodgepole basal area by 70% in infested stands and mortality exceeds 90% in mature, even-aged stands (Klutsch et al., 2009; Arapaho-Roosevelt National Forest, unpublished data). The drastic reduction in live, mature trees will shape the future trajectory of forest ecosystems in much of western

North America but little is known about how forests will recover from such widespread and severe disturbance.

Biological legacies serve as the starting point of forest recovery after disturbance. Gaining an understanding of the range of variability that will result from current infestations in North America, and how it may differ from previous disturbances, will provide critical insight into the future of these ecosystems. My first objective is to characterize the impact on stand structure of current mountain pine beetle infestations in lodgepole pine forests in northern Colorado and how this impact differs from previous outbreaks (Chapter 2). The second objective is to assess the future trajectory of these forests based on residual living trees and new recruitment (first part of Chapter 3). Lastly, I model forest recovery based on my empirical findings, and predict the future implications of various levels of forest management in response to pine beetle mortality (second part of Chapter 3, Chapter 4).

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Chapter Two

Effects of Mountain Pine Beetle on Tree Recruitment and Advance Regeneration Density in Harvested and Uncut Lodgepole Pine Stands: A Comparison using Historic Records

Abstract

The extent and severity of overstory lodgepole pine (*Pinus contorta* Dougl.) mortality from mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has created management concerns associated with forest regeneration, wildfire risk, human safety, and scenic, wildlife and watershed resources in western North America. In northern Colorado and southern Wyoming the long-term ecological and socioeconomic consequences of the outbreak hinge upon the response of tree regeneration in both harvested and untreated forests. I used historic U.S. Forest Service stand and post-harvest seedling surveys to compare the current bark beetle outbreak to pre-outbreak conditions within adjacent stands. I compared the density and species composition of advance regeneration in uncut stands and post-harvest recruits in clearcut harvest units during pre-outbreak (1980-1996) and outbreak (2002-2007) periods. In the pre-outbreak period only 5% of uncut stands had well-stocked understory (i.e., > 3,000 trees ha^{-1}) compared to 15% with a similar density during the current outbreak. The proportion of stands lacking advance regeneration was the same in both periods (~30%). Post-harvest seedling recruitment was consistently high and did not differ statistically between the current bark beetle outbreak and the pre-outbreak periods. The density of lodgepole pine recruits exceeded minimum stocking levels in 94% of stands, often by an order of magnitude. This comparison of historic U.S. Forest Service records provides evidence that the density of seedling recruitment will be at least as high after extensive mountain pine beetle-caused mortality as under relatively healthy, pre-outbreak conditions, and that the species

composition of stands regenerating after this outbreak may differ between treated and untreated stands.

Introduction

In Colorado, nearly 470,000 hectares (~1.16 million acres) of pine forest have been infested by mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) since the turn of the century (CSFS, 2008). Bark beetles killed 10.5 million lodgepole pine trees (*Pinus contorta* subsp. *latifolia*) in Colorado between 2002 and 2007, a ten-fold increase in mortality over the previous five-year period (Thompson, 2009). In infested stands, live lodgepole basal area is typically reduced by 70% and may exceed 90% in mature, even-aged stands (Klutsch et al., 2009; Sulphur Ranger District, unpublished data). Increased annual mean and winter minimum temperatures, prolonged drought, and aging forest stands have been implicated in the current decline in the health of western forests (Jenkins et al., 2008; Amman, 1982). The geographic extent and severity of overstory mortality caused by recent MPB outbreaks provides a dramatic example of how climate change may impact North American forests (Logan et al., 2003; van Mantgem et al., 2009; Raffa et al., 2008).

Lodgepole pine usually regenerates rapidly and forms even-aged stands after wildfire or forest harvest (Lotan & Perry, 1983). For example, following wildfire in Yellowstone National Park, up to 500,000 new lodgepole seedlings established per hectare with a median density of 3,100 stems ha^{-1} (Turner et al., 2004). Clearcut harvest treatments typically stimulate lodgepole recruitment, as in early research in the Gallatin and Lewis

& Clark National Forests in Montana, where post-harvest seedling recruits averaged 17,462 and 54,795 seedlings ha^{-1}, respectively (Lotan, 1964). In contrast to wildfire and harvesting, for up to a decade following a mountain pine beetle outbreak in British Columbia, seedlings failed to establish in 95% of untreated lodgepole pine stands (Astrup et al., 2008).

Availability of viable seed and adequate seedbed commonly determine the density of lodgepole pine regeneration after canopy disturbance (Lotan & Perry, 1983; Astrup et al., 2008). For example, intentional exposure of mineral seedbed by mechanical scarification is used to insure optimal seedbed conditions following harvesting in lodgepole pine stands (Landhäusser, 2009; Lotan, 1964). In Alberta, Canada, lodgepole regenerated prolifically after harvest, establishing 9,450 seedlings ha^{-1} in sites with mechanical site preparation, but recruitment was an order of magnitude lower in sites without site preparation (767 seedlings ha^{-1}) (Landhäusser, 2009). The high-severity, canopy-replacing wildfires typical of lodgepole pine ecosystems commonly consume most the forest floor and competing vegetation and expose extensive mineral seedbed (Blackwell et al., 1992). In such cases, where disturbance creates extensive seedbed, seedling density may vary with distance to seed source, elevation, fire severity, and percent serotinous cone-bearing trees in the fire-killed canopy (Turner et al., 2004; Kashian et al., 2004). In contrast, sparse seedling recruitment after bark beetle attack in British Columbia lodgepole pine forests has been attributed to the limited amount of forest floor disturbance relative to either logging or wildfire (Astrup et al., 2008).

The current bark beetle outbreak has led to a dramatic increase in forest harvesting in central Colorado (CSFS, 2008; USDA, 2005). On the Sulphur Ranger District (Arapaho-Roosevelt National Forest) at the center of the current outbreak area, lodgepole pine forests susceptible to MPB infestation comprise nearly half the total area and the majority of the forested area in the district (USDA, 2009; USDA, 2008). Since the early 1980s, growing human populations in mountain communities, decreased public support for active forest management, increased production costs and harvesting restrictions caused a decline in the forest industry and timber harvesting on U.S. Forest Service land in Colorado (Fig. 1) and elsewhere (Cubbage, 1995; Longwell & Lynch, 1990). However, the current level of MPB-caused mortality has generated renewed public support for forest management. Since the year 2000, there have been 3,700 hectares of lodgepole pine-dominated forests salvage-logged to reduce fuel loads and regenerate new stands. This represents a 2.5-fold increase in harvesting over the previous decade. Clearcut treatments have become more extensive in the years since the onset of the current bark beetle outbreak and now represent 90% of all the area treated (Fig. 1).

As an initial step in evaluating the effect of mountain pine beetle on tree regeneration, I utilized current and historic U.S. Forest Service stand inventory and post-harvest seedling records to address the following questions: 1) Do species composition and density of advance regeneration differ between uncut stands attacked by mountain pine beetle and pre-outbreak stands? 2) Does tree seedling recruitment differ between stands salvage-logged as a result of the current mountain pine beetle outbreak and relatively healthy stands harvested prior to the current outbreak?

Methods

Study Area

This study was conducted in the Williams Fork Drainage of the Arapaho-Roosevelt National Forest in the Colorado Front Range, approximately 100 km west of Denver (Fig. 2). Local climate is temperate and continental with long, cold winters and short, cool summers. Mean annual air temperature is 0.6 °C with January and July average temperatures of -10 °C and 12.2 °C, respectively (Fraser Experimental Forest, unpublished data). Total annual precipitation averages 600 mm; snowfall received between October and May comprises 64% of total annual precipitation and summer rains contribute the balance. Lodgepole pine stands dominate the lower elevations (i.e. 2750 to 3050 m) and south aspect slopes (Huckaby & Moir, 1998). Mixed-species forests of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and lodgepole pine occupy valley bottom and north-facing slopes and extend to treeline (3300 - 3500 m). Quaking aspen (*Populus tremuloides*) occurs in small clonal stands, scattered throughout the lower elevations.

Historic Records

Data were obtained from historic stand exam and seedling stocking surveys gathered by the Sulphur Ranger District. To compare the effects of overstory mortality on advance regeneration and post-harvest recruitment I compared pre-outbreak (n = 32) and outbreak stands (n=30). Stands harvested between 1980 and 1996 (pre-outbreak) experienced mild tree mortality (~17% of basal area) associated with MPB and were harvested as predominately healthy trees. The second time period consists of stands harvested since

2002 (outbreak) in response to MPB mortality. In these areas MPB infestation reduced live basal area below 11.5 m^2 ha^{-1} (50 ft^2 $acre^{-1}$). To minimize differences due to site conditions I limited my analysis to stands located within a portion of the 75 km^2 Williams Fork drainage, and clearcut harvest treatments in lodgepole pine-dominated stands (> 60% of basal area) (Table 1). In these conditions, clearcut regeneration treatments leave less than 9.2 m^2 of residual basal area per hectare (40 ft^2 $acre^{-1}$), less than 4.6 m^2 of dead residual basal area (20 ft^2 $acre^{-1}$) and a stand density index less than 30%. Stands harvested in the 1980-1996 period (pre-outbreak) and stands harvested in 2002-2007 (outbreak) were situated in close proximity (Fig. 2)

Advance regeneration

Density and species composition of advance regeneration were assessed from pre-harvest stand surveys. Advance regeneration ($\leq$ 140 cm tall, $\geq$ 4 years old) was enumerated in either 2.1 or 3.6 meter radius plots (1/300 and 1/100 acre). Plots were randomly located within sampled stands and surveyed at a density of 1 plot per 2 hectares. Overstory trees were surveyed using variable radius prism plots (basal area factor 10 or 20).

Post-harvest Recruitment

U.S. Forest Service post-harvest seedling surveys are designed to determine the proportion of a treated area stocked with an adequate density of healthy tree seedlings (Ford-Robertson, 1971) and these surveys were conducted in the same manner described above for advance regeneration. The majority of seedling surveys documented in the Sulphur District are conducted the third year following harvest, and are the focus of my study. For the purposes of my investigation I define recruits as trees established following harvest operations.

Statistical Analysis

I compared seedling densities between pre-outbreak and outbreak stands and tested the significance of site characteristics as predictors of advance regeneration and recruitment. Due to the spatially clumped distribution of recruitment, approximately one-quarter of sample plots had no new seedlings after harvest while others had a large number (> 400 recruits plot^{-1}). Due to this variability I compared population means using the multi-response permutation procedure (MRPP). MRPP is a non-parametric method which does not assume normality or homogeneity of variance (Cai, 2006). The null hypothesis under MRPP assumes observations are independent and identically distributed (Cai, 2006). Site characteristics (canopy condition at time of harvest, pre-harvest overstory species composition and basal area, elevation and aspect) were tested as predictors of advance regeneration density and post-harvest recruitment using a backwards elimination regression approach (Neter et al., 1989). I used a negative binomial error distribution to analyze this over-dispersed data, and assessed goodness of fit with Pearson's χ^2 statistic (SAS, 2008; White & Bennetts, 1996).

