2018

MOUNTAIN PINE BEETLE INDUCED CHANGES TO LODGEPOLE PINE FOREST STAND DYNAMICS AT LUBRECHT EXPERIMENTAL FOREST

Ben G. O'Connor
The University Of Montana

Recommended Citation

O'Connor, Ben G., "MOUNTAIN PINE BEETLE INDUCED CHANGES TO LODGEPOLE PINE FOREST STAND DYNAMICS AT LUBRECHT EXPERIMENTAL FOREST" (2018). *Graduate Student Theses, Dissertations, & Professional Papers*. 11308.
https://scholarworks.umt.edu/etd/11308

MOUNTAIN PINE BEETLE INDUCED CHANGES TO LODGEPOLE PINE FOREST STAND DYNAMICS AT LUBRECHT EXPERIMENTAL FOREST

By

BENJAMIN GEORGE O'CONNOR

B.S. Resource Conservation, University of Montana, Missoula, MT, 2008

Professional Paper

presented in partial fulfillment of the requirements
for the degree of

Master of Science
Forestry

The University of Montana
Missoula, MT

December 2018

Approved by:

Scott Whittenburg, Dean of the Graduate School
Graduate School

Christopher R. Keyes, Research Professor, Chair
Department of Forest Management

Edwin Burke, Professor
Department of Forest Management

Daniel Spencer, Professor
Department of Environmental Studies

Thomas Perry, Forester
Montana Department of Natural resources and Conservation

ACKNOWLEDGEMENTS

I would first like to thank my committee members for all of their time, energy, and input throughout the process. Foremost, Dr. Christopher Keyes for his constant availability and belief in me as a graduate student. His positivity, humor, guidance and expertise on the subject matter were all very influential to my success. Dr. Burke for his wealth of forestry and dendrology knowledge. Dr. Spencer for opening my eyes to the social aspects of natural resource management and improving my writing skills. Mr. Thomas Perry for his academic and practical forestry expertise, study site orientation, and historical data management.

My gratitude goes out to my peers at the Applied Forest Management Program – Justin Crotteau, Haley Anderson, and Katelynn Bowen – for their support and advice in navigating through the graduate school process. I would also like to thank Taylor Margot and Thayer Nicholaus for their help with data collection. Lastly, I am very appreciative of the support of my parents, Dennis and Virginia O'Connor.

TABLE OF CONTENTS

CHAPTER 1: Mountain pine beetle induced changes to lodgepole pine forest stand dynamics at Lubrecht Experimental Forest: Overview

CHAPTER 2: Disturbance interactions between mountain pine beetle (*Dendroctonous ponderosae*) epidemics and wildfire occurrence in lodgepole pine (*Pinus contorta*) stands: Literature review

CHAPTER 3: Mountain pine beetle induced changes to lodgepole pine forest stand dynamics at Lubrecht Experimental Forest: Case study

LIST OF FIGURES

CHAPTER 3

LIST OF TABLES

CHAPTER 3

University of Montana

CHAPTER 1:

Mountain pine beetle induced changes to lodgepole pine forest stand dynamics at Lubrecht Experimental Forest: Overview

Ben O'Connor

Chair of the Supervisory Committee:
Christopher Keyes, Research Professor
Department of Forest Management
College of Forestry and Conservation

Insect outbreaks and wildfire constitute the two most significant disturbance agents of subalpine forests of western North America, especially the Rocky Mountain West (Raffa et al. 2008; Lynch et al. 2006). Mountain pine beetles (hereafter MPB) are native to western North America and have coexisted with subalpine forests of the Rocky Mountains for thousands of years. At endemic populations they are generally present in low numbers, and primarily kill weak trees. When environmental and forest stand conditions are favorable their populations can increase rapidly to outbreak conditions. Epidemic population levels occur when an outbreak expands to encompass an even larger geographic area, causing extensive tree mortality over large spatial scales (Romme et al. 2006). However, the specific factors determining sustained outbreaks are unclear (Raffa et al. 2008). Previous research has focused primarily on the influence of climatic factors on MPB outbreaks, and only to a lesser extent focused on forest conditions; studies addressing forest stand characteristics are limited in spatial extent. The literature suggests that regional climatic conditions catalyze an outbreak, but stand conditions influence outbreak progression, severity, and extent.

Among western tree species, none is more intertwined with MPB than lodgepole pine (*Pinus contorta* var. *latifolia)*. Disturbance history and frequency as well as physical site conditions encompass the complex interactions that influence lodgepole pine forest characteristics and MPB outbreaks (Li et al. 2005). If weather conditions accommodate winter survival and reproduction, outbreak severity is limited by available susceptible lodgepole pine host trees (Safranyik 1978). Although beetles and host trees interact on an individual level, broad scale stand composition and structure influence host tree availability, nutritional quality, and defensive fitness (Raffa et al. 2008). Stand characteristics in lodgepole pine that meet these criteria are: a stand density of 300-600 trees per acre, an average age > 80 years, and an average diameter at breast height > 8 in (Amman et al. 1990). In a study at the subwatershed-scale across the Northern Rockies, Williams et al. (2018) identified a mean basal area > 93.2 ft^2/ac and a quadratic mean diameter > 7.1 in as a threshold that predisposed lodgepole pine forest to MPB attack. An outbreak can occur when susceptible stand conditions exist over a large spatial scale and coincide with favorable climatic patterns.

The MPB is an aggressive native bark beetle of western North America that attacks numerous *Pinus* spp, but consistently has the largest impact on lodgepole pine. The vast spatial scale and overall loss of forest resources from the recent outbreaks have raised questions and concerns among land managers and the general public alike. Since the mid-1990s, over 27,400 square miles of pine forests in the western U.S. have experienced MPB caused tree mortality (Hart et al. 2015). Depending on mortality levels, MPB outbreaks can have significant effects on forest stand structure and dynamics following an outbreak. Understory regeneration, coarse woody debris and overall stand trajectories can also be affected by MPB outbreaks.

In Canada, where the effects of MPB on lodgepole pine have been catastrophic, Taylor and Carroll (2003) determined that a century of fire suppression efforts led to a decrease in area burned, resulting in an average age increase of lodgepole pine forests and subsequently an increase in highly susceptible age classes of lodgepole pine. Although the definitive effects of a century of fire suppression on the age class distribution of lodgepole pine are uncertain, it is likely that average tree age has increased as a result. An increase in average tree age over the last century may have led to more landscape connectivity and greater abundance of MPB host material, contributing to the magnitude of recent outbreaks. In addition, both natural and human-caused disturbances in the late 1800s to early 1900s may have ultimately facilitated a landscape homogeneity that contributed to outbreak severity and extent.

Large stand-replacing fires in lodgepole pine ecosystems in the late 1800s and early 1900s would have resulted in even-aged stand regeneration across burned areas. Future fire events would have likely re-burned through some of these areas, breaking up the connectivity of future MPB habitat. Fire suppression effectively decreased the natural mosaic that occurred at the interface of high-severity and mixed-severity fire regimes. Even-aged stands that regenerated after fires remained intact as fire suppression gained momentum in the western U.S. Similarly, extensive and intensive logging that occurred in the 1890s-1930s had a comparable effect on post-harvest stand homogeneity. Large areas were clearcut and either replanted or naturally regenerated, resulting in even-aged regeneration cohorts. Several decades to a century later as individual trees matured, these stands contained the host characteristics to accommodate a large scale outbreak.

Stands that possess high risk characteristics can be treated to reduce stand homogeneity and MPB susceptibility. Tree host characteristics including age, diameter at breast height, phloem thickness, vigor, growth rate (average annual increase in volume) and density can help assess stand vulnerability to MPB outbreaks (Nelson et al. 2008; Hicke and Jenkins 2008). Silvicultural alteration of stand structure and composition may help mitigate outbreak risks. Treatments that include partial cutting to remove large trees and clearcutting have been recommended to reduce forest vulnerability to MPB mortality, and to encourage species and age class heterogeneity (Mitchell et al. 1983; Whitehead and Russo 2005). Thinning mature lodgepole pine stands from below to a spacing of 13 ft or more to increase vigor and tree defenses has proven effective at limiting mortality when MPB populations are low to moderate, however, at epidemic levels damage still occurs (Whitehead and Russo 2005). While management actions on a stand scale can increase vigor and decrease local mortality, they are ineffective at reducing outbreak potential on a landscape scale unless widely implemented (Raffa et al. 2008; Klutsch et al. 2009). Such understanding of beetle-host dynamics and land use history can help forest managers avoid repeating the factors that led to the most recent outbreaks and widespread forest mortality.

This professional paper consists of two core chapters that address the topic of MPB outbreaks in subalpine forests. Chapter 2 is a literature review focused on disturbance interactions between MPB epidemics and wildfire occurrence in western North America. Influential and contemporary publications were examined to explore working hypotheses regarding how MPB outbreaks influence wildfire potential and severity over time. Chapter 3 is a case study at the University of Montana's Lubrecht Experimental Forest. The objective was to examine changes to lodgepole pine forest stand dynamics following MPB outbreak.

References

Amman, G., McGregor, M., & Dolph Jr, R. (1990). Forest insect and disease leaflet 2: Mountain pine beetle. *USDA Forest Service, Washington, DC*.

Hart, S. J., Schoennagel, T., Veblen, T. T., & Chapman, T. B. (2015). Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proceedings of the National Academy of Sciences*, 201424037

Hicke, J. A., & Jenkins, J. C. (2008). Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. *Forest Ecology and Management*, *255*(5-6), 1536-1547

Klutsch, J. G., Negron, J. F., Costello, S. L., Rhoades, C. C., West, D. R., Popp, J., & Caissie, R. (2009). Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management*, *258*(5), 641-649.

Li, C., Barclay, H. J., Hawkes, B. C., & Taylor, S. W. (2005). Lodgepole pine forest age class dynamics and susceptibility to mountain pine beetle attack. *Ecological Complexity*, *2*(3), 232-239.

Lynch, H. J., Renkin, R. A., Crabtree, R. L., & Moorcroft, P. R. (2006). The influence of previous mountain pine beetle (Dendroctonus ponderosae) activity on the 1988 Yellowstone fires. *Ecosystems*, *9*(8), 1318-1327.

Nelson, W. A., Potapov, A., Lewis, M. A., Hundsdörfer, A. E., & He, F. (2008). Balancing ecological complexity in predictive models: a reassessment of risk models in the mountain pine beetle system. *Journal of Applied Ecology*, *45*(1), 248-257.

Mitchell, R. G., Waring, R. H., & Pitman, G. B. (1983). Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science*, *29*(1), 204-211.

Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G., & Romme, W. H. (2008). Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *AIBS Bulletin*, *58*(6), 501-517.

Romme, W. H., Clement, J., Hicke, J., Kulakowski, D., MacDonald, L. H., Schoennagel, T. L., & Veblen, T. T. (2006). Recent forest insect outbreaks and fire risk in Colorado forests: a brief synthesis of relevant research. *Colorado Forest Research Institute*.

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. *In Proceedings of a Symposium: Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. April 25–27, 1978. Pullman, Washington. *Edited by* Kibbee, D.L.,Berryman, A. A., Amman, G. D., and Stark, R. W. University of Idaho, Moscow, Idaho pp. 77–84.

Taylor, S. W., & Carroll, A. L. (2003, October). Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. In *Mountain pine beetle symposium: Challenges and solutions* (pp. 41-51). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC.

Whitehead, R. J., & Russo, G. L. (2005). *Beetle-proofed lodgepole pine stands in interior British Columbia have less damage from mountain pine beetle* (Vol. 402). Pacific Forestry Centre.

Williams, H., Hood, S., Keyes, C., Egan, J., & Negrón, J. (2018). Subwatershed-level lodgepole pine attributes associated with a mountain pine beetle outbreak. *Forests*, *9*(9), 552.

University of Montana

CHAPTER 2:

Disturbance interactions between mountain pine beetle (*Dendroctonous ponderosae*) epidemics and wildfire occurrence in lodgepole pine (*Pinus contorta*) stands: Literature review

Ben O'Connor

Chair of the Supervisory Committee:
Christopher Keyes, Research Professor
Department of Forest Management
College of Forestry and Conservation

Abstract

Lodgepole pine (*Pinus contorta* var. *latifolia*) is a dominant subalpine tree species throughout much of western North America. Historically fire has played an integral role in the maintenance and perpetuation of lodgepole pine on the landscape. The species has co-existed and evolved with fire for millennia and many stands possess serotinous cones requiring the heat of fire to open and release seeds. Mountain pine beetles (*Dendroctonous ponderosae*) are a native insect species that play a pivotal role as disturbance agents in subalpine forests, particularly those dominated by lodgepole pine. Certain forest stand structural characteristics combined with favorable seasonal weather conditions can facilitate mountain pine beetle (hereafter MPB) outbreaks occurring over relatively short temporal scales and across large spatial scales. Major epidemics in the last decade throughout the western United States and Canada have raised concerns about extensive areas of dead subalpine forests and the potential for an increased probability of wildland fire events. Experiments, observational studies, and simulation modelling provide extensive information on the subject. There are areas of agreement and disagreement on

disturbance interactions between MPB epidemics and wildfire occurrence. The areas of agreement focus on the changes to stand structure and fuel characteristics in the years to decades following a MPB outbreak. The areas of disagreement focus largely on changes in the likelihood of fire after a MPB outbreak (more specifically, the probability of increased likelihood and severity of surface and crown fires in a MPB infected stand, as compared to an unaffected stand). This literature review explores the state of the knowledge on how MPB outbreaks impact subsequent wildfire risk and hazard.

Epidemics result in significant impacts to foliar moisture content, fuel availability and overall fuel characteristics in an infected forest stand in the years to decades following an attack. Despite changes in fuel dynamics, other environmental factors including fire weather, topography, stand structure, and disturbance history are more important drivers of subsequent surface and crown fire potential and severity in the years to decades following an outbreak. Although local trends can suggest a disturbance interaction, they appear spatially and temporally isolated. Regional generalizations suggesting an increase in fire probability, severity and extent from MPB epidemics cannot be made considering the complexity of mechanisms involved and the local variability in their influence.

2.1 Introduction

Mountain pine beetle populations can reach epidemic levels given the right circumstances of stand structure and environmental conditions, causing extensive mortality in lodgepole pine, and in turn resulting in above-normal fuel accumulations capable of supporting intense fires (Parker et al. 2006). The concept that increased fuel loading from insect activity can affect the probability and severity of wildland fires has historically been accepted by forestry and fire personnel alike (Lynch et al. 2006). However, proving causation or a linked interaction between beetle outbreaks and altered fire occurrence is difficult, as drought is a driver of both wildfire and MPB outbreaks (Hart et al. 2015). Although there is some evidence of a relationship between MPB outbreaks and fire potential, the strength of the relationship changes with time since the outbreak. Previous disturbances, fire management, fire weather, drought and topography can also affect the relationship (Harvey et al. 2014a, b; Lynch et al. 2006). Several studies have addressed the disturbance interactions between MPB epidemics and wildfire. A general consensus exists on changes to fuel characteristics throughout the post outbreak stages, including decreased foliar moisture content and canopy bulk density followed by increased fine and large dead surface fuels. How these changes manifest in fire occurrence, severity and extent diverge among different studies. A few different working hypotheses have emerged concerning the strength and impact of the disturbance interactions. These include a heightened fire potential from larger fuel loads, increased or decreased fire potential depending on time since outbreak, and minimal differences in fire potential when compared to an unaffected stand, as other environmental factors are stronger drivers of fire occurrence.