Results

Advance Regeneration

The density of advance regeneration did not differ significantly between uncut pre-outbreak (870 stems ha^{-1}) and outbreak stands (1,700 ha^{-1}; MRPP $p = 0.21$; Fig. 3).

Lodgepole pine was the most common species in the pine-dominated areas I studied, comprising 64% and 53% of advance regeneration, in the pre-outbreak and outbreak periods, respectively. Advance regeneration of subalpine fir was more plentiful in outbreak than pre-outbreak stands, averaging 769 and 257 trees ha^{-1}, respectively ($p = 0.07$). Engelmann spruce was the least-abundant conifer species and its density did not differ between time periods (i.e., 59 and 37 stems ha^{-1} in pre-outbreak and outbreak stands; $p = 0.46$).

Overstory stand structure had a mixed influence on advance regeneration (Table 1). The density of lodgepole advance regeneration declined with increased overstory basal area in both pre-outbreak ($\beta = -0.012$, $p = 0.01$) and outbreak stands ($\beta = -0.021$, $p = 0.03$). However, overstory basal area was not significantly associated with density of either subalpine fir or Engelmann spruce.

Post-harvest Recruitment

Similar to advance regeneration in uncut stands, third-year post-harvest seedling recruits did not differ statistically between historical pre-outbreak (4,430 recruits ha^{-1}) and the current MPB outbreak (5,736 recruits ha^{-1}; MRPP $p = 0.12$, Fig. 4). Lodgepole pine accounted for 97% of recruitment and the density of lodgepole pine did not differ between pre-outbreak and outbreak harvest units ($p = 0.17$). Mean harvest size was 4-fold greater during the outbreak periods (i.e., 17 and 4 hectares in outbreak and pre-outbreak periods), though I found no relationship between harvest unit size and post-harvest recruitment in either era ($p = 0.40$). Lodgepole recruitment declined significantly with increasing elevation in both pre-outbreak ($\beta = -5.18$, $p = 0.06$) and outbreak harvest units ($\beta = -5.35$, $p = 0.08$).

Discussion

Advance Regeneration

Although the current MPB outbreak has affected nearly 470,000 ha in Colorado, there will be no forest harvest on the vast majority of federal lands. For example, on the Sulphur Ranger District 74,000 hectares of lodgepole pine forests are considered at risk of MPB infestation, but because of steep slopes and limited road access, only 40% of this area is potentially treatable (USDA, 2008). Due to staffing, time and economic constraints this district's planned and proposed treatments are unlikely to exceed 15% of the potentially treatable area (Sulphur Ranger District, unpublished data). In the untreated stands that will dominate the post-outbreak landscape, density and composition of advance regeneration will be critical to forest regeneration. Average density of advance regeneration was 870 and 1700 stems ha^{-1} during pre-outbreak and outbreak periods, respectively. Of pre-outbreak stands just 5% were considered well-stocked (i.e., $\geq$ 3000 trees ha^{-1}) compared to 15% in outbreak period stands (Fig. 3). Windfall is expected to topple greater than 50% of beetle-killed trees within a decade (Mitchell & Preisler, 1998), and stimulate growth of lodgepole pine advance regeneration in untreated stands (Murphy, et al. 1999).

Sparse seedling regeneration has been documented following severe bark beetle outbreak in some areas. In British Columbia, for example, tree regeneration was inhibited for 10 years after beetle attack and overstory loss (Astrup et al., 2008). In contrast, advance regeneration was abundant beneath beetle-killed Colorado stands in my study. This is likely due to the thin forest floor layer and scarcity of competing vegetation in Colorado lodgepole forests and the thick moss that is known to retard seedling colonization in many British Columbia forests (Blackwell, et al., 1992; Astrup et al., 2008). In addition, subalpine fir advance regeneration responded to the increased light, water and nutrients created by overstory pine mortality in Colorado stands compared to the pre-outbreak period.

Post-harvest Recruitment

Lodgepole pine typically produces abundant but highly variable regeneration following canopy removal (Turner et al., 2004; Lotan & Perry, 1983). Lodgepole recruitment ranged from 0 to greater than 500,000 seedlings ha^{-1} following fire in Yellowstone National Park (Turner et al., 2004; Kashian et al., 2004). Lodgepole pine density was also highly variable in post-harvest seedling records I surveyed; across harvest units densities varied from 150 and 19,000 seedlings ha^{-1} in the pre-outbreak and outbreak periods (Fig. 4). Lodgepole pine recruited prolifically in the first three years after harvest (~4,700 recruits ha^{-1}), and seedling density was comparable in pre-outbreak and outbreak harvest units. Seed source availability was not an obstacle to lodgepole recruitment as pre-harvest overstory was dominated by pine in both eras (71% to 100% of basal area, average SDI 40%). In contrast to lodgepole pine, shade tolerant Engelmann spruce and subalpine fir were a minor component (< 3%) of total regeneration in both pre-outbreak and outbreak harvest units.

Certification of successful post-harvest regeneration on U.S. Forest Service land requires a minimum of 370 stems ha^{-1} in at least 70% of sample plots within a treatment unit (USDA, 1997). In southern Rocky Mountain lodgepole forests, managers typically consider that development of well-stocked stands will require post-harvest seedling densities about ten-fold higher than the minimum threshold. In my study, post-harvest recruitment surpassed minimum stocking requirements in 100% and 94% of pre-outbreak and outbreak harvest units, respectively. More than half of pre-outbreak and outbreak harvest units (68% and 57%) were considered well-stocked (i.e., $\geq$ 3000 stems ha^{-1}). Seedling density failed to meet required stocking in only 3 units; all were from the post-outbreak period but appear to be associated with site rather than stand characteristics. Two of the poorly stocked units were among the highest in the study area (~3,100 meters). These plots represent the end point of the significant relationship in declining seedling recruitment with increasing elevation across all harvest units. The other poorly stocked unit occurred at the lowest elevation site (2,600 meters) in a lower landscape position. In the southern Rockies, competition with graminoid vegetation (e.g., *Calamagrostis rubescens, Carex geyeri*) in mesic, lower slope locations is known to inhibit lodgepole recruitment (Lotan, 1975). This may have contributed to sparse recruitment in the third harvest unit.

Clearing size is often integral in determining seed availability in harvested lodgepole pine forests (Alexander, 1986; Lotan & Perry, 1983) however, size was not a significant predictor of recruitment in my analysis area in pre-outbreak and outbreak harvest units.

Pre-outbreak units ranged between 0.5 and 14 hectares and were on average smaller than outbreak harvest units which were between 2 and 55 hectares. Pre-outbreak treatments in my dataset principally targeted small pockets of lodgepole susceptible to MPB, and were designed to maximize seed dispersal from adjacent uncut stands, increasing natural regeneration (Alexander, 1986; Lessard et al., 1987). In contrast, harvest unit size in the outbreak period was primarily determined by access to beetle-killed lodgepole pine. Although outbreak harvest units were generally larger than pre-outbreak units, dead trees often drop the majority of their cones through the harvest process and disperse seed throughout cut areas, providing adequate seed source for natural regeneration.

Overall, both advance regeneration and post-harvest seedling recruitment densities were similar between pre-outbreak and outbreak periods. Lodgepole was the dominant species of advance regeneration in uncut outbreak forests as it was in the past and it will likely become the dominant overstory species and continue to recruit as dead overstory trees topple. In addition, I expect an increased density of subalpine fir in outbreak stands will significantly influence species composition following the current outbreak, leaving future stands less susceptible to MPB because of a greater proportion on non-host tree species. In harvested units, similar density and stocking in both periods indicate MPB does not significantly influence post-harvest recruitment and treatment will result in abundant lodgepole regeneration.

This comparison of historic U.S. Forest Service records provides evidence that the density of seedling recruitment will be at least as high after extensive mountain pine beetle-caused mortality as before the outbreak, and that the future species composition may differ between treated and untreated stands. My study area includes some of the earliest results of the management response to the current mountain pine beetle outbreak. This comparison offers an initial estimate of forest recovery following unprecedented overstory mortality, in harvested and uncut lodgepole pine stands in Colorado. The use of historic U.S. Forest Service data in this study was a rapid, inexpensive means of answering important resource management questions.

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Table 1. Overstory conditions in pre-outbreak (n = 32) and outbreak stands (n = 30) on the Sulphur Ranger District, Arapaho-Roosevelt National Forest, Colorado.

	Basal area (m^2 ha^{-1})			Trees per hectare			Quadratic mean diameter (cm)		
	mean	max	min	mean	max	min	mean	max	min
Pre-outbreak	32.5	59.0	17.4	1,947	2,958	341	16.8	34.5	9.9
Outbreak	20.0	50.5	4.6	1,829	5,280	185	14.7	29.2	3.6