The historical perspective that MPB epidemics cause an increase in fire potential and severity with time since outbreak has been pervasive among public land management entities throughout the 20th century (Lynch et al. 2006). This hypothesis is intuitive, as steady accumulation of dead fuels is visually evident in the years following a MPB outbreak, and fuel accumulations can support intense fire events (Parker et al. 2006). Fire behavior models predict higher rates of spread, intensity, and crown fire potential in outbreak stands compared to unaffected stands because of increased fuels and surface winds (Jenkins et al. 2008; Page and Jenkins 2007a). However, further investigation has revealed the relationship is not linear.

Another hypothesis suggests that surface and crown fire potential and severity rise and fall in accordance with mortality levels and changing fuel characteristics in the years to decades following outbreak occurrence (Agne et al. 2016; Page and Jenkins 2007a; Jenkins et al. 2008; Jolly et al. 2012). When compared to endemic stands where MPB numbers are low and only weak trees are killed occasionally (Romme et al. 2006), fire risk may increase or even decrease depending on the post outbreak stage. Another component of this theory is that the fire weather conditions necessary to facilitate ignition and spread are lower in outbreak stands than in unaffected stands. A sustained crown fire could occur under moderate fire weather conditions in an outbreak stand (Kaufmann et al. 2008; Harvey et al. 2014a), whereas extreme conditions would be required in an endemic stand.

Another working hypothesis is that any seemingly present interaction between MPB outbreaks and wildfire occurrence, severity and extent is insignificant. The overall impact of a disturbance interaction is negligible on the landscape scale. Lodgepole and subalpine forests burn under extreme fire weather conditions, and high-severity stand-replacing fires are a component of disturbance regimes (Kulakowski and Veblen 2006). Changes to fuel characteristics are overridden by environmental factors and unaffected stands are just as likely to burn as outbreak stands given the right conditions.

2.2 Current and historic role of mountain pine beetles in subalpine forests of western North America

2.2.1 Range and associated tree species

As an insect species native to pine forests throughout western North America, MPB exists as far north as central British Columbia and Alberta, Canada, and as far south as northern Baja California, Mexico. Its longitudinal range extends from the Pacific coast to the Black Hills of South Dakota. MPB habitat covers a large elevational gradient ranging from 11,000 feet in southern California down to almost sea level in British Columbia (Amman et al. 1990). The primary host species infested and killed by MPB throughout the intermountain west include lodgepole pine, ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*), whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) (Jenkins et al. 2008). Although not true hosts, MPB can also attack Douglas-fir (*Pseodotsuga menziesii*), true firs (*Abies*), western larch (*Larix occidentalis*), incense-cedar (*Calocedrus decurrens*) and western hemlock (*Tsuga heterophylla*). Attacks on these species occur when MPB populations are high and the nearby primary host species are saturated. Brood development is rare in tree species that are not true hosts (Amman et al. 1990). This review will focus primarily on lodgepole pine as it is the tree species most widely distributed and heavily attacked by MPB.

2.2.2 Life cycle

The four stages of beetle development include egg, larva, pupa and adult. Female beetles begin an attack by chewing through the inner bark and phloem of a host tree. Aggregating pheromones are released, which attract hundreds of other male and female beetles to the same tree. Once a tree is saturated with beetles, males can produce anti-aggregating pheromones to inhibit overcapacity (Amman et al. 1990). Breeding occurs under the bark of the host tree between adults. After breeding, females construct vertical galleries in the phloem or inner bark that average 10 in in length (but can range from 4-48 in in accordance with attack density). Small white eggs are laid singly into niches along the sides of the vertical galleries and are covered with boring dust; eggs generally hatch in 10-14 days. The annual period of egg laying varies geographically, but usually occurs between late June and late August (Safranyik and Carrol 2006; Amman et al. 1990). Once hatched, the beetles pass through four larval stages called instars and each stage ends with molting. The larvae construct mines or tunnels running at horizontal right angles to the vertical parent galleries and feed on the phloem tissue of the inner bark. Larval mine width increases with each successive instar stage as the larvae increase in size. Larvae normally reach the third or fourth instar stage before cold fall temperatures stop development. They continue feeding and growth the following spring when temperatures warm again, and transform to pupae by early summer (Safranyik and Carrol 2006). In the fourth and final larval instar stage an oval cell is excavated, where pupation occurs and the adult is formed.

Newly formed adults are pale colored and soft, often called callow adults. They feed on fungal spores and tree tissue for a period of time before hardening and turning dark brown to black. One generation per year is typical, however in unseasonably warm summers adults may re-emerge and produce a second brood. At higher elevations, or when below average summer temperatures occur, maturation can require two years. The MPB life cycle is spent almost entirely beneath the bark of the host tree save for a few days in the summer when adults emerge from the tree, fly to attack a new host tree, and begin the cycle again (Safranyik and Carrol 2006; Amman et al. 1990).

Successful colonization can occur only with tree mortality. Mass attack and the introduction of blue stain fungal spores, when beetles bore through the bark, both serve to weaken a trees’ defenses through girdling of the cambium and altered nutrient flow. Beetles benefit from the presence of blue stain fungi through improved moisture composition in the phloem, nutrient availability for development, and brood protection from other fungi (Safranyik and Carrol 2006). These fungal, insect, and conifer interactions have been a part of forests for millennia.

2.2.3 Historic activity levels

Mountain pine beetles are native to western North America and have coexisted with subalpine forests of the Rocky Mountains for thousands of years. They are generally present in low numbers, and primarily kill weak trees. When stand and environmental conditions are favorable their populations can increase rapidly to outbreak or epidemic population levels, causing high tree mortality over large spatial scales (Romme et al. 2006). Significant outbreaks over the last few decades have brought MPB and wildfire occurrence to the forefront of forestry and wildfire discussion and research. Since 1990, tens of thousands of square miles of forested lands in western North America have been affected by bark beetle outbreaks (Raffa et al. 2008). A recent synthesis of MPB and lodgepole, with a focus on Colorado and Wyoming, noted multiple outbreak insect epidemics of this scale have not been seen during the last century of scientific study. However, determining historic activity levels and whether MPB outbreaks in the early 2000s were unprecedented is difficult beyond 100 years. Decomposition can occur quickly in moist environments, and reliable modern records exist only for the last century. The possibility of similar environmental conditions and outbreak magnitude occurring in the past cannot be excluded (Kaufmann et al. 2008).

As climate change continues to impact forest health and resilience of regeneration and recovery to MPB and wildfire disturbances, a major concern is the presence of MPB activity outside of their historic range. Recent widespread outbreaks among high elevation whitebark pine forests of the Greater Yellowstone Ecosystem are considered outside the historic range of variability, where previous outbreaks were rare and short lived (Logan et al. 2010). Range expansion in Canada and successful breeding and invasions of lodgepole pine forests and neighboring boreal jack pine (*Pinus banksiana*) forests has raised significant concern of MPB establishment in the Boreal Plains Ecoregion of eastern Canada (Safranyik et al. 2010). The presence of MPB disturbances outside of their historic range could have far-reaching ecological impacts on forested ecosystems. Range expansion is likely a result of warmer temperatures and other factors aligning to influence outbreaks (Safranyik et al. 2010).

2.3 Biophysical drivers affecting MPB epidemics

Suitable stand conditions occurring over a large spatial scale must coincide with favorable climatic conditions in order for MPB populations to transition from endemic to outbreak levels. The abundance and impact of MPB populations on subalpine forests is dependent on stand conditions, environmental factors, proper host material and parasites, and predators (Jenkins et al. 2008). Stand characteristics associated with high levels of MPB mortality are: an average age > 80 years, a stand density of 300-600 trees per acre, and an average diameter at breast height > 8 in (Amman et al. 1990). Endemic populations are always present, but attacks with few cohorts can often be repelled by the superior defenses of healthy trees. Less vigorous and stressed trees offer an easier target for MPB attack but are nutritionally inferior and less common across the landscape. Other factors affecting tree health such as defoliators, pathogens, and root herbivores can decrease tree resistance and act as a compounding effect on tree mortality and beetle success (Raffa et al. 2008). Following a population increase, healthier trees are targeted as the stressed trees' resources are exhausted. Higher density attacks on vigorous trees can overcome defenses. A preliminary population spike can occur when external factors (i.e. drought and warm weather) decrease host resilience and facilitate beetle reproduction. Once population density passes a critical threshold, positive feedbacks can result where high numbers successfully attack new healthy stands and expand the epidemic spatially (Raffa et al. 2008; Safranyik and Carrol 2006).

Predators and parasites may regulate endemic numbers but do not have a significant impact on reducing populations at outbreak levels. Nematode parasites can hinder production and predate on eggs. Wasps, checkered beetles and dolichopodid flies prey on both immature and adult beetles (Amman et al. 1990). Numerous woodpecker species feed on overwintering larvae which can have a compounded effect on larvae mortality as the holes they create can dry out the bark and increase exposure (Amman et al. 1990).

Predation is an important factor on population density, however the life cycle and success of MPB outbreaks depends on temperature. Particularly high seasonal temperatures can accelerate beetle development and alter regular emergence timing. Unusually cold temperatures, especially in the spring and fall, can result in high mortality at all life stages (Amman et al. 1990). Cold temperatures (-40^{o} F for approximately one week) can kill overwintering larvae and end an outbreak at any developmental stage, particularly if low temperatures occur in the late autumn or early spring (Romme et al. 2006). Seasonal temperature variability serves as a mechanistic driver of MPB populations.

In summary, the most important biophysical drivers of MPB epidemics are stand conditions, drought and temperature. Suitable homogenous stand conditions over a large spatial scale create an abundant food and habitat source (Amman et al. 1990; Safranyik and Carrol 2006). Drought stress weakens trees, increasing mortality from an attack, and warm summers accelerate growth and production while warm winters decrease mortality (Romme et al. 2006). Environmental factors impact MPB populations, and on a larger scale MPB outbreaks can impact ecosystems.

2.4 Ecological impacts of MPB outbreaks

2.4.1 Ecological impacts on associated biotic communities

The effects of a MPB outbreak on future stand conditions and associated biotic communities depend on a multitude of factors. Pre-outbreak tree species composition (pure lodgepole or mixed species), mortality rates, cone serotiny, and the occurrence, severity and timing of a fire event could all influence forest succession. Associated plant communities likely respond to the increased resource availability (water, nutrients and sunlight) through tolerance, competition and dispersal mechanisms. Current species composition affects the way fire and mountain pine beetle disturbances impact forests, which in turn influences future trajectories of forest ecosystems (Kauffman et al. 2008). The effects of a MPB outbreak are visually evident within 1 to 2 years, however the impact on associated biotic communities continues during the years and decades that follow. Extensive tree mortality over large spatial scales causes an alteration in forest composition, structure and function. Insect and wildlife populations shift in response to habitat alterations. Attacked trees become suitable habitat for numerous vertebrate, arthropod and nematode species (Raffa et al., 2008).

Overstory tree mortality and the subsequent loss of canopy cover causes increased water and sunlight availability in the understory (Jenkins et al. 2008). Following a loss of canopy cover, understory species of grasses, herbs and shrubs experience a growth release. This will change the ratio of shade-tolerant to shade-intolerant species and can persist for more than 60 years (Raffa et al. 2008). A lodgepole pine dominated study site in north central Colorado experienced a MPB event that reduced lodgepole pine density by 42%, which changed species composition and density (Klutsch et al. 2011). Post epidemic lodgepole density was nearly equivalent to non-host species including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and quaking aspen (*Populus tremuloides*) (Klutsch et al. 2011). Changes in species composition from an outbreak would likely alter fire behavior.

Depending on their extent and severity, MPB outbreaks can also affect watershed hydrology. The initial loss of forest canopy will decrease the amount of rain and snow intercepted and evaporated back into the atmosphere, therefore increasing net precipitation. Increased albedo may affect the timing of snowmelt, and the amount of water loss in a system through transpiration will decline with increasing levels of tree mortality. At a study site in Colorado (Romme et al. 2006) noted that an increase in stream flow will not be realized unless annual precipitation exceeds roughly 20 in and overstory mortality surpasses 15-20%. Ecological impacts to biotic communities occur over decades or centuries and can vary substantially depending on outbreak severity, extent, and subsequent successional pathways.

2.4.2 Impacts to fuels

Changes to fuel characteristics occur over a much shorter temporal scale. Fuel structure and moisture content are key mechanisms in determining the probability and severity of surface and crown fire occurrence (Klutsch et al. 2011). Fuel characteristics change significantly from initial stand conditions at the onset of an outbreak to post epidemic conditions years to decades following the outbreak (Page and Jenkins. 2007). Temporal scales are critical in an assessment of impacts on fuel characteristics from MPB outbreaks. During and after an outbreak lodgepole forests transition through several stages, which in turn affect fuel continuity and structure.

Following tree mortality, needles turn red within 1 year and foliar moisture content decreases. The "red stage" generally lasts 2-4 years and is characterized by decreased canopy bulk density late in the stage and an accumulation of litter and fine woody fuels on the forest floor (0-3in in diameter), which reach peak levels within a few years after the outbreak (Jolly et al. 2012; Page and Jenkins 2007b; Jenkins et al. 2008). This is the stage where visual forest changes are most noticeable as the red needles of dead trees contrast sharply with live trees. Length of the "red stage" can vary depending on environmental conditions before the dead fuels transition again.

The "gray stage" begins 4-15 years after outbreak when dead foliage is no longer present in the canopy and dead trees turn gray (Hicke et al. 2012). The timing of foliage loss from the canopy can vary temporally likely due to wind and snowfall. Fine dead woody surface fuels may decrease during this period from decomposition (Jenkins et al. 2008), but seedlings, saplings and shrubs will likely increase (Klutsch et al. 2011; Page and Jenkins 2007b). Canopy bulk density declines throughout the "gray stage" in accordance with mortality levels, and changes to live surface fuels are related to species composition and resource availability. The final stage begins as killed trees begin to fall and change surface fuel characteristics once again.

The “old stage” occurs 15-30 years after outbreak and is characterized by snag fall and increased sapling and seedling density (Page and Jenkins 2007a). A study on the fall rate of MPB killed lodgepole pines in Central Oregon found decay to be the factor most affecting fall rate, and heat as the primary driver of decay (Mitchell and Preisler 1998). Consequently, trees on north and east aspects and occurring at higher elevations generally stood longer than those on warmer south and west aspects at lower elevations. Trees in thinned stands fell sooner than in unthinned stands likely due to increased sunlight and temperature. When DBH was not a factor, 50% of trees in unthinned stands had fallen in about 9 years (Mitchell and Preisler 1998). That study corroborates another that observed fuel changes 1-20 years after an outbreak and found a continuous and significant increase in large fuels for a minimum of 20 years post outbreak (Romme et al. 1986).

Studies agree that following an outbreak small dead surface fuels increase over a short period of about a decade as needles and branches accumulate. Surface fuel loading will vary in accordance with decomposition, understory growth, and release and regeneration (Jenkins et al. 2008). As snags begin to fall, large diameter dead fuel depth increases over the next several decades and regeneration increases ladder fuels (Page and Jenkins 2007b). Considerable differences in fuel characteristics exist in epidemic stands compared to endemic stands, but how these changes manifest in fire occurrence, severity and behavior is speculative.

2.5 Interactions between MPB outbreaks and subsequent fire activity

2.5.1 Post outbreak phases

As previously discussed, fuel characteristics change dramatically through multiple stages in the years to decades following an outbreak. Changes to fuel complexes over time result in periods where fire potential and severity increase or decrease (Page and Jenkins 2007a; Jenkins et al. 2008). Simulation modelling and observational studies have attempted to quantify the effects of fuel changes on surface and crown fire potential and behavior through the "red", "gray" and "old" stages. The terms "current" and "post epidemic" are also frequently used and it is assumed that post epidemic begins late in the "red stage" and early "gray stage" when new mortality is no longer occurring.