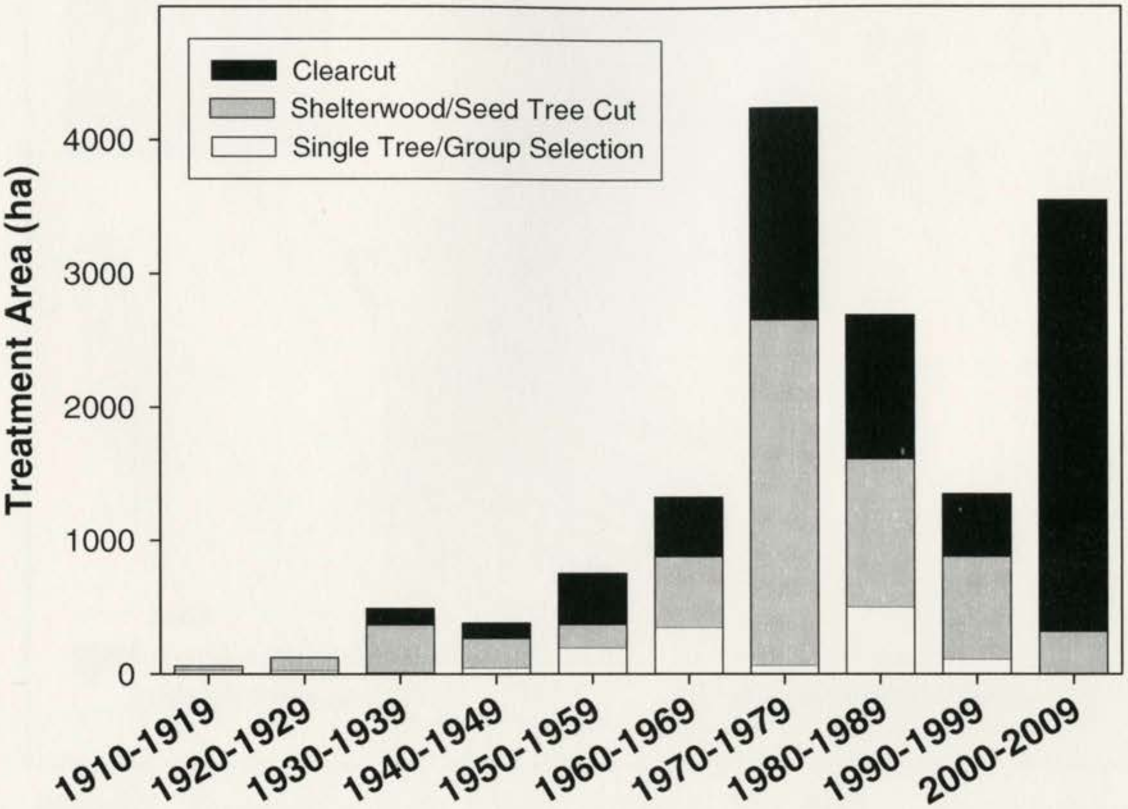

Figure 1. Commercial harvesting activities within the Sulphur Ranger District, Arapaho-Roosevelt National Forest, Colorado. Records exist since establishment of the Arapaho National Forest in 1908.

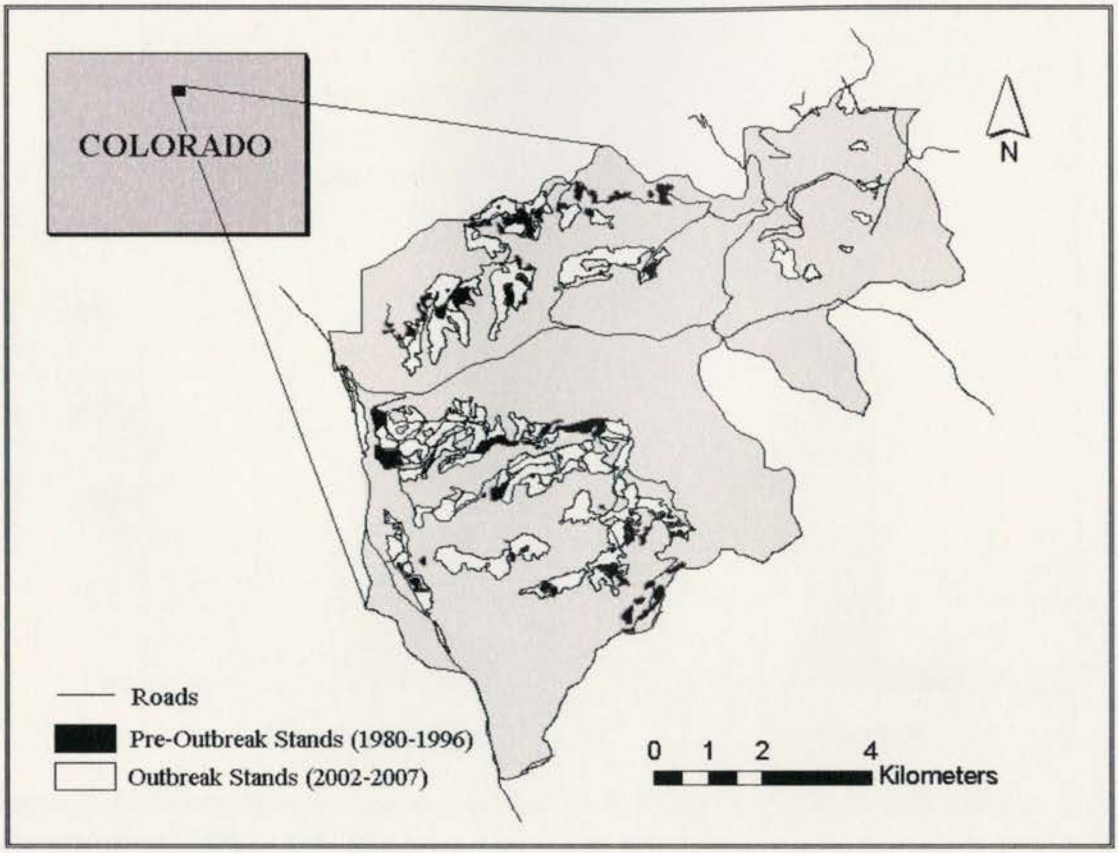

Figure 2. Harvest units in the 7,500 ha Williams Fork drainage (grey), Sulphur Ranger District, Arapaho-Roosevelt National Forest, Colorado. USGS hydrologic unit code 14010001. Harvest units range from 0.5 to 55 hectares. Elevation ranges from 2,600 to 3,200 meters above sea level.

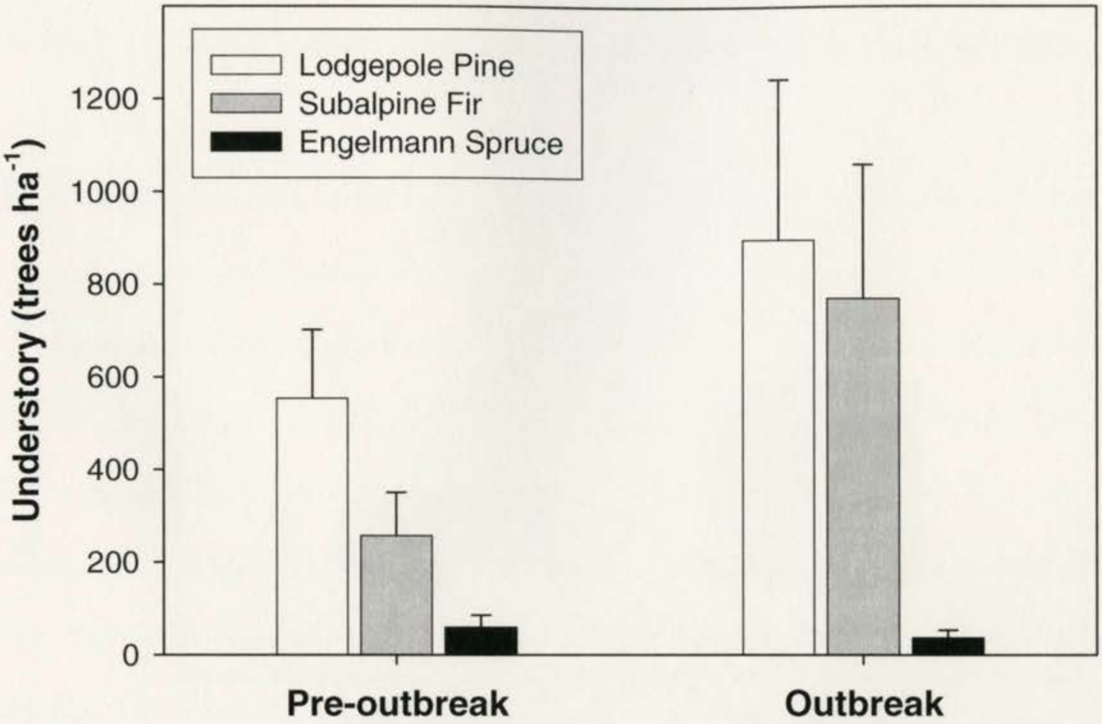

Figure 3. Advanced regeneration density (≤ 140 cm tall) in uncut pre-outbreak and outbreak stands (means and SE)

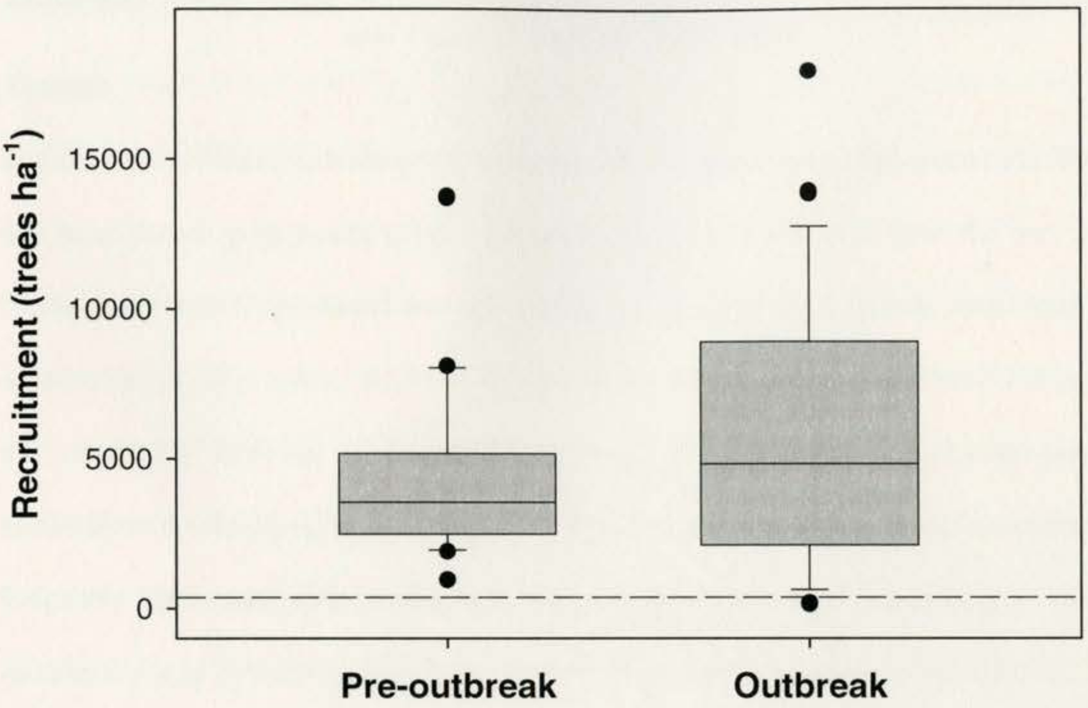

Figure 4. Post-harvest recruitment in pre-outbreak (n = 32) and outbreak (n = 30) stands three years after harvest. Lodgepole pine accounts for 97% of all recruits. Boxes show the median, 25th and 75th percentiles, and whiskers represent 10th and 90th percentiles. Dashed line represents the minimum density (370 trees ha^{-1}) of undamaged seedlings required to certify successful stocking (USDA, 1997).

Chapter Three

Initial and Future Stand Development following Mountain Pine Beetle in Harvested and Uncut Lodgepole Pine Stands

Abstract

In the southern Rockies, widespread mortality of lodgepole pine (*Pinus contorta* Dougl.) due to mountain pine beetle (*Dendroctonus ponderosae* Hopkins) since the turn of the century has lead to increased salvage logging in response to concerns associated with wildfire risk, public safety, wildlife, ecosystem services, and forest recovery. I compared the effects of differing levels of forest management on site conditions, seedling establishment and growth of advance regeneration to uncut areas in beetle-infested lodgepole pine stands with greater than 70% overstory mortality. The density of seedling recruitment was three times higher in harvested than untreated stands (6,487 versus 2,021 seedlings ha^{-1}), however 80% of harvested and untreated survey plots met or exceeded U.S. Forest Service stocking requirements. Lodgepole pine advance regeneration showed increased leader growth from 2008 to 2009 in harvested and untreated stands in response to canopy removal and decreased foliar cover due to overstory mortality, respectively. Stand growth simulations suggested clearcut harvest units will be dominated by a single cohort of lodgepole pine for more than a century and partial cut stands will be dominated by subalpine fir for at least two centuries. In untreated stands lodgepole pine will continue to be the dominant species for fifty years following outbreak, but after a century will be surpassed by subalpine fir which will make up the majority of stand basal area. Clearcut treatments will return to pre-outbreak stand conditions within 80 to 120 years, while partial cut and untreated areas will be dominated by subalpine fir and be less susceptible to future mountain pine beetle outbreaks.

Introduction

Recent mortality of lodgepole pine (*Pinus contorta* Dougl.) due to mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) in western North America is unprecedented in synchrony and severity (Raffa et al., 2008). Increased annual minimum temperatures and persistent drought conditions are implicated in the recent eruption in MPB populations (Romme et al., 2006). In Colorado, nearly all of the 600,000 hectares of lodgepole pine forests are threatened by current infestations (CSFS, 2008; USDA, 2009). Pine beetle has reduced live lodgepole basal area by up to 70% in pine-dominated stands, and mortality exceeds 90% in mature, even-aged stands (Klutsch et al., 2009; Sulphur Ranger District, unpublished data). Emerging concerns over fire risk, public safety and forest regeneration have prompted an increase in management activities in heavily affected stands (Fettig et al., 2007; Trzcinski & Reid, 2008).

Mountain pine beetle is considered an important disturbance agent in lodgepole pine-dominated forests, influencing aspects of nutrient cycling, species succession and stand structure (Fettig et al. 2007; Schoennagel et al., 2004). At endemic levels MPB typically kills the least vigorous and physiologically stressed trees (Roe & Amman, 1970; Shore et al., 2006). However, at current epidemic population levels, MPB has killed many of the largest most vigorous trees and now threatens increasingly younger and smaller diameter trees (CSFS, 2008). Although mountain pine beetle has persisted in the Rocky Mountains for millennia, little is known about future forest demography and structure following the severity of current mortality (Aukema et al., 2006).

Following harvest, lodgepole typically produces abundant regeneration, however recruitment densities may differ dramatically based on availability of seed source and site conditions. Disposal of harvest residue and seedbed preparation are important considerations for natural seedling regeneration and fuels concerns (Lotan, 1975). In Alberta, Canada, lodgepole regenerated prolifically after harvest, establishing 9,450 seedlings ha^{-1} in sites with mechanical site preparation, but recruitment was an order of magnitude lower in sites without site preparation (767 seedlings ha^{-1}) (Landhäusser, 2009). In the Gallatin and Lewis & Clark National Forests in Montana, sites with similar site preparation had differing recruitment based on site conditions and prevalence of serotinous cones (17,463 and 54,796 seedlings ha^{-1}, respectively) (Lotan, 1964). Site preparation and treatment of harvest residue are important factors regulating natural recruitment after harvest.

In the Sulphur Ranger district on Colorado's Arapaho-Roosevelt National Forest, forest health, fire risk and public safety concerns prompted forest harvest on nearly 3,700 hectares of lodgepole pine stands in response to MPB. Since the onset of the current MPB outbreak, clearcutting has accounted for greater than 90% of treatments in the Sulphur District, more than at any other time in the previous century. The objective of my study was to compare the effects of varying management intensities on forest recovery in areas heavily impacted by MPB to a no-action alternative. My comparison focuses on the following questions: 1) How do forest harvesting and mountain pine beetle infestation affect the density and growth of advance regeneration? 2) How do various overstory treatments and slash management options alter site conditions and influence forest regeneration compared to untreated areas? 3) How will differing management intensities affect species composition and stand structure of future forest stands?

Methods

Study Area

This research took place in lodgepole pine-dominated subalpine forests at the USDA Forest Service, Fraser Experimental Forest (FEF), Colorado. The FEF is a 93 square-kilometer research forest located 81 kilometers northwest of Denver, Colorado. Elevation ranges from 2,650 to 3,900 meters above sea level; one-quarter of the total area falls below 3,000 meters, where my study took place. The mean annual temperature is 1°C, ranging between -40°C and 32°C annually. Annual precipitation averages 71 to 76 centimeters with two-thirds falling as snow (Alexander & Watkins, 1977). Lodgepole pine stands dominate the lower elevations (i.e. 2750 to 3050 m) and south aspect slopes (Huckaby & Moir, 1998). Mixed-species forests of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*) and lodgepole pine occupy valley bottom and north-facing slopes and extend to treeline (3300 - 3500 m). Quaking aspen (*Populus tremuloides*) occurs in small clonal stands, scattered throughout the lower elevations.

MPB began to cause widespread overstory pine mortality in the FEF in 2002. Harvest operations in response to mortality occurred in the fall of 2007 and winter of 2007-2008. The study area is within 10 harvested units, paired with 10 adjacent uncut forest stands. Overstory removal prescriptions ranged across a gradient from partial (focused on dead pine removal) to clearcutting to reduce canopy fuels. Harvest residue ranged from lop and scatter (deep residue) to whole tree harvesting (minimal residue). Individual stands varied between 4 and 61 hectares in size, with a total study area of approximately 250 hectares.

Overstory

Overstory species composition, mortality and basal area were sampled on 5 meter wide, 150 meter long belt transects (n = 69). I used overstory conditions to quantify mortality, harvest removal and surface level light environment, and therefore I use the term overstory for all trees greater than 2.5 centimeters in diameter at breast height (DBH). Tree diameter measures and local, species-specific allometric equations were used to calculate leaf area index (LAI) for each transect, in order to characterize the surface level light environment (Kaufmann et al., 1982).

Seedlings & Groundcover

Seedling plots were established 150 meters apart in a gridded system with a random starting point. Seedling plots enumerate advance regeneration and recruitment in a 3.6 meter radius plot (1/100 acre) (Ford-Robertson, 1971). I define recruits as tree seedlings (conifers) or root sprouts (aspen), aged to be a maximum of two years old and thus established after harvest operations in untreated and treated stands; advance regeneration is defined as less than 2.5 cm at DBH, ranging from three years to decades old. Sampling occurred in the summer of 2009. The height of each tree was measured and placed into one of three categories: < 15 cm tall, 15 cm to 76 cm tall, > 76 cm tall to 2.5 cm DBH. All untreated stands and harvest units were sampled at a density of approximately 1 seedling plot per 2 hectares (n = 115). Trees less than 15cm tall were aged, using annual bud scars, to distinguish new recruitment from advance regeneration (Murphy et al. 1999). A minimum of one lodgepole and subalpine fir were randomly selected in each plot (where present) and measured to determine annual leader growth in 2008 and 2009 (Murphy et al. 1999).

Ocular estimates of groundcover were made within four 1 m^2 plots (n = 460) within each seedling plot, one in each cardinal direction. The percent cover was estimated for graminoid, forb, shrub, rock, bare soil, forest floor and harvest residue; the depth of forest floor and harvest residue was also measured.

Forest Growth Simulation

Based on my observations of existing overstory and tree regeneration I modeled the response of species composition and stand structure to MPB and forest management. I used the Central Rockies Variant extension of the Forest Vegetation Simulator (FVS) (Dixon, 2002), a set of allometric equations defining growth rates by tree species in Colorado, New Mexico, Arizona and South Dakota forests, to model future tree and stand conditions over time. The response of 10 uncut MPB-infested stands, 3 partial cut and 3 clearcut stands were modeled individually using 2009 measurements of overstory conditions (from 5 m x 150 m transects), advance regeneration and seedling recruitment (from 3.6 m radius plots). U.S. Forest Service, Forest Inventory and Analysis data (FIA, unpublished) were used to estimate future recruitment and mortality each decade over the course of the simulation, based on overstory basal area. Simulations were refined using a site index of 65 developed for lodgepole pine at the Fraser Experimental Forest (Alexander, 1966) for all simulations. Site index is a measure of forest site quality based on the height of dominant trees at 100 years of age (Alexander, 1966).

Statistical Analysis

I used a backward elimination regression approach in a generalized linear mixed model to assess statistical significance of site conditions on seedling recruitment (measured in groundcover plots) (Neter et al., 1989). Overstory and groundcover conditions varied considerably within single harvested and untreated stands, and were not of singular interest; therefore stands were treated as a random effect. Overstory and groundcover conditions were considered as continuous fixed effects. Seedling counts were skewed and non-normal, so I used a zero-inflated Poisson error distribution, as recommended for over-dispersed data (Lambert, 1992; SAS, 2008). I compared recruitment and advance regeneration densities using the multi-response permutation procedure (MRPP) (Cai, 2006), a non-parametric method that does not assume normality or homogeneity of variance. The null hypothesis under MRPP assumes that observations are independent and identically distributed (Cai, 2006). Growth of advance regeneration from 2008 and 2009 height measurements on the same individuals, were compared using a paired t-test. Horizontal coordinates for each sample plot ($n = 114$) were used to test for spatial correlation of seedling regeneration using a variogram analysis and was not found to be significant (Littell et al., 2006). Statistical significance is reported at the $\alpha = 0.05$ level unless otherwise noted.