During the "red stage", surface fuel composition is largely unchanged from pre outbreak conditions as is surface fire potential. However decreased foliar moisture content and intact canopy fuels increase crown fire potential through shorter ignition times and increased foliar flammability (Jolly et al. 2012). In a comparison of average needle ignition times under controlled conditions, red needles ignited nearly 3 times faster than green needles. Decreased non-fiber carbohydrates and fats also exacerbated this effect. A shorter ignition time lowers the surface fire intensity required for a transition to crown fire, as well as the heat released from burning trees (Jolly et al. 2012). "Red stage" outbreak stands experience increased potential for crown fire initiation and spread than endemic stands and are most likely to experience crown fires during extreme fire weather (Jenkins et al. 2008). In addition, the dry needles in effect lower the height at which crown ignition occurs, which enables surface to crown fire transition to occur with lower fire intensity and flame length than in a stand unaffected by MPB (Keyes

2006). These findings support an increased probability of crown fire during the “red stage” and the potential for crown fires to occur under milder conditions than in unaffected stands.

Through the “gray stage”, canopy bulk density declines and fine surface fuel loading increases. Torching potential remains high but active crown fire potential decreases from a lack of crown fuel continuity (Hicke et al. 2012; Jenkins et al. 2008). Simulation models found common trends of reduced crown fire potential during the “gray phase” as a higher critical rate of spread was required to sustain active crown fires (Page and Jenkins 2007b; Klutsch et al. 2011; Hicke et al. 2012). Fire activity during this stage is likely to be influenced by mortality levels and regeneration. Decreases in crown fire potential coincide with the hypothesis of rises and falls in fire probability throughout the stages.

The “old stage” or post epidemic conditions are characterized by heavy large diameter fuel loading and the proliferation of regeneration, causing the greatest fire hazard. Fallen snags can increase surface fire intensity, and the released understory can serve as “ladder fuels” for crown fire initiation (Romme et al. 2006). Canopy bulk density begins to increase from the growth release of regeneration and suppressed trees, and crown fire potential may increase (Hicke et al. 2012). Heavy large diameter fuel loading results in increased durations of burning and higher total heat release per unit area (Jenkins et al. 2008). A retrospective study by Lynch et al. (2006) observed that past beetle activity in Yellowstone National Park had increased the probability of burning in 1988. Evidence was found in support of heightened burning probability during the “old stage”. The odds of burning increased by 11% for stands that experienced an outbreak from 1972-1975, whereas outbreaks from 1980-1983 did not increase the risk of burning. Fuel conditions from outbreaks in 1980-1983 would have been in late “red stage” or "gray stage". Perhaps climatic conditions were a larger driver of fire occurrence in these stands and heavy fuel accumulations of the "old stage" were required to see a relationship.

2.5.2 Forest regeneration

Succession following a MPB outbreak and wildfire event is largely influenced by fire extent and severity, serotiny levels, pre-disturbance species composition and time elapsed between outbreak and fire events. Throughout its range lodgepole pine can grow in pure or mixed stands with a variety of other species including Engelmann spruce, subalpine fir, and aspen at high elevations, and Douglas-fir, aspen and ponderosa pine at lower elevations. Each species has unique fire adaptations which facilitate survival or reproduction as well as influence fire behavior (Kauffman et al. 2008). Post disturbance regeneration will be influenced by fire severity and species composition.

Mixed conifer stands can burn under a moderate-severity regime likely resulting in the mixed conifer mosaic of pre-fire conditions, or under a high-severity regime possibly leading to pure lodgepole regeneration (Agee 1998; Kaufmann et al. 2008). Given a viable seed source, a ruderal strategy gives lodgepole pine the capacity for rapid seedling establishment and growth (Grime 1974), leading to even-aged pure lodgepole pine stands. Harvey et al. (2014b) found serotiny to be the key mechanism of lodgepole pine forest resilience to MPB and wildfire disturbances, and the prevalence of mature cone bearing trees as the most important factor of seedling density.

Time since outbreak and fire intensity greatly influence the success of post fire lodgepole pine regeneration. Seedling density was lower when burning occurred in the gray stage, likely a result of cone deterioration and seed predation (Harvey et al. 2014b). Similarly, under extreme burning conditions serotinous cones were consumed and contributed a minimal seed source whereas seed contribution was higher under moderate burning conditions (Harvey et al. 2014b). Custom fuel models developed by Page and Jenkins (2007a) predicted that total heat release from surface fire was 99% higher in post epidemic stands than endemic stands, and that burning duration was 63% longer under normal fire season fuel moistures. Duration and intensity of burning could negatively impact regeneration, soil characteristics, and ecosystem recovery (Lynch et al. 2006). Potential negative impacts of intense fire behavior in the “old stage” could be a loss of viable seed sources, soil scarification, and an alternate path of succession.

2.5.3 Fuel availability

Fuel loads do not substantially increase in epidemic stands, but rather shift states from a live to dead category as fuel moisture declines. Live and dead fuels can both support fire spread under extreme conditions (Romme et al. 2006). A higher ratio of dead to live fuels supports the notion of increased crown fire potential during the “red stage” under less extreme conditions than similar stands of live trees (Kaufmann et al. 2008; Harvey et al. 2014a). Fuel distribution changes as dead needles fall to the forest floor and a gradual shift from “red stage” to “gray stage” occurs. At this time the 10-hour (.25-1” intercept diameter) and 100-hour (1-3” intercept diameter) fuels will be available to burn during dry months but changes in structure and orientation may limit fire spread. Without other surface fuels needles will generate small flame lengths and low intensity surface fires; crown fire initiation and spread is unlikely due to decreased canopy bulk density and crown continuity (Kauffman et al. 2008; Gibson and Negron 2009). Under post outbreak conditions, higher solar radiation and increased air movement will contribute to fuel desiccation (Page and Jenkins 2007b). 1,000-hour fuels (3-8" intercept diameter) will likely become available to burn sooner than in endemic stand conditions. There are many other mechanisms at work besides fuel availability when evaluating fire activity.

2.5.4 Others factors influencing fire activity in outbreak areas

An observed increase in fire occurrence and severity in an epidemic stand compared to an endemic stand does not necessarily imply linked disturbance between beetles and fire. Disturbance history, MPB mortality levels, stand structure, topography and vegetation type may all heavily influence fire activity. Stand structure and species composition resulting from previous disturbances combined with differences in slope and aspect strongly influence fire behavior and severity (Turner et al. 1994). Two adjacent stands with a shared disturbance history and similar topography would likely experience similar fire behavior regardless of differences in MPB activity. Disturbance history shapes species composition and stand structure, both of which change successionally with time (Kulakowski and Veblen 2006). Therefore topography and disturbance history affecting stand structure and species composition may be stronger drivers of fire activity than altered fuel characteristics from MPB mortality. Turner et al. (1994) also suggest the influence of these factors will decline as the latter disturbance increases in intensity. This coincides with the notion that under extreme fire weather conditions and high severity fire regimes the impacts of beetle activity on fuels and subsequent fire behavior are diminished.

2.5.5 Management implications

Fire suppression in western North America has reduced landscape heterogeneity and increased the occurrence of MPB susceptible host stands. In Canada a substantial decrease in annual area burned in the last half century has resulted in lodgepole forests where almost 70% of trees are over 80 years old (Raffa et al. 2008). Patchiness is reduced in the absence of fire, enabling MPB outbreaks to occur over large spatial scales. The accumulation of fuels resulting from a century of fire suppression has created conditions that may contribute to extensive high severity fires, resulting in homogenous successional trajectories. The complexity of the problem requires management strategies to be adaptive and implemented accordingly in space and time (Raffa et al. 2008). Fuel treatments in sensitive outbreak areas and along the urban interface to reduce extreme fire behavior are a logical strategy, but on a larger scale forests should be managed for landscape resilience and heterogeneity.

2.6 Conclusions

It is difficult to make broad generalizations about the disturbance interactions between MPB epidemics and fire occurrence and severity because of the complexity of influencing factors involved. Depending on the time since outbreak and the post outbreak fuel conditions analyzed, one could find evidence supporting any of the working hypotheses. Surface and crown fire metrics must be considered independently, as well as combined through the post outbreak stages. Additionally, topography, disturbance history, geographic location, and fire weather conditions at the time of time of burning all compound the difficulty of drawing conclusions. The severity of an outbreak and the stage at which fire occurs can cause tremendous variation in fire activity.

Fire behavior in a given stand will vary depending upon the percentage of beetle killed trees (Romme et al. 2006).

The literature offers considerable insight on the subject, but as noted by Hicke et al. (2012), there is a lack of specificity about study questions. In addition, time since outbreak and the fuel and fire characteristics being measured are imperative in describing results. Models are useful in predicting general fire behavior, but environmental conditions that are difficult to incorporate such as real time fire weather, slope and aspect can be more dominant drivers of fire behavior than variations in fuels and stand conditions. In a post fire observational study, Agne et al. (2016) found fire behavior different than that predicted by models. Surface fire severity decreased with higher mortality and crown fire was common during the “gray stage” despite decreased canopy fuels. Lodgepole pine and MPB interact over a vast geographic range spanning the majority of subalpine forest ecosystems in western North America and associated tree and plant species vary considerably. Research areas from are scattered across western North America and study results may only be relevant locally. Page and Jenkins (2007b) noted that comparing results to other areas may be limited.

The conclusions drawn from analyzing disturbance interactions between MPB epidemics and wildfire occurrence depend on the scale of interpretation. From a narrower individual stand view, disturbance interactions between beetle outbreaks and subsequent fire events are assured as fuel characteristics are substantially altered (Kauffman et al. 2008). From this view, changes to fuels from beetle activity alter fire behavior compared to unaffected stands. If we scale out to a landscape perspective, minor differences in fire behavior between stands are insignificant if fire occurs regardless and equivalent succession paths occur. Hart et al. (2015) compared areas of beetle activity across the western U.S. from 2000-2013 with areas burned in the major fire years of 2006, 2007 and 2012. They concluded that area burned did not increase in direct response to MPB activity. MPB outbreaks of the early 21st century have not increased wildfire fire extent in the western United States.

We then must consider whether altered fire intensity and severity in MPB epidemic stands are decreasing forest resilience and changing successional trajectories. Disturbance interactions can be additive, synergistic or negative. They fall into two broad categories of ecosystem resistance or ecosystem resilience (Buma 2015). Resistance is a measure of how linked disturbances affect the likelihood, extent or severity of another disturbance (Buma 2015). MPB outbreaks have been suggested to increase or decrease likelihood and severity of fire events on a local scale depending on a multitude of factors. They have not been shown to increase extent (Hart et al. 2015; Kulakowski and Veblen 2007). Resilience is a measure of how compound disturbances affect ecosystem recovery (Buma 2015). In a study of post fire regeneration in the Northern Rockies where fires burned through forests ranging widely in MPB severity, Harvey et al. (2014b) concluded that MPB activity did not significantly change the post fire ecosystem and structure. Essentially, MPB outbreaks did not weaken subalpine forest resilience.

High severity stand replacing fires are natural occurrences in subalpine ecosystems, and a weak linked disturbance between MPB outbreaks and fire occurrence does not equate to an altered disturbance regime or decreased forest resilience. Further studies between MPB outbreaks and fire probability and severity over a wide range of temporal scales from time of burning to decades and centuries later may be required to incorporate first, second, and third order fire effects between unaffected and outbreak stands, and better help us understand this complex disturbance interaction.

2.7 References

Agee, J. K. (1998). The landscape ecology of western forest fire regimes. *Northwest Science, 72,* 24.

Agne, M. C., Woolley, T., & Fitzgerald, S. (2016). Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. *Forest Ecology and Management, 366,* 73-86.

Amman, G., McGregor, M., & Dolph Jr, R. (1990). Forest insect and disease leaflet 2: Mountain pine beetle. *USDA Forest Service, Washington, DC.*

Buma, B. (2015). Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere*, *6*(4), 1-15.

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, *250*(5461), 26.

Gibson, K., & Negrón, J. F. (2009). Fire and bark beetle interactions. In *In: Hayes, JL; Lundquist, JE, comps. The Western Bark Beetle Research Group: A unique collaboration with Forest Health Protection: Proceedings of a symposium at the 2007 Society of American Foresters conference. Gen. Tech. Rep. PNW-GTR-784. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station: 51-70* (Vol. 784, pp. 51-70).

Hart, S. J., Schoennagel, T., Veblen, T. T., & Chapman, T. B. (2015). Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proceedings of the National Academy of Sciences*, 201424037.

Harvey, B. J., Donato, D. C., Romme, W. H., & Turner, M. G. (2014a). Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. *Ecological Applications*, *24*(7), 1608-1625.

Harvey, B. J., Donato, D. C., & Turner, M. G. (2014b). Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. *Proceedings of the National Academy of Sciences*, *111*(42), 15120-15125.

Hicke, J. A., Johnson, M. C., Hayes, J. L., & Preisler, H. K. (2012). Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management, 271,* 81-90.

Jenkins, M. J., Hebertson, E., Page, W., & Jorgensen, C. A. (2008). Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management, 254*(1), 16-34.

Jolly, W. M., Parsons, R. A., Hadlow, A. M., Cohn, G. M., McAllister, S. S., Popp, J. B., & Negron, J. F. (2012). Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. *Forest Ecology and Management*, *269,* 52-59.

Kaufmann, M. R., Aplet, G. H., Babler, M. G., Baker, W. L., Bentz, B., Harrington, M., & Keane, R. E. (2008). The status of our scientific understanding of lodgepole pine and mountain pine beetles – a focus on forest ecology and fire behavior. *GFI technical report 2008-2. Arlington, VA: The Nature Conservancy. 13 p.*

Keyes, C. R. (2006). Role of foliar moisture content in the silvicultural management of forest fuels. *Western Journal of Applied Forestry*, *21*(4), 228-231.

Klutsch, J. G., Battaglia, M. A., West, D. R., Costello, S. L., & Negrón, J. F. (2011). Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. *Western Journal of Applied Forestry*, *26*(3), 101-109.

Kulakowski, D., & Veblen, T. T. (2006). The effect of fires on susceptibility of subalpine forests to a 19th century spruce beetle outbreak in western Colorado. *Canadian Journal of Forest Research*, *36*(11), 2974-2982.

Kulakowski, D., & Veblen, T. T. (2007). Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology*, *88*(3), 759-769.

Logan, J. A., Macfarlane, W. W., & Willcox, L. (2010). Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications*, *20*(4), 895-902.

Lynch, H. J., Renkin, R. A., Crabtree, R. L., & Moorcroft, P. R. (2006). The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems*, *9*(8), 1318-1327.

Mitchell, R. G., & Preisler, H. K. (1998). Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. *Western Journal of Applied Forestry*, *13*(1), 23-26.

Page, W., & Jenkins, M. J. (2007). Predicted fire behavior in selected mountain pine beetle–infested lodgepole pine. *Forest Science*, *53*(6), 662-674.

Page, W. G., & Jenkins, M. J. (2007). Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. *Forest Science*, *53*(4), 507-518.

Parker, T. J., Clancy, K. M., & Mathiasen, R. L. (2006). Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agricultural and Forest Entomology*, *8*(3), 167-189.

Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G., & Romme, W. H. (2008). Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *AIBS Bulletin*, *58*(6), 501-517.