Results

Overstory Stand Condition

Lodgepole pine represented 45% to 100% of the total basal area in untreated stands, 80% (29.9 m^2 ha^{-1}) on average (Fig. 1). Pine beetle infestation killed between 60% and 93% of the overstory lodgepole pine overstory (mean = 74%); beetle-killed pine represented 60% of total stand basal area, on average. Aspen accounted for 10% of total basal area and subalpine fir and Engelmann spruce constituted roughly 5% each. Alder (*Alnus incana* supsp. *tenuifolia*) was found in 15% of overstory transects and constituted less than 0.1% of total basal area. Harvest removed between 39 and 86% of total basal area, leaving an average of 22.0 and 4.3 m^2 ha^{-1} in partial and clearcut stands, respectively. Leaf area index (LAI) ranged between 0.04 and 2.94 and was a highly significant predictor of spruce and fir advance regeneration densities, but not lodgepole. Overstory basal area of subalpine fir was a significant predictor of advance regeneration of that species.

Advance Regeneration

Subalpine fir was the most common species (< 2.5 cm DBH), accounting for 52% of advance regeneration (averaging 2,061 stems ha^{-1}) and occurring in 59% of study plots (Fig. 2). Lodgepole pine and aspen accounted for 18% and 25% of advance regeneration, respectively (averaging 698 and 969 stems ha^{-1}) and were found in 46% and 44% of plots. Engelmann spruce was the least abundant and least common of the four dominant tree species, averaging 254 stems ha^{-1} and found in 26% of study plots. Advance regeneration, averaged 3,953 stems ha^{-1} among all species.

Seedling Recruitment

The density of recruitment was three times higher in harvested units (6,487 ha^{-1}) compared to untreated stands (2,021 ha^{-1}). Aspen was the most abundant recruiter after harvest accounting for 51% of all recruits in treated areas, establishing on average 3,337 stems ha^{-1}, significantly more than untreated areas (335 stems ha^{-1}, 17% of recruitment in untreated stands). Lodgepole pine was more plentiful in harvested than untreated stands where it accounted for 43% and 29% of recruitment, respectively (2,803 and 589 recruits ha^{-1}, respectively) (Fig. 3). Subalpine fir averaged fewer recruits in harvested areas (329 recruits ha^{-1}, 5% of recruitment) as compared to untreated areas (1,064 recruits ha^{-1}, 53% of recruitment). Engelmann spruce recruits did not differ between treatments, averaging 16 stems ha^{-1} in harvested stands and 31 stems ha^{-1} in untreated areas. Lodgepole pine was the most widely distributed recruit in harvested stands, found in 57% of sample plots, ranging between 247 and 31,600 stems ha^{-1} (Fig. 4) Subalpine fir was the most abundant and widely distributed recruit in untreated areas, found in 62% of sample plots and ranging between 247 and 7,400 stems ha^{-1} (Fig. 5); subalpine fir was found in 43% of plots in harvested areas.

Across all treatments (untreated and harvested) percentages of various types of groundcover, measured in meter-square plots, were tested as predictors of seedling recruitment using regression analysis. Parameter estimates indicate the mean increase in number of recruits ha^{-1} for each 1 percent increase in groundcover. Bare soil ($\beta = 25.5$), forbs ($\beta = 12.6$) and harvest residue ($p = 0.10$, $\beta = 6.7$) were significant predictors of lodgepole recruitment, increased percent groundcover of each was associated with increased lodgepole recruitment. Amongst all survey plots bare soil, forb and harvest residue cover ranged between 0 – 79%, 0 - 60% and 0 – 100%, respectively. Lodgepole pine recruitment declined with increased LAI ($\beta = -1438.0$). Subalpine fir recruitment declined with increased forest floor depth ($\beta = -4.5$). Engelmann spruce and aspen recruitment was unrelated to groundcover or canopy LAI.

Seedling Growth

Among lodgepole pine advance regeneration, I saw a significant increase in annual leader growth from 2008 to 2009 in harvested and untreated stands, increasing by 1 cm and 1.4 cm, respectively ($p < 0.01$; Fig. 6). On average, advance regeneration of pine had significantly more leader growth in untreated stands compared to harvested areas (6.1 vs. 4.3 cm yr^{-1}). However, lodgepole recruitment (≤ 2 years old) grew more in harvested areas as compared to untreated stands (2.6 and 2.0 cm yr^{-1}, respectively) (Fig. 7). Subalpine fir advance regeneration had significantly less leader growth in harvested stands compared to untreated stands in 2008 and 2009 (2.7 and 5.6 cm $year^{-1}$, respectively). Subalpine fir leader growth in harvested and untreated stands did not differ between 2008 and 2009. LAI was not a significant predictor of growth of pine or fir advance regeneration.

Forest Growth Simulation

I observed differences in projected future stand conditions between untreated, partial cut and clearcut treatments. Among all treatments, stands reached maximum stem counts within 20 years, and steadily declined throughout the 200 year simulation (Fig. 8).

Species composition changed most rapidly in partial cut stands, which were dominated by aspen (~35% of basal area) in the first 3 decades. After 100 years of simulated growth, both partial and clearcut stands had similar total basal areas (44.8 and 36.2 m2 ha^{-1}, respectively) however partial cut stands were dominated by subalpine fir and clearcut stands were dominated by lodgepole pine. Untreated stands were similar to partial cut units, averaging 41.9 m^2 ha^{-1} of basal area with subalpine fir making up 57% of the total. After two centuries, untreated and partial cut stands are projected to be dominated by subalpine fir (> 80% of total basal area). Clearcut units will have stand attributes similar to pre-outbreak stands in 80 to 100 years and after 200 years lodgepole will continue to be the dominant overstory species (45% of basal area).

Discussion

Forest recovery following extensive beetle mortality is thought to hinge on advance regeneration established prior to the outbreak (Roe & Amman, 1970; Veblen et al., 1991). I found advance regeneration in 94% of all plots, averaging 3,953 trees ha^{-1}, across my study area. Species composition of advance regeneration in harvested and uncut stands was more evenly distributed among subalpine fir (51%), lodgepole pine (19%) and quaking aspen (24%) than the current overstory which is dominated by lodgepole (Figs.1 & 2). These finding suggest there is an adequate density of advance regeneration to achieve well-stocked future stands, and that these stands will be less susceptible to MPB infestations because of the greater proportion of non-host tree species, notably subalpine fir.

In beetle infested lodgepole pine stands, harvest is intended to stimulate new recruitment (Lotan, 1975). In my study area, harvest stimulated abundant lodgepole pine recruitment averaging 2,803 recruits ha^{-1} but recruitment was patchy, with recruits occurring in 57% of plots and varying between 0 and 31,000 stems ha^{-1} (Figs. 3 & 4). Aspen was the most abundant recruit in harvested stands, on average adding 3,337 stems ha^{-1}; however, recruitment varied between 0 and 43,000 stems ha^{-1}, and was found in 43% of survey plots. In contrast, subalpine fir was the most abundant new recruit in untreated stands, averaging 1,064 stems ha^{-1} and found in 62% of survey plots; recruitment varied between 0 and 7,400 recruits ha^{-1} (Figs. 3 & 5). Lodgepole pine recruitment also occurred in untreated stands but was limited to one-third of survey plots and varied between 0 and 10,000 stems ha^{-1}. I found pronounced heterogeneity in overstory and groundcover conditions in harvested stands, as compared to untreated stands, which may have contributed to greater variability in seedling recruitment.

Certification of successful post-harvest recruitment on U.S. Forest Service land requires a minimum of 370 stems ha^{-1} in at least 70% of sample plots within a treatment unit (USDA, 1997). In southern Rockies lodgepole pine forests, managers typically consider development of well-stocked stands will require post-harvest seedling densities to exceed the minimum stocking threshold by an order of magnitude. Required seedling stocking was similar in harvested and untreated stands with 77% and 79% of plots meeting requirements, respectively (USDA, 1997). In untreated stands, 18% of plots were considered well-stocked, exceeding 3000 stems ha^{-1}, compared to 56 % of harvested stands.

Site conditions are a critical component of seedling establishment following harvest and differ greatly depending on cutting method and treatment of harvest residue (Alexander, 1986; Lotan, 1964; 1975). I found increased LAI had a negative impact on lodgepole pine recruitment while increased groundcover of soil, harvest residue and forbs were associated with increased recruitment of lodgepole. Prior to analysis I expected LAI and bare soil cover would be important predictors as lodgepole is a shade intolerant species preferring a seedbed of bare mineral soil (Lotan & Perry, 1983). A high density of cones in harvest residue provided increased seed source in areas with increased residue, and therefore increased recruitment. I suspect increased herbaceous plant cover, not considered a competitor to new recruitment, was an indication of moist micro-sites with favorable growing conditions. Across all treatments, I found increased forest floor depth was associated with decreased subalpine fir recruitment and increased LAI was associated with increased fir recruitment. Fir was the most dominant species in untreated stands due to an increased shade tolerance in comparison to pine, spruce and aspen (Kobe & Coates, 1997). Surface rock cover was found to be the most significant predictor of aspen recruitment ($p = 0.07$, $\beta = -1181.2$). This might indicate that rocky soils present an obstacle to new aspen sprouts, which emerge from existing root structures or that aspen roots simply are less abundant in rocky soils.

Advance regeneration has been shown to increase annual leader growth following canopy reduction after years to decades of suppressed growth beneath the canopy. Following overstory removal in Idaho, undamaged lodgepole pine advance regeneration increased annual leader growth after a three year time lag, but took up to ten years to fully adjust to new growing conditions (Murphy et al., 1999). I found that lodgepole seedlings (≤ 2 years old) grew significantly more in harvested compared to untreated stands (Fig. 7). As anticipated, subalpine fir showed less growth in harvested areas, as compared to untreated stands, with 25% of trees showing no new leader growth in 2009. Subalpine fir favors shade during early development and does not compete well with lodgepole and spruce when light intensity exceeds 50% of full shade as it has a low tolerance of high temperatures and is susceptible to heat girdling (Alexander et al., 1990). Although I found lodgepole pine advance regeneration in harvested stands had significantly less leader growth (4.3 cm yr^{-1}) compared to untreated stands (6.1 cm yr^{-1}), growth increased significantly from 2008 to 2009 in both harvested and untreated stands indicating a response to diminished canopy cover (due to harvest and overstory mortality, respectively) (Fig. 6).

In Colorado, the extent and severity of overstory lodgepole pine mortality due to MPB has raised concerns over the future trajectory of forests (Rocca & Romme, 2009). To provide an estimate of forest recovery, changes in species composition and the effects of management, I projected stand characteristics in untreated, partial cut and clearcut stands over 200 years (Fig. 8). Growth simulations showed all stands steadily declined in total stem density over the course of the simulation, reaching their highest densities within the first twenty years. Although lodgepole was a substantial component of all stands initially, it declined in total basal area over the course of the simulation in untreated and partial cut stands, in favor of subalpine fir. The dominance of subalpine fir in these stands is the result of high lodgepole pine mortality in untreated stands and the selective removal of dead lodgepole in partial cut stands. Following clearcut treatments, lodgepole remained the dominant species and after ~100 years of growth and had similar attributes to the current stands prior to MPB infestation.