Romme, W. H., Clement, J., Hicke, J., Kulakowski, D., MacDonald, L. H., Schoennagel, T. L., & Veblen, T. T. (2006). Recent forest insect outbreaks and fire risk in Colorado forests: A brief synthesis of relevant research. *Colorado Forest Research Institute*.

Romme, W. H., Knight, D. H., & Yavitt, J. B. (1986). Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *The American Naturalist*, *127*(4), 484-494.

Safranyik, L., & Carroll, A. L. (2006). The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *In The mountain pine beetle: a synthesis of its biology, management and impacts on lodgepole pine*. *Edited by* Safranyik, L. and Wilson, B. Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, Victoria, British Columbia. pp. 3-66.

Safranyik, L., Carroll, A. L., Régnière, J., Langor, D. W., Riel, W. G., Shore, T. L., Peter, B., Cooke, B. J., Nealis, V. G., & Taylor, S. W. (2010). Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist*, *142*(5), 415-442.

Turner, M. G., Hargrove, W. W., Gardner, R. H., & Romme, W. H. (1994). Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science*, *5*(5), 731-742.

University of Montana

CHAPTER 3:

Mountain pine beetle induced changes to lodgepole pine forest stand dynamics at Lubrecht experimental forest: Case study

Ben O'Connor

Chair of the Supervisory Committee:
Christopher Keyes, Research Professor
Department of Forest Management
College of Forestry and Conservation

3.1 Introduction

Between 1999 and 2014, extensive mountain pine beetle (*Dendroctonous ponderosae*) outbreaks in subalpine forests of the northern Rocky Mountains have caused significant changes to forest landscapes, particularly those dominated by lodgepole pine (*Pinus contorta* var *latifolia*). Since 1990, tens of millions of hectares of forested lands across western North America have been affected by pine beetle outbreaks (Raffa et al. 2008). The most important biophysical drivers of mountain pine beetle (hereafter MPB) epidemics are stand conditions, drought, and temperature (Romme et al. 2006). Following a MPB epidemic, forest managers are faced with the task of implementing management strategies that aid forest recovery and promote forest resilience, as well as evaluating silvicultural strategies to reduce future threats to lodgepole pine forests (Crotteau et al. 2016, Keyes et al. 2014). Salvage logging has been utilized as a silvicultural tool, however the effects of salvage logging on post outbreak forest stand dynamics, and subsequently future stand development trajectories and beetle susceptibility, are uncertain.

Recent widespread MPB outbreaks throughout western North America have demonstrated the necessity for a stronger understanding of both the factors contributing to an outbreak, and the changes that occur to forest and fuel characteristics in the years to decades following one. Forest and fire managers need to be informed of how outbreak affects forest stand dynamics and wildfire hazard. How an outbreak impacts overstory species composition, stand density, tree growth, and regeneration determines future stand development trajectories. How 1,000-hour fuels (3+" diameter) - also known as coarse woody debris (CWD) - change following an outbreak defines the intensity and severity of wildfires.

To address this issue, I analyzed the aftermath of a bark beetle outbreak in a lodgepole pine stand at the University of Montana's Lubrecht Experimental Forest (LEF). LEF encompasses 28,000 acres in western Montana's Blackfoot River drainage. During the 1999-2014 period, lodgepole pine forests at LEF experienced extensive mortality as a result of MPB activity. This was especially true at Section 1 (Figure 1), the forest's highest elevations, located in T13N R14W S1. There, lodgepole pine was abundant and mortality was widespread, with most mature lodgepole pines eventually being killed. The majority of lodgepole pine killed in Section 1 was salvage logged to minimize fuel loading and facilitate reforestation. However, some parts were reserved as study areas and left unharvested. In 2009, permanent research plots were installed in those reserves. The purpose was to observe changes over time to an affected stand that was not salvage logged, but was instead left to grow, decay, and regenerate naturally and without interference. This enabled analysis of post outbreak forest stand dynamics (overstory growth and mortality, regeneration, species composition shifts, stand density), as well as indications of stand development trajectories, future MPB susceptibility and wildfire hazard.

This case study examined the following questions:

1. What was the effect of MPB outbreak on lodgepole pine stand mortality?
2. How did the outbreak affect overstory and understory structure, species composition, stand density and tree growth rates?
3. What changes occured to standing dead snags and CWD surface fuel accumulations following the outbreak and after the passage of time?

To answer these questions, I: 1) evaluated the overstory stand characteristics before, during and after the outbreak; 2) assessed understory species composition, density and growth rates from 2010 to 2017; and 3) quantified changes to CWD.

Results of this case study analysis will help forest managers in the northern Rocky Mountains design silvicultural strategies to promote forest productivity and increase resilience to future disturbances in lodgepole pine forests, and anticipate aspects of fire hazard following MPB outbreak.

3.2 Methods

3.2.1 Study area

The study area is located on the University of Montana's Lubrecht Experimental Forest (T13N R14W S1). The site has a north aspect, with slopes roughly 20-30% and elevations ranging from 5200-5800 ft. The forest is characterized by the No. 218 Lodgepole Pine forest cover type of the middle elevations interior of western forest cover types (SAF 1980). Soils are typified by Evaro Gravelly Loam, which are loamy-skeletal, mixed, Typic Cryochrepts derived from Belt colluvium parent material (Nimlos 1986). Prior to the MPB outbreak the overstory consisted of an even-aged mixture of primarily lodgepole pine with a small amount of western larch (*Larix occidentalis*). Also present in low densities were Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea Engelmannii*) and subalpine fir (*Abies lasiocarpa*). The understory was comprised of advanced regeneration which included subalpine fir, Douglas-fir, western larch and Engelmann spruce.

The study area experienced an extensive MPB outbreak around the mid-2000s. With salvage logging set to commence in late 2009, three 2.47 ac reserve units were installed in October and November immediately prior to harvest. Each of the three reserves was chosen due to its representativeness of the greater unit. Within each reserve unit the measurement area was 1.24 ac, allowing for a 1.24 ac buffer from the salvage boundary.

Salvage logging operations began outside the reserves in the fall of 2009 and were completed during the summer of 2010. Lengthy roads, steep slopes and ephemeral streams precluded winter logging. The local contractor that performed the operation was Euchre Mountain Logging, (Condon, MT). House logs and saw logs were taken to Pyramid Mountain Lumber in Seeley Lake, Montana, with pulp logs headed to Smurfit-Stone Container Corporation pulp mill in Missoula, Montana. The reserve unit study areas were established with permanent monumentation in the summer of 2010 and initial vegetation and fuels data was collected at that time.

3.2.2 Data collection

Overstory tree vegetation data were collected in August 2010 using a 1/8-acre (41.63’) circular fixed radius plot based around reserve unit center. All trees with a diameter at breast height (DBH) ≥ 4 in were measured, species and status (dead/alive) was recorded. Measurements of each trees’ DBH were taken to the nearest 0.1 in using a diameter tape. Total height and height to live crown base were measured using a clinometer. Each qualifying tree was marked with a hard tag nailed to the tree facing plot center. The total overstory sample of all three plots comprised n=122 stems, yielding an average of 96 trees per acre (TPA) live stems and 229 TPA dead stems.

Understory tree vegetation data were collected simultaneously using four equidistant 1/100-acre (11.78’) radius circular subplots at each reserve, for a total of 12 subplots. Subplots were placed at cardinal directions just within the perimeter of the overstory plot, with centers 29.8 ft from plot center. Measurements were taken from all live trees > 4.5’ tall and < 4” DBH. Species was recorded, DBH was measured to the nearest .01” with a digital caliper, and total height was measured to the nearest .01’ with a height pole. Impressible soft tags were attached to lateral branches at breast height, with regeneration plot number and tree number impressed on the tag, (e.g. 1.3 = regen plot 1, tree 3). The total understory sample of all 12 plots was comprised of 113 stems, yielding an average understory density of 942 stems per acre (SPA).

Surface fuels were inventoried according to standard line-intercept sampling methods (Brown 1971) during July 2010. At each plot, four transects were installed at right angles along sub-cardinal directions. Each transect originated 10 feet from plot center to buffer against trampling. Transect lengths varied according to fuel size classes and were as follows: 1-hour (0-.25 in) and 10-hour fuels (.25-1 in), 6 ft; 100-hour fuels (1-3 in), 20 ft; 1,000-hour fuels (3+ in), 50 ft. Each 1,000-hour fuel particle was classified as sound or rotten, and its diameter was measured at the point of intersect. Total transect length for all 3 reserve units was: 1-hour and 10-hour fuels, 72 ft; 100-hour fuels, 240 ft; 1,000-hour fuels, 600 ft.

In the fall of 2017 data collection occurred again with similar protocols followed at all 3 reserve sites. Overstory measurements were taken for all live trees, and standing dead and fallen dead trees were categorized as such to determine mortality rates. All understory trees within subplots were categorized as live or dead. DBH and height measurements were taken for a subset of 62 of the original 113 saplings. For that subset, the fittest individuals (as suggested by size and form) were selected for re-measurement, with representation from all four species present. Only CWD (1,000-hour) surface fuels were remeasured along the same transects using line-intercept sampling methods.

3.2.3 Data analysis

Overstory stand characteristics including species composition, DBH size class distribution, basal area (BA) distribution, quadratic mean diameter (QMD), stand density index (SDI) and stocking were compared between pre-outbreak, mid to late-outbreak (2010), and post-outbreak + 7 years (2017). Pre-outbreak overstory conditions were simulated; at the time of plot installation in 2010 many trees still contained red needles indicating mortality had occurred recently (Figure 2). Thus, for the purpose of reconstructing stand structure prior to MPB outbreak, overstory trees recorded as dead in 2010 were analyzed as live. This simulation gave the added benefit of 3 separate evaluations of stand characteristics, and changes that occurred with increasing levels of mortality.

Complete understory datasets were used to observe shifts in species composition and density from 2010 to 2017. The sapling growth subset was used to evaluate height and diameter growth among the fittest individuals, and to compare growth rates among species. 1,000-hour surface fuel measurements were compared between 2010 and 2017 to quantify increases in CWD resulting from MPB mortality.

3.3 Results

3.3.1 Overstory structure

Pre-outbreak species composition of the overstory was dominated by lodgepole pine, which made up 88.5% of all trees. Western larch, subalpine fir, Douglas-fir and Engelmann spruce comprised the remaining 11.5% (Figure 3a). There was an average of 325 TPA (range 240-368 TPA). QMD for all species was 10.9 in (range 9.9-11.6 in). Most species had a QMD near the overall QMD except for western larch and Engelmann spruce; both of those had > 20 in trees in a single plot, consequently raising their QMD. Total average BA was 208 ft^2/ac (range 178-249 ft^2/acre). This resulted in a SDI of 369 and average spacing between overstory trees of 11.7 ft (Table 1).

Evaluating just lodgepole pine, the pre-outbreak density was 288 TPA (range 200-352 TPA). QMD was 10 in with very little variation among plots (Table 1). The majority of lodgepole pine trees fell in the 8-12 in DBH class (n = 73), followed by 4-8 in (n = 18), 12-16 in (n = 16) and 16-20 in (n = 1) (Figure 4). Lodgepole pine BA was 157 ft^2/ac, (range 117-182 ft^2/ac). This equated to a SDI of 288 (range 211-337).

By 2010 (mid-outbreak), overstory species composition had shifted considerably with lodgepole pine being reduced to 67%. Western larch increased to 18%, and Douglas-fir, Engelmann spruce and subalpine fir all increased in representation, covering the remaining 15% roughly equally (Figure 3b). Density for all species declined substantially to 96 TPA, a decrease of 71% (Table 1, Figure 5). Two of the three plots decreased to 56 TPA and 48 TPA (77% and 87% decline respectively), with the remaining plot dropping to 184 TPA (50% decline). Stand wide BA declines were significant as well at 63% (range 54-74%). By 2010, western larch had passed lodgepole pine in BA composition to account for 41.50% of the total BA on site (Figure 3b). As a result of higher mortality rates for smaller diameter trees, the QMD for all species increased by nearly 20% to 13.4 in (range 9.6-15.7 in). The overall SDI dropped to 126, a decrease of 66%.

Lodgepole pine density had by mid-outbreak decreased from 288 TPA to 64 TPA (range 8-168 TPA), indicating 81% loss and 19% survivorship (Table 1). In contrast to the overall QMD trend, lodgepole pine QMD fell 7% to 9.3 in as larger trees experienced higher levels of mortality. This was reflected in changes to the diameter distribution as all lodgepole pine > 12 in DBH were killed by the mid-outbreak measurement period in 2010 (Figure 4). Lodgepole BA declined by 83% to 29 ft^2/ac and SDI dropped 81% to 56. By 2010 the majority of mortality had occurred; however, there was still some suitable host material to be exploited.

By the fall of 2017, the MPB outbreak had subsided; red needles were no longer visible and all dead trees were either in the late “gray stage” or “old stage” (Figure 6). When compared to pre-outbreak conditions, post-outbreak stand characteristics had changed substantially as a result of MPB induced mortality to lodgepole pine. Species composition had shifted from 88.5% to 62% lodgepole pine, with western larch comprising nearly 20% of the stand, a notable increase from 6% at pre-outbreak. Douglas-fir and subalpine fir both experienced a surge in representation to 8% each, up from the original 1.5% and 2.5%. The shift in species dominance was even more profound in BA terms; lodgepole pine accounted for only 28.5% of the BA with western larch making up 47.25% of the total BA (Figure 3c). Stand density for all species present had declined to 69 TPA, equating to a 78% decrease from pre-outbreak. From both attrition of smaller stems and growth of survivors, stand QMD had increased 26% to 14.7 in.

From pre-outbreak to post-outbreak, BA declined 68% from 208 ft^2/ac to 67 ft^2/ac, and SDI had declined 71% from 369 to 107 (Table 1).

A closer look at just lodgepole pine revealed a post-outbreak density of 43 TPA (range 0-112 TPA), a decrease of 245 TPA, indicating 87% mortality and just 13% survivorship (Table 1). By causing mortality to larger trees, the outbreak reduced lodgepole pine QMD by nearly 40% from 10.0 in to 6.2 in, and the diameter distribution changed dramatically from pre-outbreak to post-outbreak (Figure 7). Notably, all lodgepole pine trees > 12 in DBH were killed. Trees in the 8-12 in DBH class declined from 195 TPA to 37 TPA, equating to 81% loss. Mortality rates were slightly higher in the 4-8 in DBH class with a change of 48 TPA to 5 TPA, equating to 90% loss (Figure 4). BA declined by 89% from 157 ft^2/ac in 2010 to just 19 ft^2/ac in 2017. SDI had a similar decrease from 288 to 36 over the course of the outbreak (Table 1).

3.3.2 Understory structure

In 2010 (mid-outbreak), the understory numbered 941 SPA, and consisted of four species: subalpine fir, Douglas-fir, western larch and Engelmann spruce (Figure 8). Species composition was dominated by subalpine fir and Douglas-fir (90% of the understory,) with western larch and Engelmann spruce present in much lower quantities (Figure 9). The majority of all saplings present in 2010 had DBH < 2 in and height < 12 ft (Figure 10).

By 2017 (post-outbreak), understory species composition and density had experienced some minor changes. Of the original 113 trees recorded, 102 were still alive (850 SPA), resulting in 90% survivorship and 10% mortality. No new ingrowth was found. The majority of sapling mortality occurred to subalpine fir and Douglas-fir, with each species losing 5 trees across the study plots, equating to a decrease of 42 SPA. One western larch was killed, a decline of 8 SPA. All of the Engelmann spruce survived (Figure 8). Subalpine fir and Douglas-fir still accounted for 90% of the understory (Figure 9).

A subsample of the fittest individuals from each species was analyzed to evaluate understory height and diameter growth over the seven year period (Figure 11). Across all species, average tree diameter grew by 0.62 in over seven years (.09 in/year). This translated to a 72.6% DBH increase from 2010 to 2017 (10.4% per year). Average height growth was 14.54 in over seven years (2.08 in/year), which equated to a 12.7% increase in height over that period (1.8% per year). However, there were considerable differences among species in both diameter and height growth. Subalpine fir had the largest absolute DBH growth, increasing by 0.71 in over the seven year study period, (0.10 in/year). Western larch was next accruing .62 in of diameter over seven years, (.09 in/year), followed closely by Douglas-fir with 0.56 in of growth, (.08 in/year). Engelmann spruce exhibited the lowest growth with .45 in over seven years, (0.064 in/ year) (Table 2). For absolute height growth, western larch was the leader adding 27.5 in over seven years (3.9 in/ year). Douglas-fir was next with 18.6 in after seven years (2.7 in/year) followed by subalpine fir at 8.3 in (1.2 in/year). Engelmann spruce had the lowest height growth at 5.6 in over seven years, (0.8 in/year) (Table 2).

Comparing relative growth among species, or how much each species increased in diameter and height as a percent of the original measurement, tells a slightly different story. Western larch was the clear leader in relative diameter growth, increasing by 188.6% in seven years, (26.9% per year), followed by Engelmann spruce at 87.2% (12.46% per year), Douglas fir at 63.6% (9.09% per year), and subalpine fir at just 53.42% over seven years, (7.63% per year) (Table 2). Western larch also displayed the greatest relative height growth, putting on 23.77% over seven years (3.40% per year). Second to larch was Douglas-fir at 13.90% (1.99% per year), followed by subalpine fir at 9.39% (1.34% per year) and Engelmann spruce at 8.23% (1.18% per year) (Table 2).

The 2010 diameter distribution (Figure 10) illustrates the interesting differences in absolute and relative DBH growth performance among species, particularly the contrast of subalpine fir to western larch. Subalpine fir had representation in the larger diameter classes, whereas western larch was only present in the smallest class. As a rule, larger trees gain more diameter than smaller trees, as was exhibited by the absolute growth results. However, despite their small initial sizes, western larch saplings had the highest relative DBH and height growth. These results indicate that the western larch occurring in the understory is growing at a pace unmatched by other species, with implications for future dominance trends in this cohort.

3.3.3 Coarse woody debris

In 2010 (mid-outbreak), total CWD averaged 21.9 tons/ac (range 17.7 - 26.6 tons/ac). Rotten material accounted for 68% of the total, averaging 15.0 tons/ac (range 9.0 - 19.5 tons/ac). Sound material averaged 7.0 tons/ac (range 5.0 - 8.7 tons/ac) (Table 3). By 2017, significant changes had occurred to both sound and rotten CWD density totals (Figure 12). Total CWD grew by 24.8 tons/ac (113.2%) to an average of 46.7 tons/ac (range 35.3 - 63.8 tons/ac). However, it was no longer dominated by rotten material. Sound material made up the majority and accounted for 76% of the total, increasing by 28.6 tons/ac (408.6%) to an average 35.6 tons/ac (range 29.9 - 42.2 tons/ac) (Table 3). Rotten material actually decreased by 3.8 tons/ac (-25.3%) to an average of 11.2 tons/ac (range 5.4 - 21.7 tons ac).

3.4 Discussion

3.4.1 Overstory structure

Prior to the MPB outbreak an even-aged mixed conifer stand dominated by lodgepole pine existed at the study site. Favorable stand and climatic conditions facilitated a dramatic increase in MPB numbers, resulting in lodgepole pine mortality beginning in the early 2000s. Pre-outbreak lodgepole BA was 157 ft^2/ac with a QMD of 10.9 in. Both of these characteristics met the criteria found to predispose stands to MPB attack by Amman et al. (1990) and Williams et al. (2018). Over the next several years lodgepole pine mortality had immediate and lasting effects on stand characteristics.

In 2017, roughly fifteen years after the MPB outbreak began, the stand contained a small portion of what previously existed. 79% of overstory trees had been killed and 68% of BA had been lost, almost exclusively among lodgepole pine. Declines in BA were lower than TPA due to the presence of other species in larger DBH classes. Most of the BA loss occurred in the first several years of the outbreak and tapered off with time (Table 1). The most suitable host material was exploited by MPB initially, followed by less suitable material as the outbreak waned. Overall QMD increased as a result of heavy mortality to lodgepole pine and more weight being given to other species.

The MPB outbreak transformed this stand from an even-aged lodgepole pine dominated stand to a two-aged mixed conifer stand. The dominant overstory trees are now composed of primarily western larch with a smaller component of Engelmann spruce and subalpine fir. Douglas-fir, lodgepole pine and subalpine fir make up the overstory co-dominants. All of the surviving lodgepole pines are < 12 in DBH and were likely on the fringe of suitable MPB host material at the time of the outbreak. Average spacing increased by nearly 60%, which may result in further lodgepole pine mortality from windthrow. In the absence of another disturbance event, such as fire, lodgepole pine very likely will remain a relatively small component of the stand.

3.4.2 Understory structure

Subalpine fir and Douglas-fir, both shade tolerant species, were most abundant in the understory in 2010 and 2017. Western larch was present in much lower densities, likely constrained by its shade intolerance and need of scarified soil surfaces for seedling establishment. Engelmann spruce was the least represented understory species. Some combination of a minimal seed source and heavy competition likely influenced this species' low understory presence.

A decline in understory density between 2010 and 2017 occurred among the most abundant species as stems grew and competed for growing space and limited resources. By 2017 subalpine fir and Douglas-fir were not ubiquitous throughout the understory but rather occurred in dense pockets with some western larch and Engelmann spruce mixed in intermittently. Mortality occurred among weaker individuals as the dense patches of regeneration gradually self-thinned. Outside of regeneration patches, dense shrub communities covered the forest floor and restricted new seedling establishment (Figure 13).

Focusing on understory species responses to overstory mortality, western larch was the most successful in terms of diameter and height growth. Although not present in abundant numbers it has responded well to increased sunlight availability and will likely continue to outgrow other species in the cohort to make up part of the future overstory. Douglas-fir is known for its morphological plasticity and ability to grow in a wide variety of moisture and sunlight availabilities. It has also reacted well to increased resources with height growth second only to western larch. Understory subalpine fir and Engelmann spruce have experienced slower growth and will likely be overtopped by the faster growing species.

In the future we can expect some continued mortality from competition, specifically among Douglas-fir and subalpine fir. Overall density should continue to decline as uncompetitive individuals are killed, and composition may shift slightly in favor of western larch and Engelmann spruce. A complete absence of lodgepole pine regeneration suggests that without fire to stimulate reproduction, that species will decline at the site. As surviving saplings emerge into the mid-story, western larch and Douglas-fir will become dominants with subalpine fir and Engelmann spruce as co-dominants in that cohort.

3.4.3 Coarse woody debris

Between 2010 and 2017 substantial changes to 1,000-hour fuel structure and location occurred as standing dead trees fell, translocating canopy fuels to surface fuels. Photos taken in 2010 (Figure 2) show an abundance of standing dead lodgepole pines, many still in the red stage, and an insignificant accumulation of sound CWD on the forest floor. By 2017 many of those snags had fallen, decreasing canopy fuels and increasing surface fuels (Figure 13). A comparison between the measurement periods reveals a 408.6% increase in sound fuels and a 25.3% decrease in rotten fuels over 7 years. The escalation in sound fuels was to be expected as recently killed trees succumbed to surface decay and gravity. There may be a few causes for the decline in rotten fuels including accelerated decomposition and litter accumulation.

Pre-outbreak diameter distribution shows the majority of lodgepole pines (84%) on site were < 12 in DBH. Although larger and older trees were present, many were still relatively young. The stand was likely in the stem exclusion stage of stand development before and during the MPB outbreak, with weaker individuals outcompeted and killed. In 2010, trees killed from stem exclusion years before could have been present as measurable rotten CWD. An elevated rate of decomposition from increased throughfall precipitation, plus increased solar radiation resulting in higher forest floor temperatures, may have spurred the microbial community responsible for decomposition. By 2017, decomposition and fine fuel accumulations from recently killed trees may have caused enough litter and duff buildup to disqualify some rotten fuels from re-measurement. Together, these factors could help account for the higher densities of rotten coarse woody debris in 2010. The outbreak seems to have accelerated the stem exclusion stage and pushed the stand into the understory re-initiation stage.

MPB killed trees that had fallen and become surface fuels by 2017 were likely killed in the early stages of the outbreak. A study in central OR found that in unthinned stands of lodgepole pine killed by MPB, 50% of trees fell within the first 9 years, and 90% fell within 14 years (Mitchell and Preisler, 1998). Fall rates were dependent on bole decay at the ground level, and surface temperature was the principal driver of decay. Colder temperatures in MT may result in slower decay and fall rates. Although many trees had fallen by 2017, there were still an average 136 TPA standing dead. In northwestern Wyoming, Romme et al. (1986) found a constant and substantial increase in large fuels for at least 20 years from lodgepole pine stands heavily damaged by MPB. Based on the current stock of standing dead overstory trees, we expect surface accumulations of coarse woody debris to continue to increase over the next several years to decades.

Crown fire potential in this stand has diminished over time. Fine canopy fuel connectivity to facilitate spread has declined, and many trees have transitioned to surface fuels. However, surface fire intensity and severity will likely continue to increase as coarse woody debris accumulates. In the event of a fire disturbance under warm and dry conditions, heat output and burning duration could be significant enough to cause mortality to both the understory and surviving overstory cohorts. Severe surface and ground fires could result in hydrophobic soil and possibly ecosystem transformation.

3.5 Conclusion

Forest stand characteristics including specific density, BA and QMD known to catalyze MPB outbreaks were all present at the study site prior to significant MPB activity. Stand characteristics that aligned with favorable environmental conditions in the early 2000s to facilitate high levels of MPB caused mortality to lodgepole pine in Section 1 of LEF. Mortality has triggered considerable shifts in overstory species composition and QMD, as well as substantial declines in density and total BA. Overstory mortality has resulted in increased sunlight and nutrient availability to the understory. The variation in growth rates of understory species from 2010 to 2017 reveals trends suggestive of future dominants and co-dominants of this cohort. CWD surface fuels increased tremendously over the study period, and that trend will likely continue for years to come due to an abundance of standing dead lodgepole pine still present in 2017. In the event of a fire disturbance, high severity surface fire could alter stand trajectories once again.

The specific effects of MPB outbreaks on forest stand and fuel characteristics will inevitably vary among location. Creating and maintaining forest resiliency before and after insect and fire disturbance events is a long term goal that forest managers should embrace when developing management plans. It is increasingly relevant as climate change is altering temperature and moisture regimes, as well as fire season length. To ensure forest ecosystems remain through a disturbance event, or regenerate following one, several strategies can be taken into consideration.

Managing lodgepole pine density to minimize MPB outbreak mortality can be effective. This strategy can be utilized in sensitive outbreak areas, and in areas of high ecological importance. Maintaining healthy stands of lodgepole pine with moderate stocking levels will help reduce both MPB mortality and fire hazard, as well as maintain other ecosystem services such as water retention, and wildlife habitat. However, implementation is difficult on a large scale and this approach will be most applicable and effective in strategic areas.

In the event of heavy MPB caused mortality to lodgepole pine, salvage logging is a practical management option to reduce fire hazard, and utilize the economic value of recently killed timber resources. Removing recently killed trees will reduce crown and surface fire hazard for years to decades into the future. Salvage logging should be considered if it aligns with long term management goals, and existing infrastructure and market prices make it a viable option.

If MPB killed trees are to remain on site, forest managers should consider the timeline of surface and crown fire hazard, as well as facilitating regeneration. If no action is taken, the potential of future MPB mortality to surviving lodgepole pine will likely remain low for several decades due to decreased density. However, crown fire hazard will exist in the first few years and continued surface fuel accumulation will increase high severity surface fire hazard and the possibility of ecosystem transformation for decades into the future. In addition, the regeneration of desired species may not occur without management action.

Depending on species composition and lodgepole pine serotiny levels, prescribed fire can be utilized to catalyze regeneration and decrease surface fuels. In a mixed conifer stand, a low intensity controlled burn could serve to both open serotinous cones, and scarify soil surfaces for the regeneration of lodgepole pine and other conifers such as western larch. Many subalpine mixed conifer stands occur in areas where the successful implementation of prescribed fire can be difficult. Coordinating seasonal timing of the burn, seedfall, and environmental conditions for desired fire effects must be taken into consideration for this strategy to be successful. Prescribed fire may help produce an uneven aged mixed species stand which will create forest resiliency to future disturbance events.

This case study exhibited measurable changes to forest stand dynamics and CWD fuel loads during and after a MPB outbreak in the Northern Rockies. This research should prove helpful to forest and fire managers in making informed decisions about preventing or dealing with the effects of MPB outbreak.

3.6 References

Amman, G., McGregor, M., & Dolph Jr, R. (1990). Forest insect and disease leaflet 2: Mountain pine beetle. *USDA Forest Service, Washington, DC*.

Brown, J. K. (1971). A planar intersect method for sampling fuel volume and surface area. *Forest Science*, *17*(1), 96-102.

Crotteau, J. S., Keyes, C. R., Sutherland, E. K., Wright, D. K., & Egan, J. M. (2016). Forest fuels and potential fire behaviour 12 years after variable-retention harvest in lodgepole pine. *International Journal of Wildland Fire*, *25*(6), 633-645.

Keyes, C. R., Perry, T. E., Sutherland, E. K., Wright, D. K., & Egan, J. M. (2014). Variable-retention harvesting as a silvicultural option for lodgepole pine. *Journal of Forestry*, *112*(5), 440-445.

Mitchell, R. G., & Preisler, H. K. (1998). Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. *Western Journal of Applied Forestry*, *13*(1), 23-26.

Nimlos, T. J. (1986). *Soils of Lubrecht Experimental Forest*. Miscellaneous Publication No. 44, Montana Forest and Conservation Experiment Station.

Romme, W. H., Knight, D. H., & Yavitt, J. B. (1986). Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity? *The American Naturalist*, *127*(4), 484-494.

Williams, H., Hood, S. M., Keyes, C. R., Egan, J. M., & Negrón, J. (2018). Subwatershed-level lodgepole pine attributes associated with a mountain pine beetle outbreak. *Forests*, *9*(9), 552.