My investigation suggests that advance regeneration met or exceeded stocking requirements in the vast majority of untreated, beetle-infested stands. In addition, I found that as leaf area decreases following overstory mortality, stands will respond with additional recruitment. Current species composition and growth projections suggest untreated and partial cut stands will be dominated by subalpine fir, a late-seral species, and be less susceptible to future MPB outbreak. Although stands dominated by subalpine fir will be less vulnerable to MPB, they will have an increased susceptibility to other insect and disease agents such as spruce budworm (*Choristoneura sericeus*), fir engraver (*Scolytus ventralis*), fir broom rust (*Melampsorella caryophyllacearum*), and various wood rotting fungi (Alexander et al., 1990). Clearcut harvesting in beetle-infested stands stimulates abundant lodgepole pine regeneration, and will likely stimulate growth of lodgepole advance regeneration and cull subalpine fir. Although lodgepole and aspen will be dominant species in untreated and partial cut stands for ~2 decades, subalpine fir will become the dominant component of these stands after 100 years of projected growth and continue to increase for another century.

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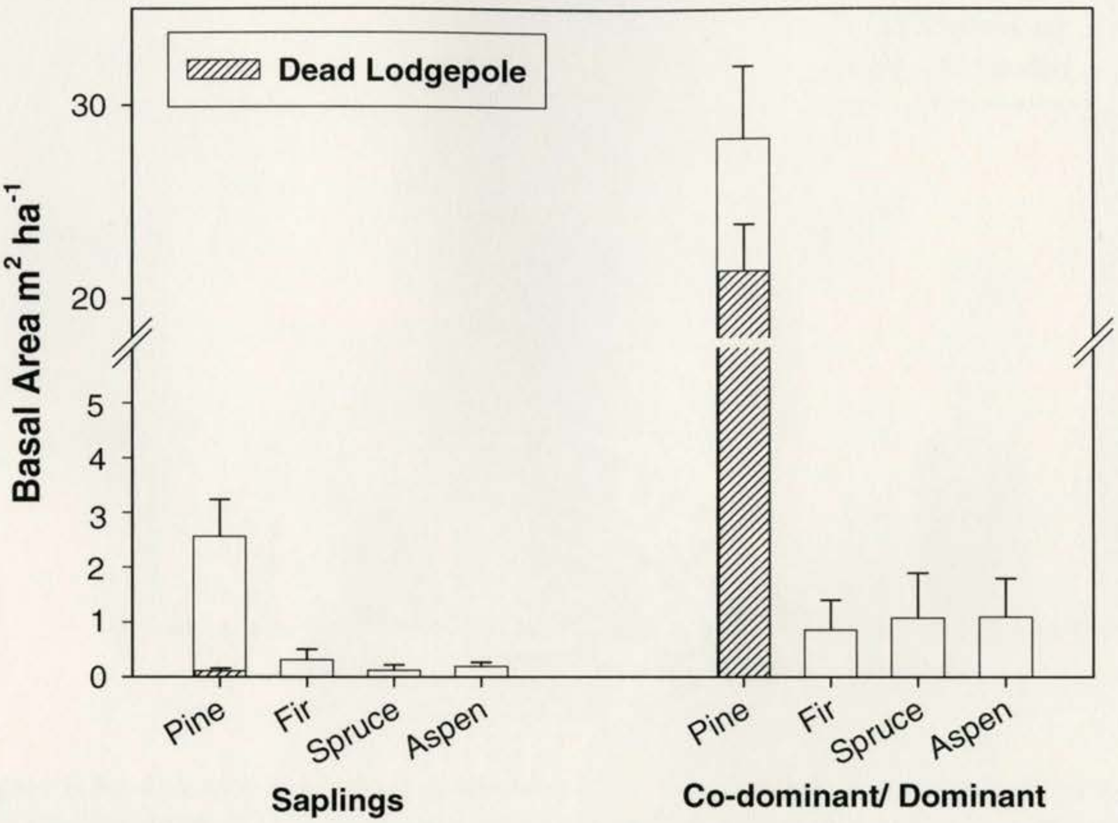

Figure 1. Composition of sapling (< 10 cm DBH) and co-dominant/dominant trees (> 10 cm DBH) in untreated areas (n = 10 stands). Hatched area represents basal area of dead lodgepole pine killed by mountain pine beetle. Error bars represent standard error.

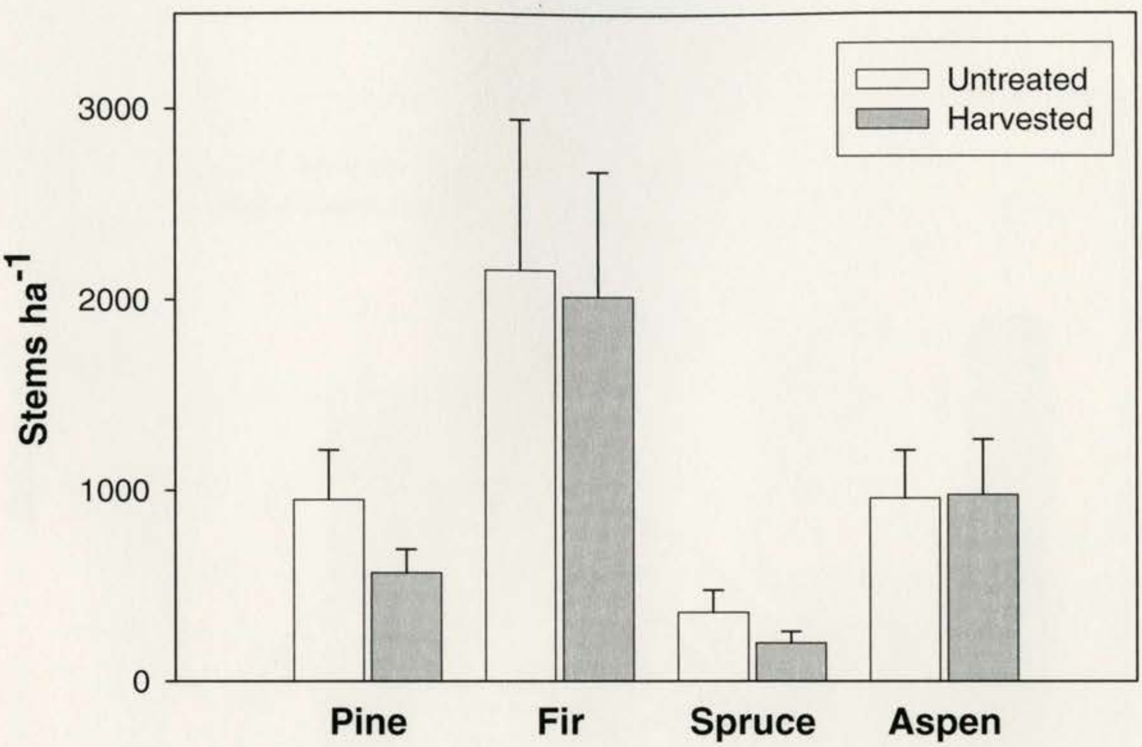

Figure 2. Mean density of advance regeneration (< 2.5 cm at DBH) in untreated (n = 39 plots) and harvested stands (n = 75 plots). All advance regeneration was established prior to treatment. Error bars represent standard error.

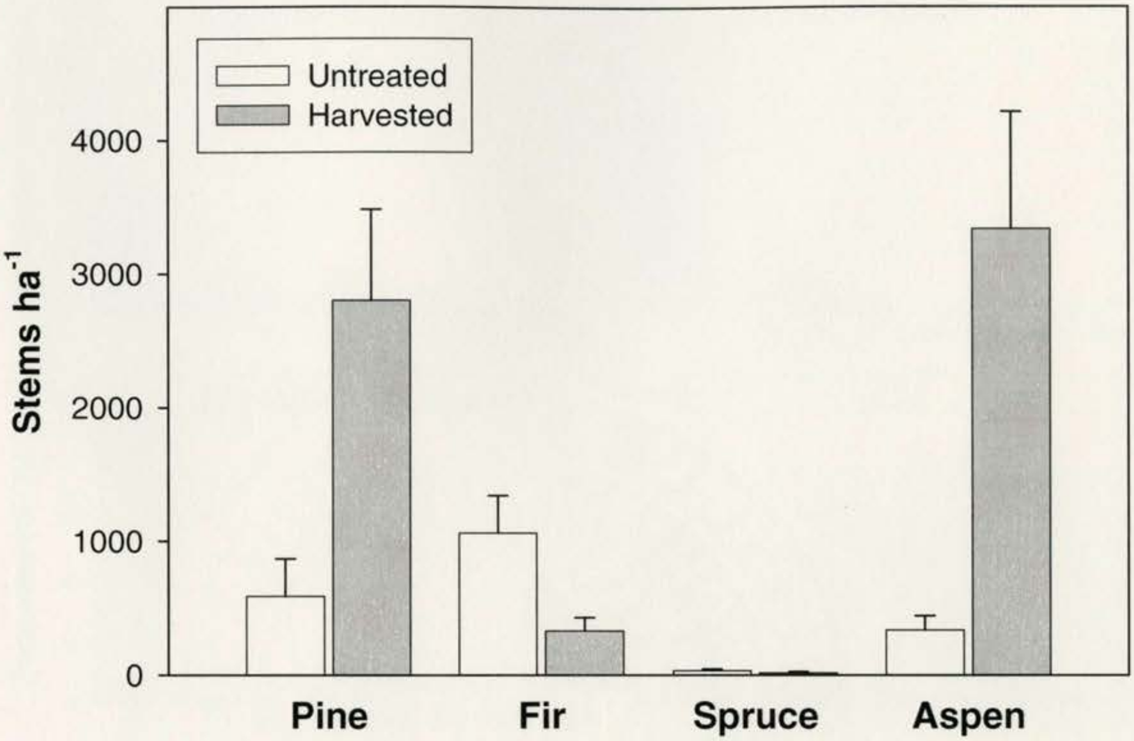

Figure 3. Density of seedlings that have established since 2008 in untreated (n = 39 plots) and harvested areas (n = 75 plots). Error bars represent standard error.