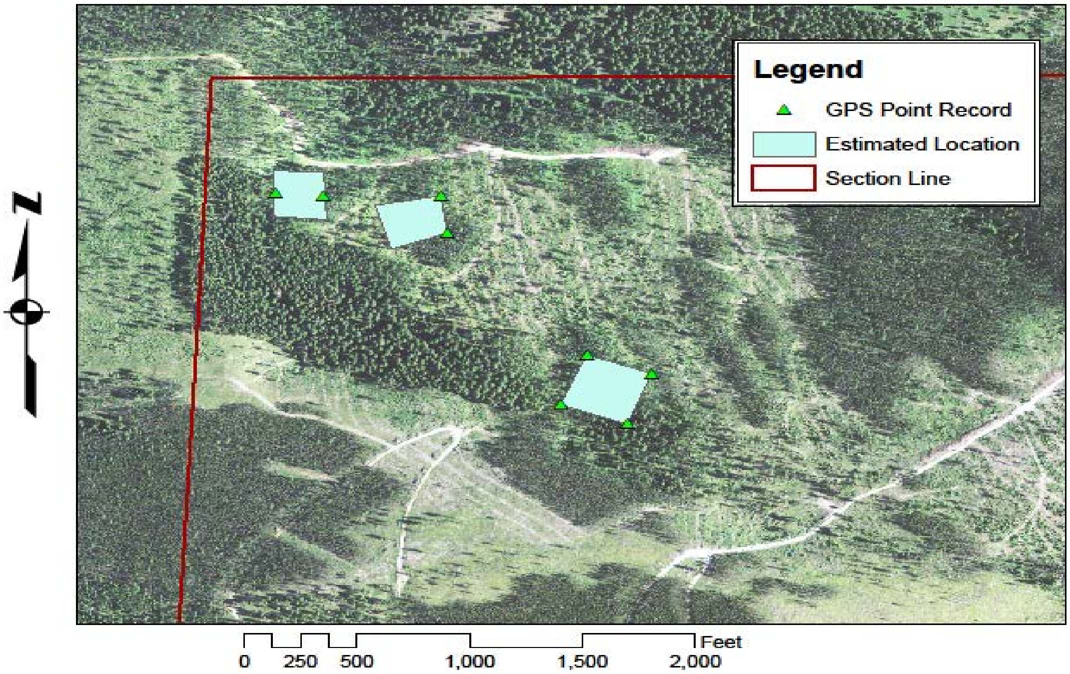


Figure 1 - Reserve locations in relation to Section 1 (T13N R14W) of Lubrecht Experimental Forest. Image from 2011 (post-harvest).

Figure 2 - Photos of study area in 2010.

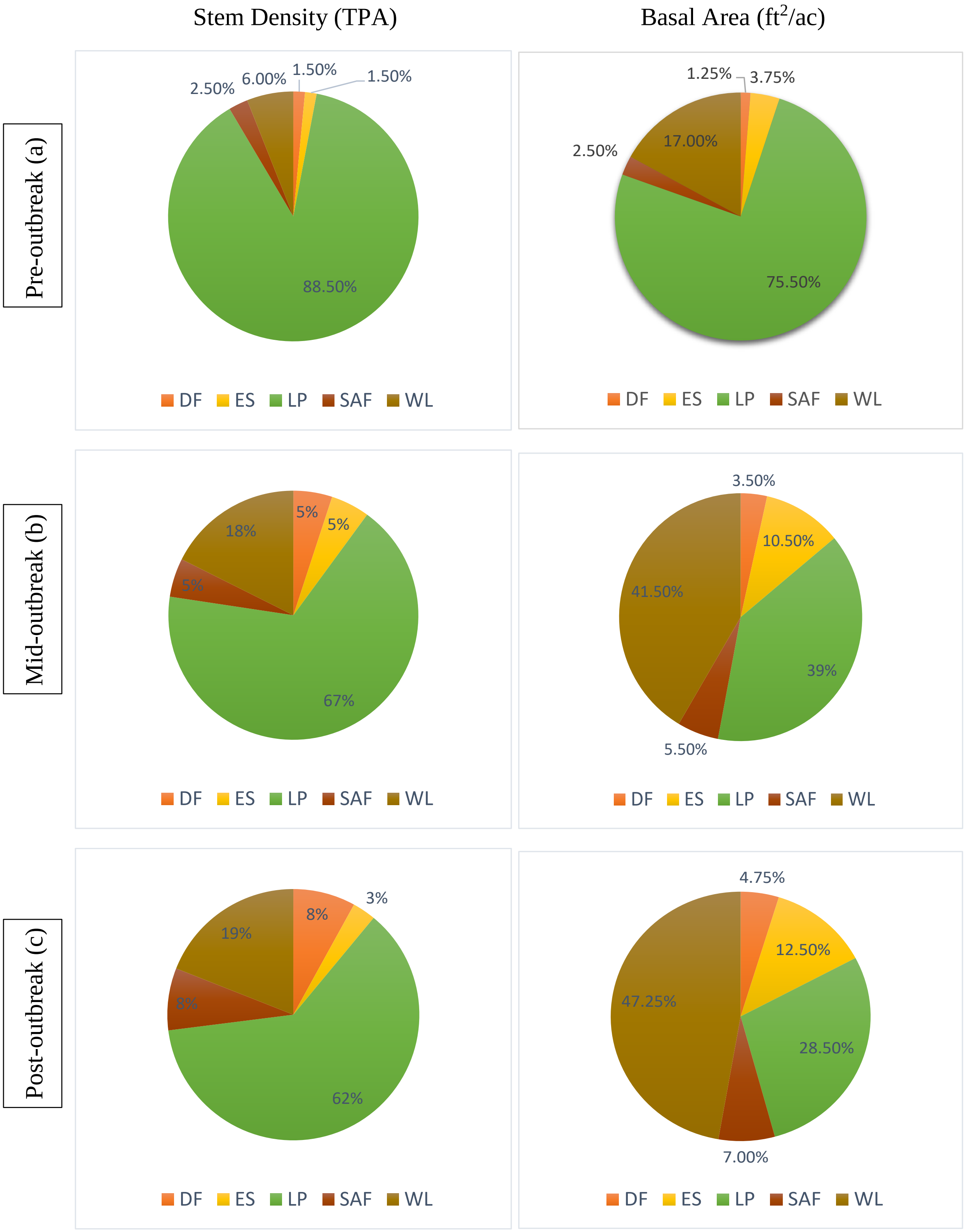


Figure 3 (a, b and c) – Overstory species composition by stem density (left column) and by basal area (right column) during the outbreak periods. Pre-outbreak (simulated) upper row, mid-outbreak (2010) middle row, and post-outbreak (2017) bottom row.

			All Species					
	Plot /Stand	Trees Per Acre	TPA % Decline	Basal Area ft^2/ac	BA % Decline	QMD (in)	SDI	Avg. Spacing (ft)
Pre-Outbreak	1	240		177.6		11.6	306.6	13.5
	2	368		197.0		9.9	362.6	10.9
	3	368		248.8		11.1	437.2	10.9
	Stand Avg	325		207.8		10.9	368.8	11.7
Mid-Outbreak	1	56	77%	68.7	61%	15.0	107.4	27.9
	2	184	50%	91.5	54%	9.6	170.9	15.4
	3	48	87%	64.8	74%	15.7	99.4	30.1
	Stand Avg	96	71%	75.0	63%	13.4	125.9	24.5
Post-Outbreak	1	56	77%	75.7	57%	15.7	116.0	27.9
	2	120	67%	64.1	67%	9.9	118.1	19.1
	3	32	91%	60.1	76%	18.6	86.1	36.9
	Stand Avg	69	78%	66.6	67%	14.7	106.7	27.9

			Lodgepole pine					
	Plot /Stand	Trees Per Acre	TPA % Decline	Basal Area ft^2/ac	BA % Decline	QMD (in)	SDI	Avg. Spacing (ft)
Pre-Outbreak	1	200		116.7		10.3	211.2	14.8
	2	352		181.8		9.7	337.0	11.1
	3	312		172.4		10.1	315.4	11.8
	Stand Avg	288		157.0		10.0	287.8	12.6
Mid-Outbreak	1	16	92%	7.9	93%	9.5	14.7	52.2
	2	168	53%	76.3	58%	9.1	145.1	16.1
	3	8	97%	3.7	98%	9.2	7.0	73.8
	Stand Avg	64	81%	29.3	83%	9.3	55.6	47.4
Post-Outbreak	1	16	92%	8.0	93%	9.6	14.9	52.2
	2	112	68%	48.9	73%	8.9	93.7	19.7
	3	0	100%	0.0	100%	0.0	0.0	0.0
	Stand Avg	43	87%	18.9	89%	6.2	36.2	24.0

Table 1 - Overstory stand metrics for all species (top), and just lodgepole pine (bottom).

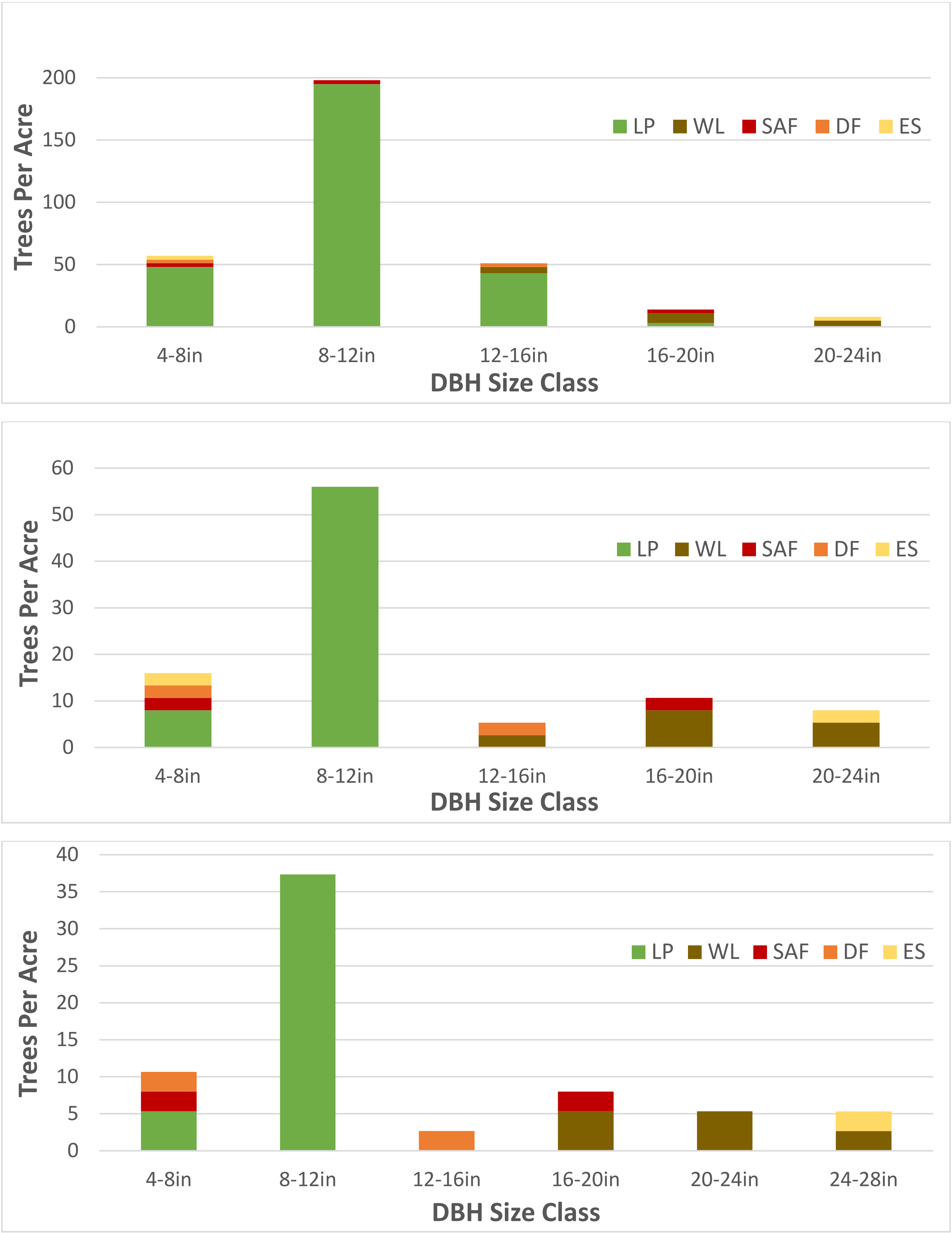
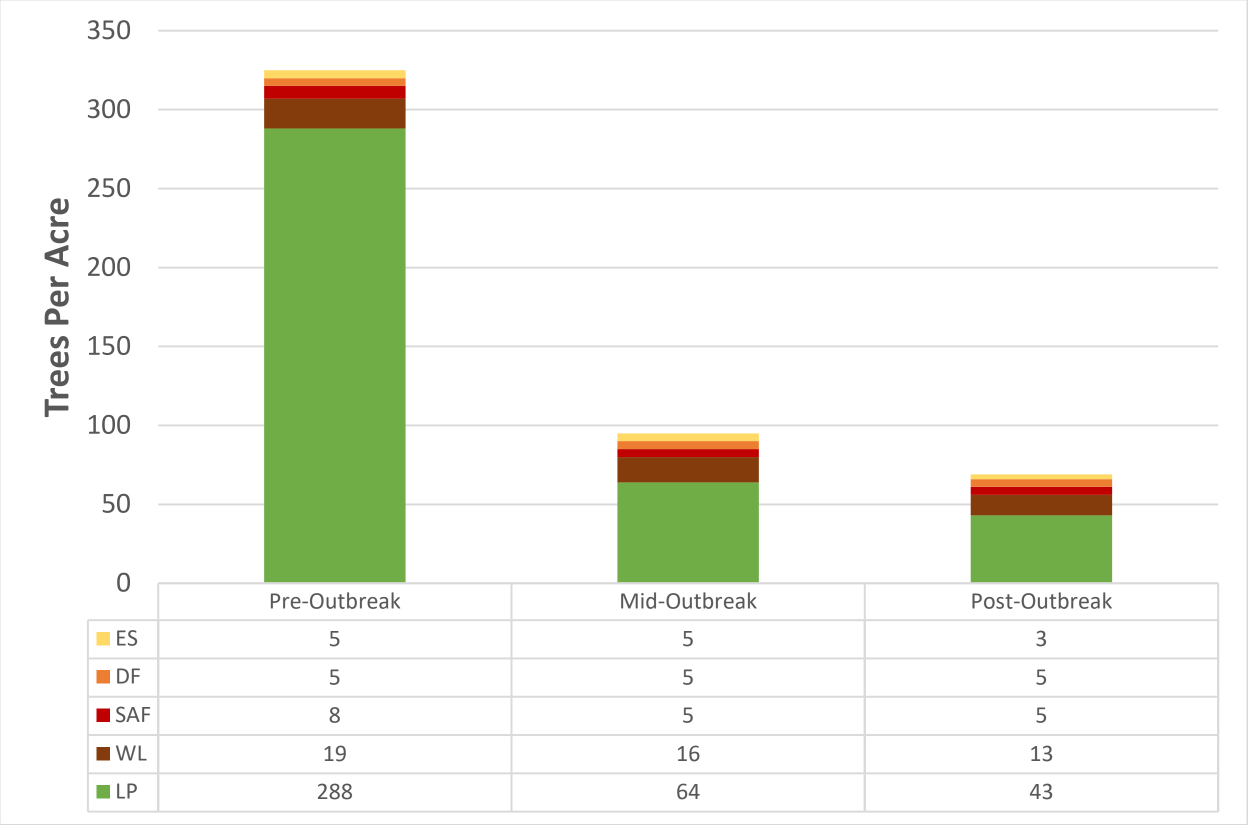


Figure 4 - Overstory diameter distribution for all species at pre-outbreak (top; simulated), mid-outbreak (2010; middle), and post-outbreak (2017; bottom).



	Pre-Outbreak	Mid-Outbreak	Post-Outbreak
🟨 ES	5	5	3
🟧 DF	5	5	5
🟥 SAF	8	5	5
🟫 WL	19	16	13
🟩 LP	288	64	43

Figure 5 - Changes to overstory species density (trees/ac) during the outbreak period. Pre-outbreak (left), mid-outbreak (center) and post-outbreak (right).

Figure 6 - Photo of study area in 2017.

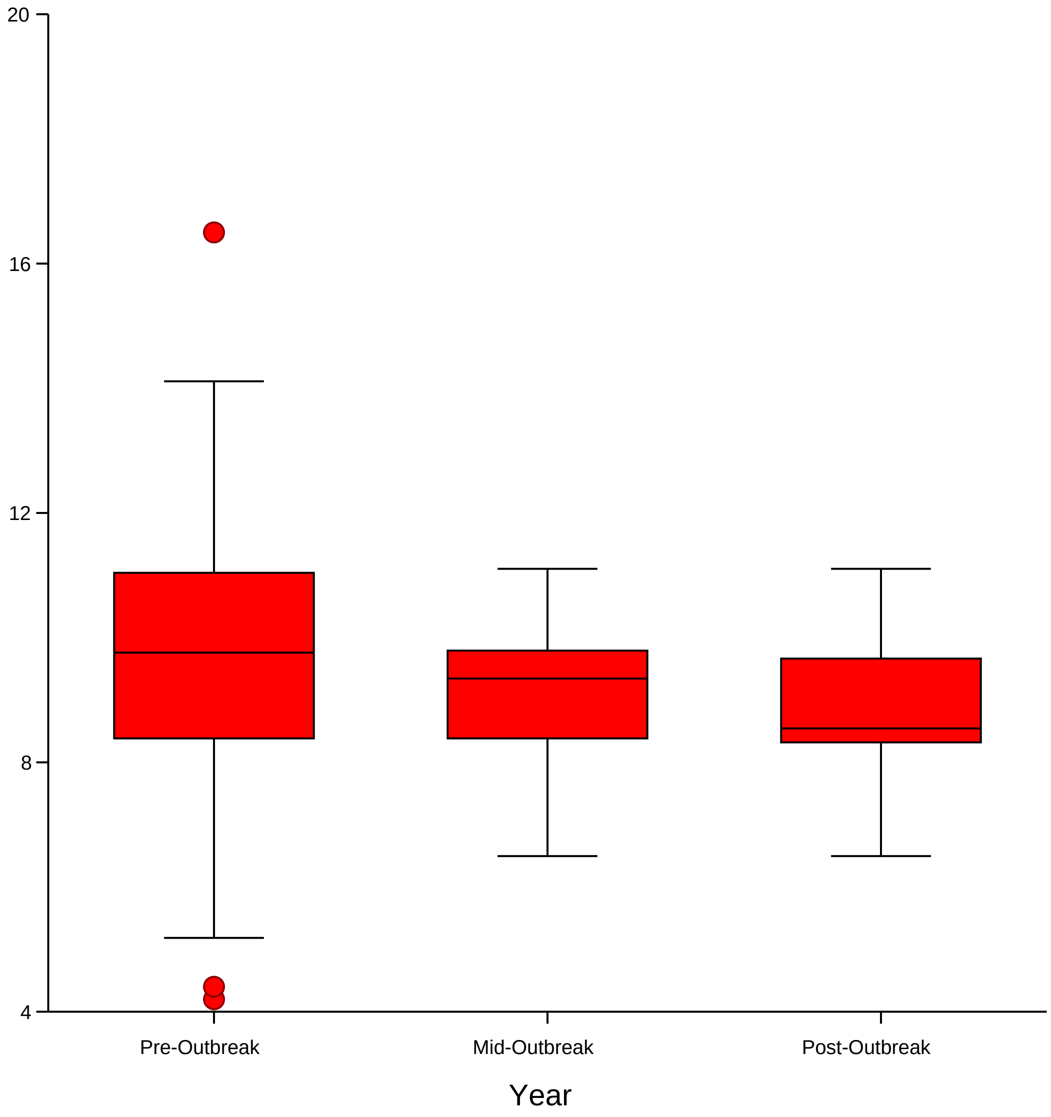


Figure 7 - Lodgepole pine diameter distributions at pre-outbreak (simulated; left), mid-outbreak (2010; center) and post-outbreak (2017; right).

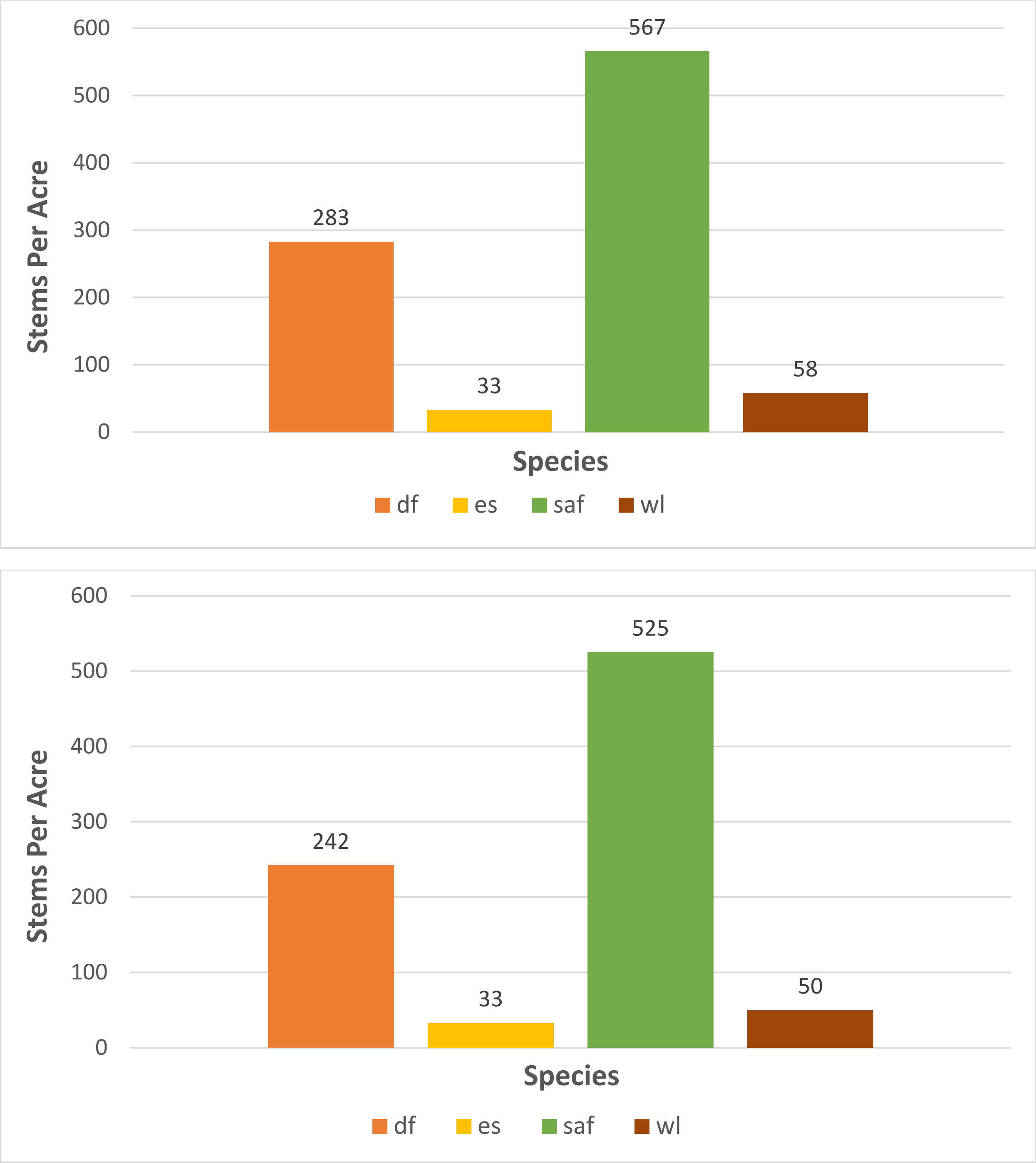


Figure 8 - Understory density (stems/ac) by species at mid-outbreak (2010; top) and at post-outbreak (2017; bottom).

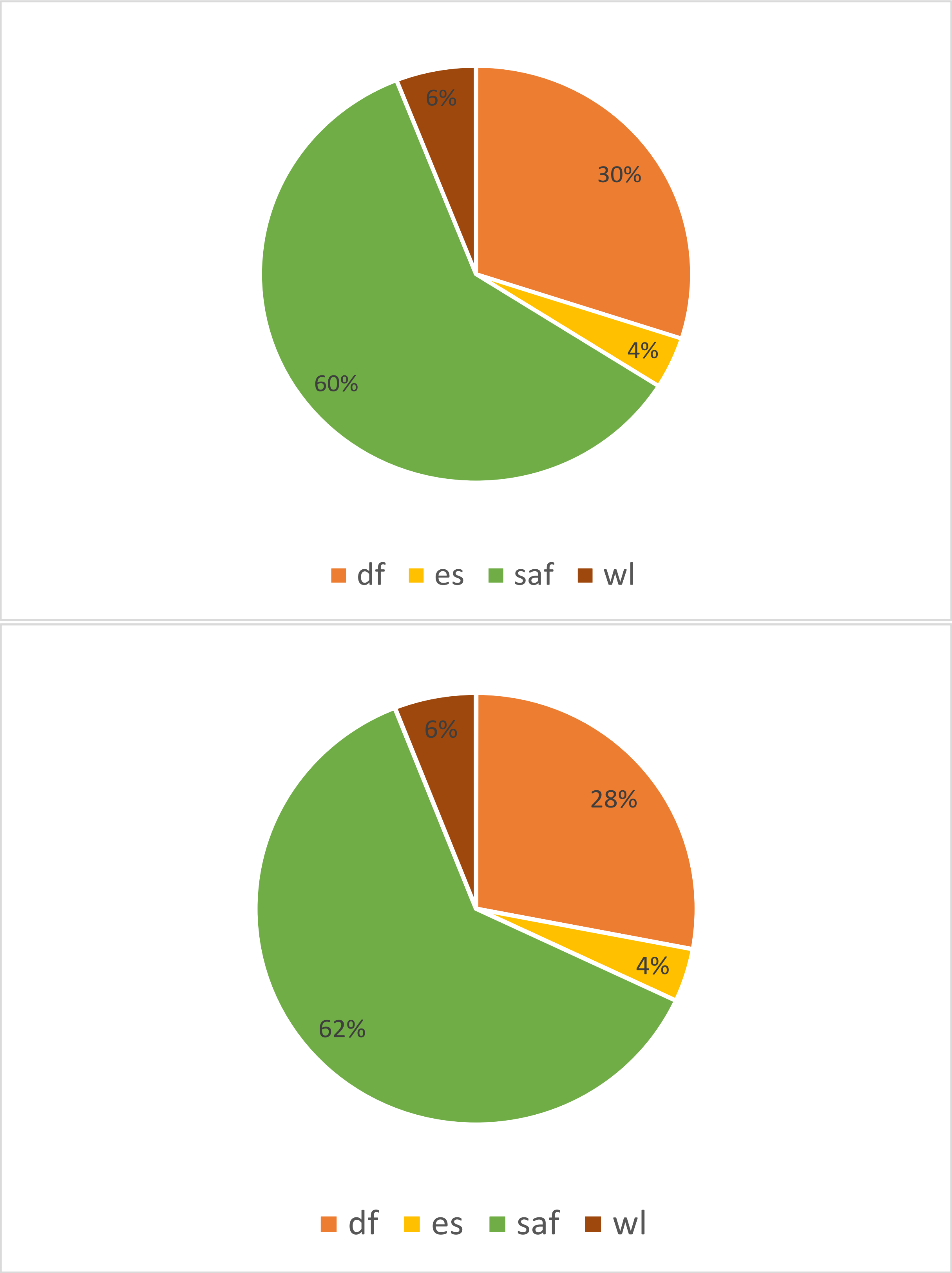


Figure 9 - Understory species composition by stems/ac at mid-outbreak (2010; top) and at post-outbreak (2017; bottom).

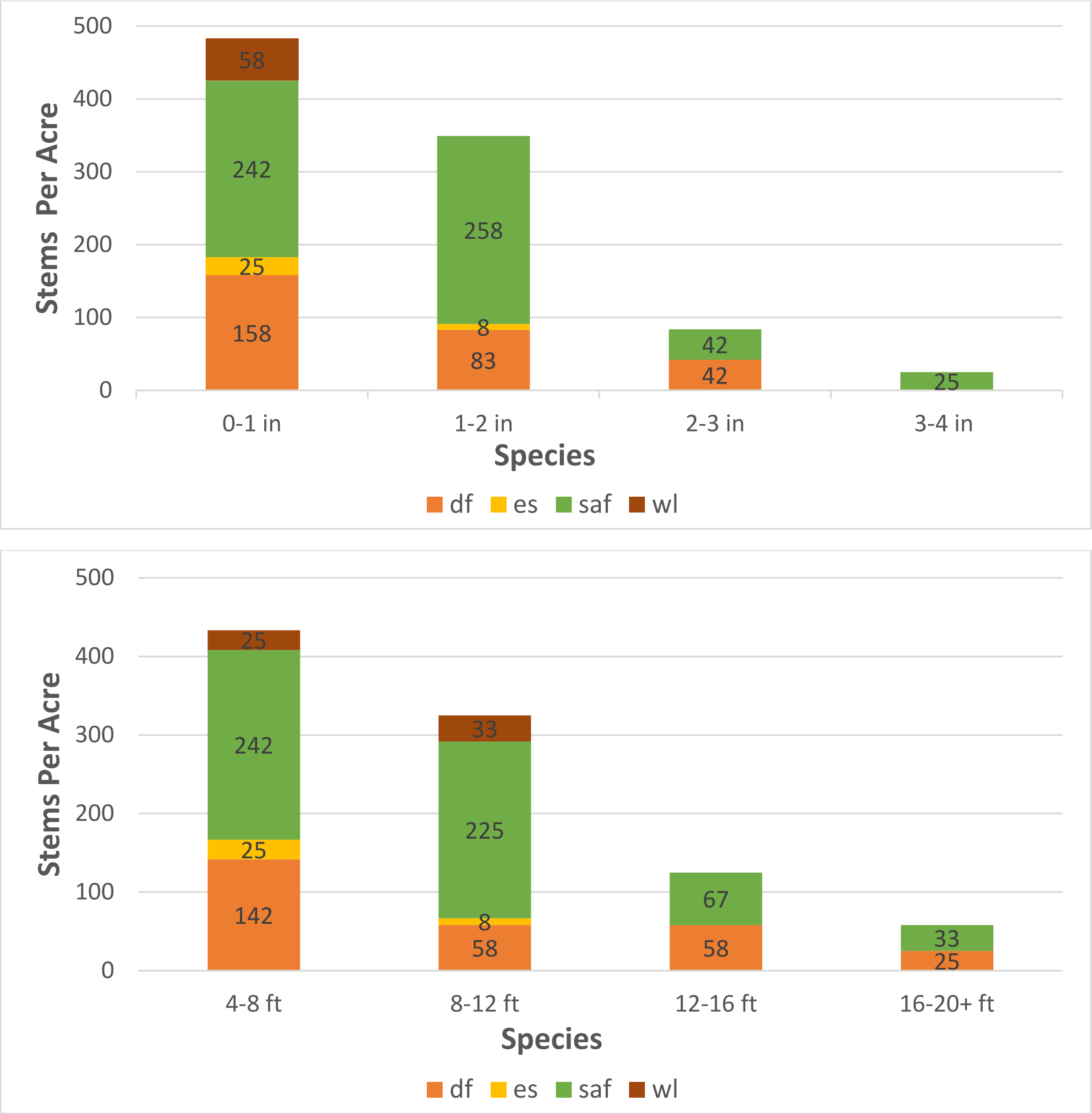


Figure 10 - Understory diameter distribution (top) and height distribution (bottom) of all saplings at mid-outbreak (2010).