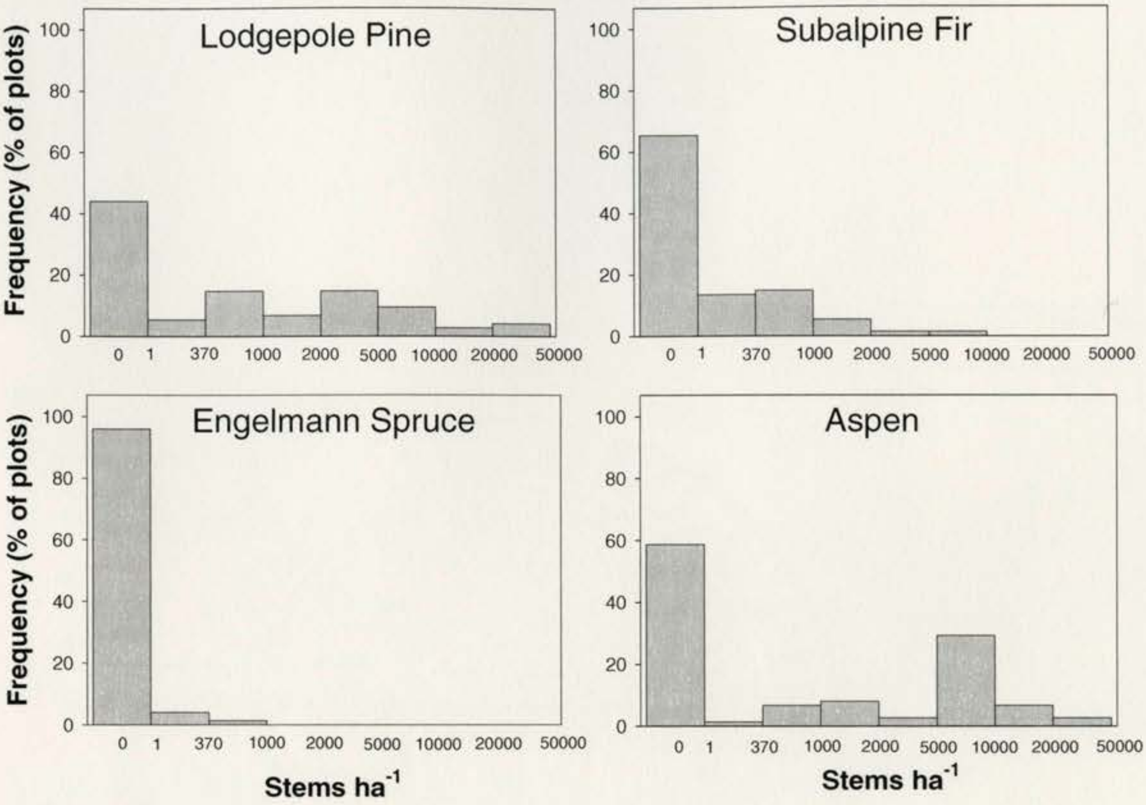

Figure 4. Seedling recruitment in harvested pine beetle-infested stands (n = 75 plots).

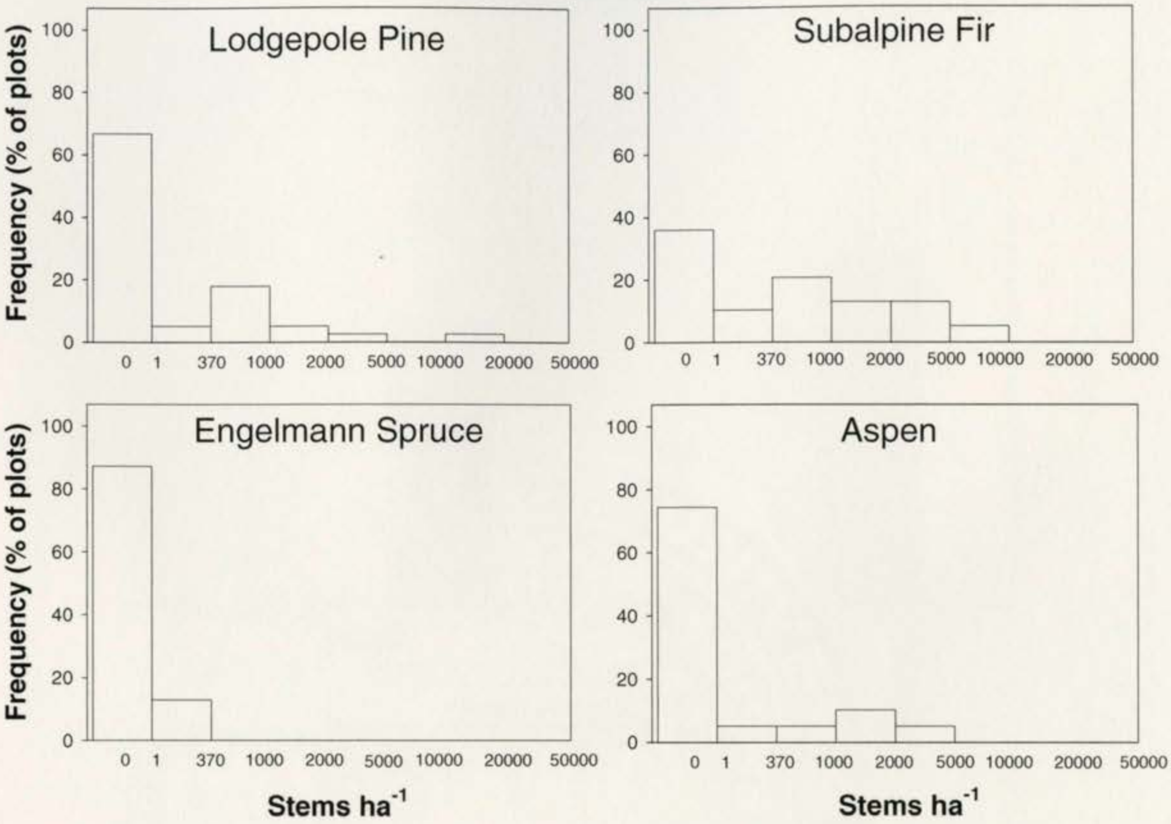

Figure 5. Seedling recruitment in untreated pine beetle-infested stands (n = 39 plots).

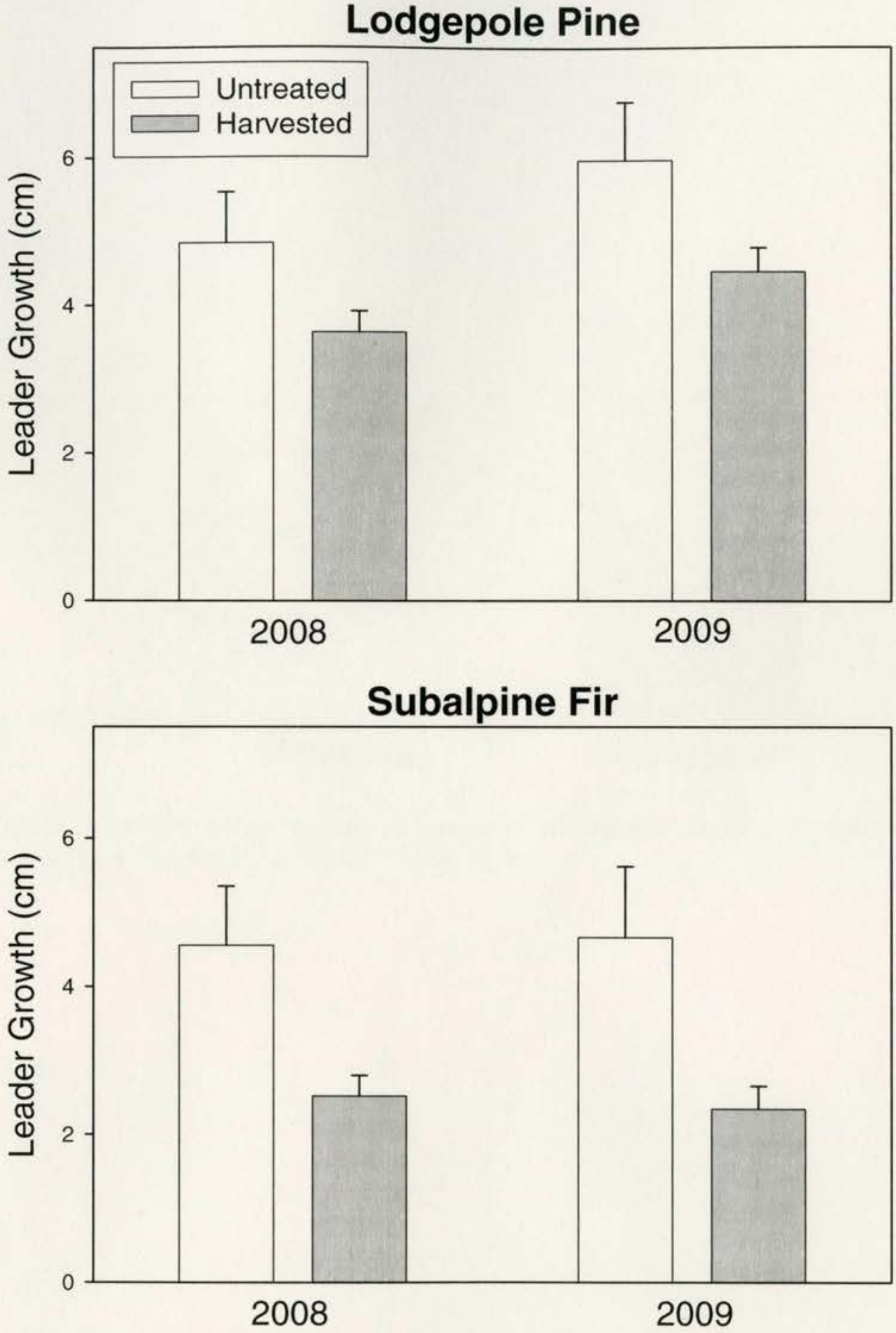

Figure 6. Annual leader growth of lodgepole pine (n = 114 trees) and subalpine fir (n = 117 trees) in 2008 and 2009 in untreated and harvested stands. Annual height growth measured between true branch whorls marked by annual bud scars. Error bars represent standard error.

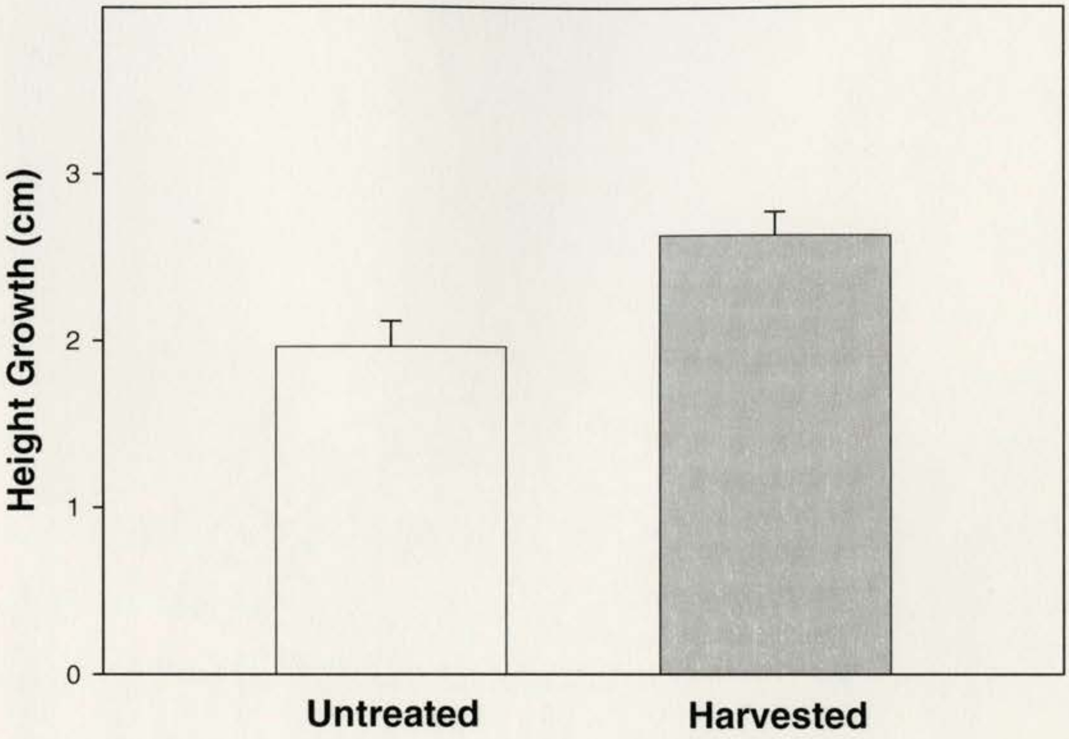

Figure 7. Annual height growth of lodgepole recruitment (trees ≤ 2 years old) in untreated and harvested stands (n = 75 seedlings).

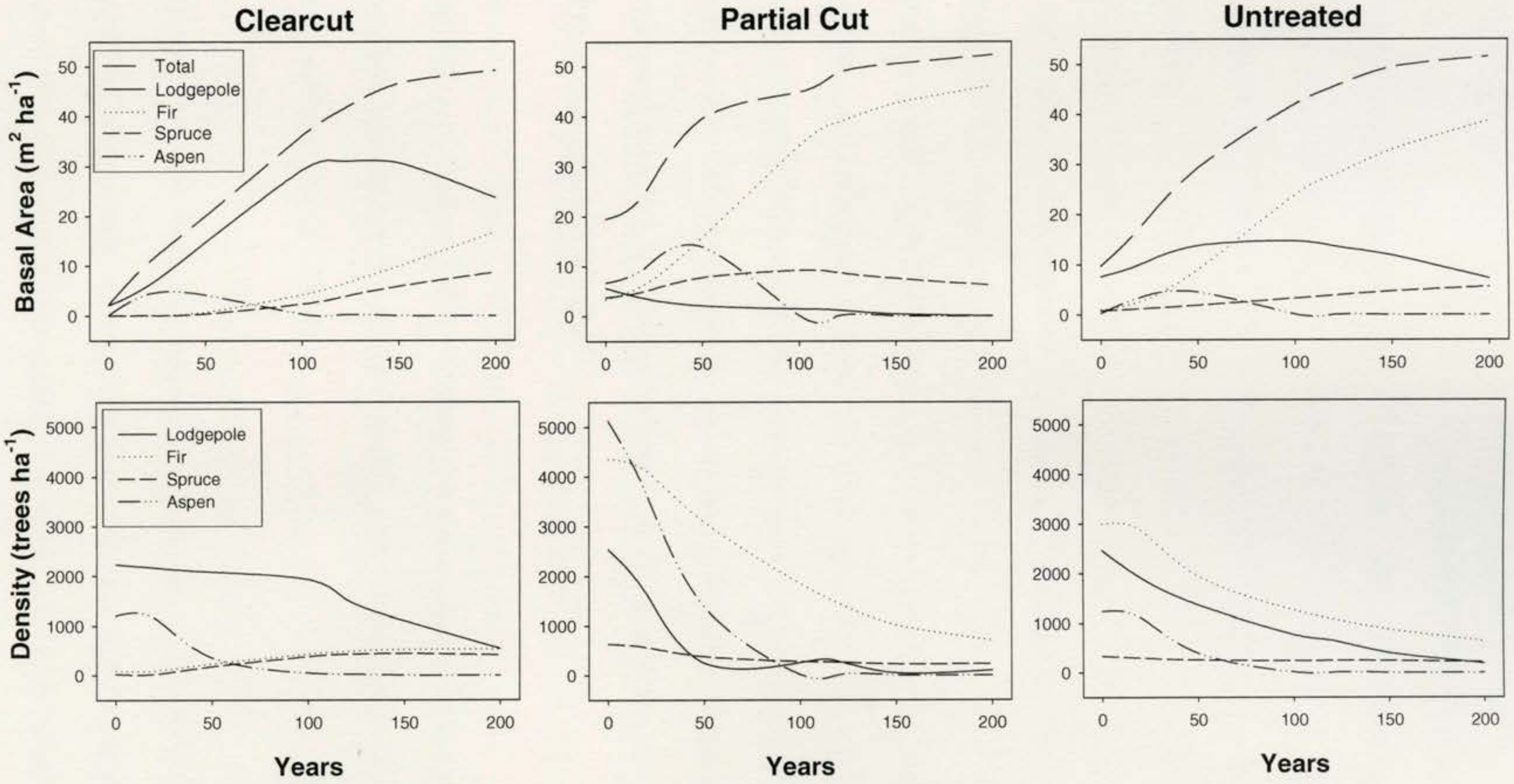

Figure 8. Projected stand development based on initial observations in clearcut (n = 3 stands), partial cut (n = 3 stands) and untreated (n = 10 stands) areas. Growth simulated using the Forest Vegetation Simulator (Dixon, 2002).

Chapter Four

Conclusions and Management Implications

Following a decade of infestation, the mountain pine beetle has transformed pine forests across western North America (Raffa et al., 2008; Aukema et al., 2006). Unlike wildfire and windthrow, insect infestations are selective mortality agents which do not significantly reduce biomass or expose extensive mineral soil (Veblen et al. 1991). Forest recovery following beetle mortality is thought to hinge on advance regeneration established prior to the outbreak and their expected growth release under a deteriorating canopy (Roe & Amman, 1970; Sibold et al., 2007; Veblen et al., 1991). Since 2000, severe overstory mortality has raised concerns over public safety, fire risk, wildlife, recreation and infrastructure. In the last decade the Sulphur Ranger District (Arapaho-Roosevelt National Forest) has harvested nearly 3,700 hectares of lodgepole pine-dominated forests to reduce crown fuel loads and regenerate lodgepole pine stands. The widespread mortality of overstory lodgepole pine is a certainty, but the future trajectory of these ecosystems is unclear.

The major conclusions and implications for management from this study conducted in lodgepole pine forests of northern Colorado, following a decade of severe mountain pine beetle outbreak, are as follows:

(1) Mountain pine beetle has reduced lodgepole pine basal area by 60 to 93%. However, understory tree surveys in Fraser Experimental Forest indicate that in 2008, 85% of survey plots met stocking requirements stipulated in the forest plan (USDA, 1997). In

addition, understory lodgepole in uncut stands responded to overstory mortality with a 23% increase in leader growth from 2008 to 2009. Moreover, seedling stocking surveys following harvest indicated recruitment exceeded Arapaho-Roosevelt stocking requirements in 77% of survey plots (USDA, 1997). Comparisons of historic seedling surveys suggest recruitment densities are equivalent or higher in stands harvested as predominately dead trees following infestation than those harvested before the outbreak. I found that untreated stands also established recruitment in response to overstory mortality and canopy foliage loss in the same time period, meeting or exceeding requirements in 79% of plots. Recruitment varied principally by species composition with untreated stands dominated by subalpine fir while harvested stands recruited lodgepole and aspen.

(2) To estimate forest development and the effects of management, I projected stand characteristics in untreated, partial cut and clearcut stands over 200 years, using the Forest Vegetation Simulator (Dixon, 2002). Growth projections suggest that untreated stands will become more evenly distributed between subalpine fir and lodgepole pine after 50 to 100 years and will have a total basal area equivalent to pre-outbreak stands after ~75 years. Beyond a century of growth, subalpine fir will dominate untreated stands, making them less susceptible to future pine beetle infestations. Partial cut stands will have similar attributes to untreated areas, and be dominated by subalpine fir within 50 years. Following clearcut treatments, lodgepole remained the dominant species and after ~100 years of growth and had similar attributes to the current stands prior to infestation.

(3) Tree recruitment has responded to overstory mortality in harvested and untreated mountain pine beetle-infested stands. These forest ecosystems will persist following clear and partial cut treatments as well as no treatment, but each alternative carries different future management implications. Clearcut harvest treatments will promote the establishment of a single cohort of lodgepole pine. High recruitment densities in these stands will likely require stand thinning within a few decades to reduce ladder fuels and to hasten growth and will be susceptible to future MPB infestations within a century. Partial cut stands, dominated by subalpine fir, will be less vulnerable to MPB, but will have an increased susceptibility to other insect and disease agents such as spruce budworm (*Choristoneura sericeus*), fir engraver (*Scolytus ventralis*), fir broom rust (*Melampsorella caryophyllacearum*), and various wood rotting fungi (Alexander et al., 1990). Untreated stands will dominate the landscape following the current mountain pine beetle outbreak as less than 15% of susceptible stands will be treated (Sulphur Ranger District, unpublished data). Uncut stands will have a more diverse species composition than partial and clearcut stands, over the first century of growth, distributed principally between lodgepole pine and subalpine fir, reducing the risk of massive overstory mortality from a single disturbance agent.

These results illustrate the critical initial stages of stand development in the lodgepole pine stands most heavily impacted by mountain pine beetle in Colorado. These two study areas represent a range of species composition, elevation, and site conditions typical of lodgepole pine forests and management techniques common to the greater outbreak area in the Rocky Mountains. Although these findings are applicable to many of the most heavily affected stands in central Colorado, these study sites are incorporated into a larger study, spanning multiple National Forests. Two additional sites in the Routt National Forest and one in the Colorado State Forest span the most severe mortality due to MPB in Colorado. Similar measurements at each site will more clearly define the future trajectory of these ecosystems following the current outbreak.

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