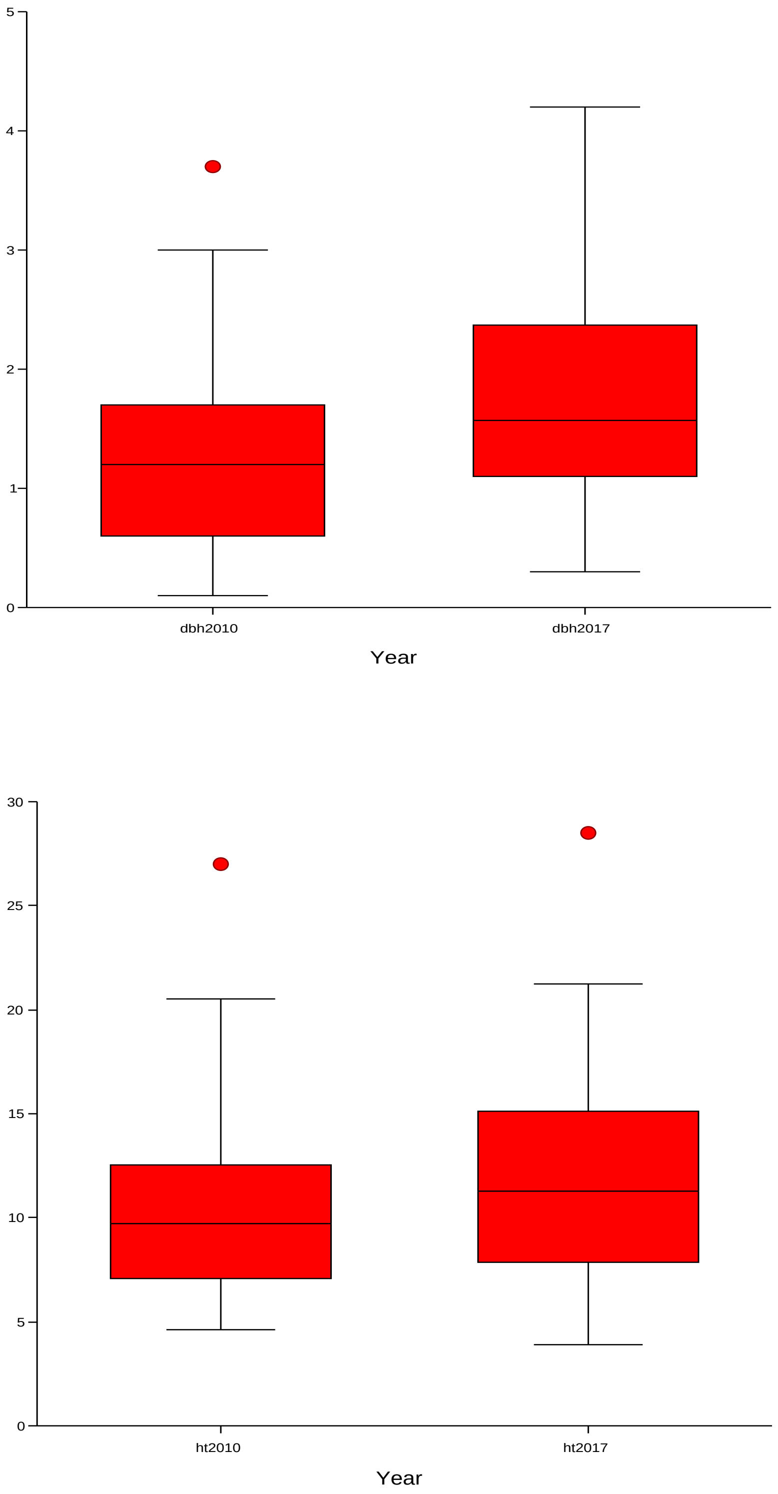
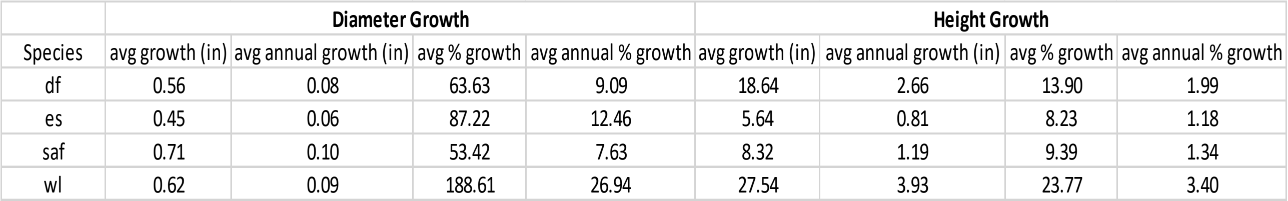


Figure 11 - Understory subsample DBH distribution (top) and height distribution (bottom) at mid-outbreak (2010) and post-outbreak (2017).



	Diameter Growth				Height Growth			
Species	avg growth (in)	avg annual growth (in)	avg % growth	avg annual % growth	avg growth (in)	avg annual growth (in)	avg % growth	avg annual % growth
df	0.56	0.08	63.63	9.09	18.64	2.66	13.90	1.99
es	0.45	0.06	87.22	12.46	5.64	0.81	8.23	1.18
saf	0.71	0.10	53.42	7.63	8.32	1.19	9.39	1.34
wl	0.62	0.09	188.61	26.94	27.54	3.93	23.77	3.40

Table 2 - Diameter and height growth of understory subsample by species.

2010				**2017**			**Differences**			**% Differences**		
	Tons/Acre			Tons/Acre			Tons/Acre			Tons/Acre		
Unit	Sound	Rotten	Total	Sound	Rotten	Total	Sound	Rotten	Total	Sound	Rotten	Total
1	5.0	16.5	21.5	34.6	6.4	41.0	+29.6	-10.1	+19.5	+592	-61.2	+90.7
2	7.1	19.5	26.6	29.9	5.4	35.3	+22.8	-14.1	+8.7	+321.1	-72.3	+32.7
3	8.7	9.0	17.7	42.2	21.7	63.8	+33.5	+12.7	+46.1	+385.1	+141.1	+260.5
Avg	7.0	15.0	21.9	35.6	11.2	46.7	+28.6	-3.8	+24.8	+408.6	-25.3	+113.2

Table 3 - Observed changes to 1,000-hour surface fuels from 2010 to 2017.

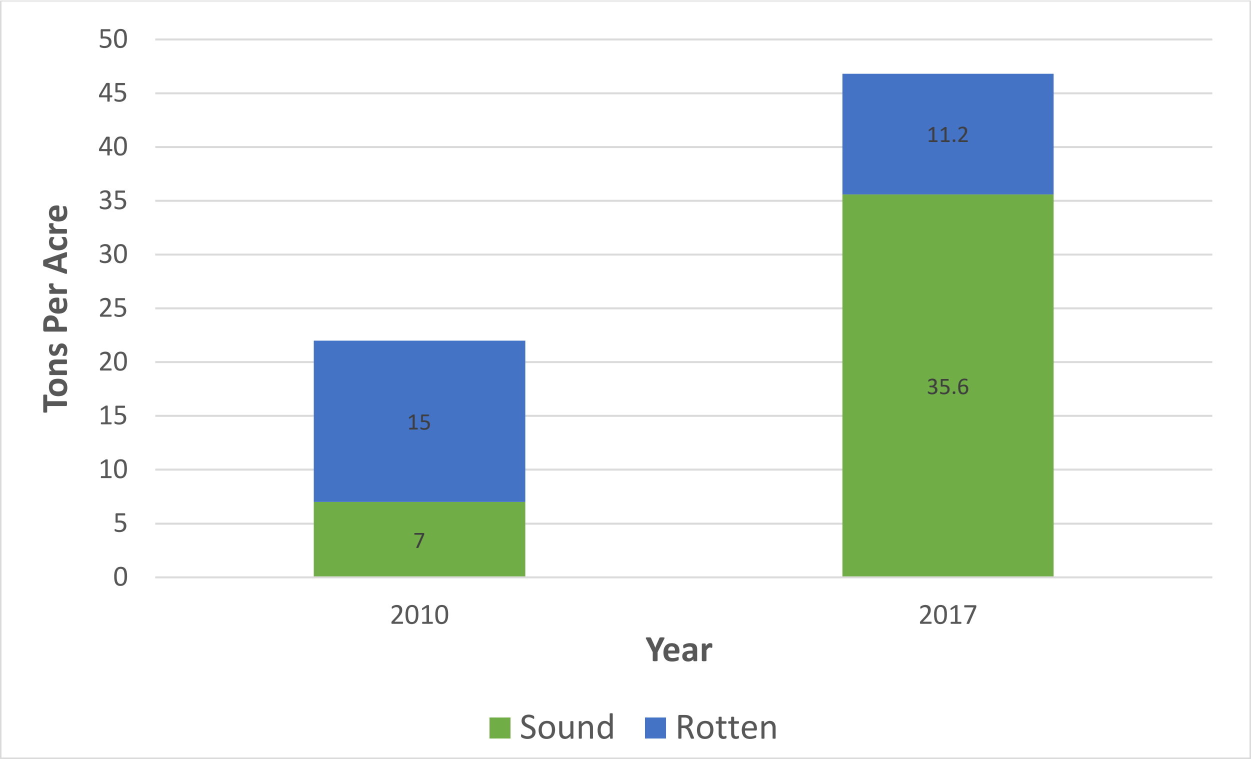


Figure 12 - Sound and rotten 1,000-hour fuels at mid-outbreak (2010; left) and post-outbreak (2017; right).

Figure 13 - Photos of study area in 2017.

BIBLIOGRAPHY

Agee, J. K. (1998). The landscape ecology of western forest fire regimes. *Northwest Science*, *72*, 24.

Agne, M. C., Woolley, T., & Fitzgerald, S. (2016). Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. *Forest Ecology and Management*, *366*, 73-86.

Amman, G., McGregor, M., & Dolph Jr, R. (1990). Forest insect and disease leaflet 2: Mountain pine beetle. *USDA Forest Service, Washington, DC*.

Brown, J. K. (1971). A planar intersect method for sampling fuel volume and surface area. *Forest Science*, *17*(1), 96-102.

Buma, B. (2015). Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere, 6*(4), 1-15.

Crotteau, J. S., Keyes, C. R., Sutherland, E. K., Wright, D. K., & Egan, J. M. (2016). Forest fuels and potential fire behaviour 12 years after variable-retention harvest in lodgepole pine. *International Journal of Wildland Fire*, *25*(6), 633-645.

Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, *250*(5461), 26.

Gibson, K., & Negrón, J. F. (2009). Fire and bark beetle interactions. In*: Hayes, JL; Lundquist, JE, comps. The Western Bark Beetle Research Group: A unique collaboration with Forest Health Protection: Proceedings of a symposium at the 2007 Society of American Foresters conference. Gen. Tech. Rep. PNW-GTR-784. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station: 51-70* (Vol. 784, pp. 51-70).

Hart, S. J., Schoennagel, T., Veblen, T. T., & Chapman, T. B. (2015). Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proceedings of the National Academy of Sciences*, 201424037.

Harvey, B. J., Donato, D. C., Romme, W. H., & Turner, M. G. (2014a). Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. *Ecological Applications*, *24*(7), 1608-1625.

Harvey, B. J., Donato, D. C., & Turner, M. G. (2014b). Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. *Proceedings of the National Academy of Sciences*, *111*(42), 15120-15125.

Hicke, J. A., & Jenkins, J. C. (2008). Mapping lodgepole pine stand structure susceptibility to mountain pine beetle attack across the western United States. *Forest Ecology and Management*, *255*(5-6), 1536-1547.

Hicke, J. A., Johnson, M. C., Hayes, J. L., & Preisler, H. K. (2012). Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management*, *271*, 81-90.

Jenkins, M. J., Hebertson, E., Page, W., & Jorgensen, C. A. (2008). Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management*, *254*(1), 16-34.

Jolly, W. M., Parsons, R. A., Hadlow, A. M., Cohn, G. M., McAllister, S. S., Popp, J. B., & Negron, J. F. (2012). Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. *Forest Ecology and Management*, *269*, 52-59.

Kaufmann, M. R., Aplet, G. H., Babler, M. G., Baker, W. L., Bentz, B., Harrington, M., & Keane, R. E. (2008). The status of our scientific understanding of lodgepole pine and mountain pine beetles – a focus on forest ecology and fire behavior. *GFI technical report 2008-2. Arlington, VA: The Nature Conservancy. 13 p.*

Keyes, C. R. (2006). Role of foliar moisture content in the silvicultural management of forest fuels. *Western Journal of Applied Forestry*, *21*(4), 228-231.

Keyes, C. R., Perry, T. E., Sutherland, E. K., Wright, D. K., & Egan, J. M. (2014). Variable-retention harvesting as a silvicultural option for lodgepole pine. *Journal of Forestry*, *112*(5), 440-445.

Klutsch, J. G., Negron, J. F., Costello, S. L., Rhoades, C. C., West, D. R., Popp, J., & Caissie, R. (2009). Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *Forest Ecology and Management*, *258*(5), 641-649.

Klutsch, J. G., Battaglia, M. A., West, D. R., Costello, S. L., & Negrón, J. F. (2011). Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. *Western Journal of Applied Forestry*, *26*(3), 101-109.

Kulakowski, D., & Veblen, T. T. (2006). The effect of fires on susceptibility of subalpine forests to a 19th century spruce beetle outbreak in western Colorado. *Canadian Journal of Forest Research*, *36*(11), 2974-2982.

Kulakowski, D., & Veblen, T. T. (2007). Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. *Ecology*, *88*(3), 759-769.

Li, C., Barclay, H. J., Hawkes, B. C., & Taylor, S. W. (2005). Lodgepole pine forest age class dynamics and susceptibility to mountain pine beetle attack. *Ecological Complexity*, *2*(3), 232-239.

Logan, J. A., Macfarlane, W. W., & Willcox, L. (2010). Whitebark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications*, *20*(4), 895-902.

Lynch, H. J., Renkin, R. A., Crabtree, R. L., & Moorcroft, P. R. (2006). The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. *Ecosystems*, *9*(8), 1318-1327.

Mitchell, R. G., & Preisler, H. K. (1998). Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. *Western Journal of Applied Forestry*, *13*(1), 23-26.

Mitchell, R. G., Waring, R. H., & Pitman, G. B. (1983). Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. *Forest Science*, *29*(1), 204-211.

Nelson, W. A., Potapov, A., Lewis, M. A., Hundsdörfer, A. E., & He, F. (2008). Balancing ecological complexity in predictive models: a reassessment of risk models in the mountain pine beetle system. *Journal of Applied Ecology*, *45*(1), 248-257.

Nimlos, T. J. (1986). *Soils of Lubrecht Experimental Forest*. Miscellaneous Publication No. 44, Montana Forest and Conservation Experiment Station.

Page, W., & Jenkins, M. J. (2007). Predicted fire behavior in selected mountain pine beetle–infested lodgepole pine. *Forest Science*, *53*(6), 662-674.

Page, W. G., & Jenkins, M. J. (2007). Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. *Forest Science*, *53*(4), 507-518.

Parker, T. J., Clancy, K. M., & Mathiasen, R. L. (2006). Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agricultural and Forest Entomology*, *8*(3), 167-189.

Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G., & Romme, W. H. (2008). Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *AIBS Bulletin*, *58*(6), 501-517.

Romme, W. H., Clement, J., Hicke, J., Kulakowski, D., MacDonald, L. H., Schoennagel, T. L., & Veblen, T. T. (2006). Recent forest insect outbreaks and fire risk in Colorado forests: A brief synthesis of relevant research. *Colorado Forest Research Institute*.

Romme, W. H., Knight, D. H., & Yavitt, J. B. (1986). Mountain pine beetle outbreaks in the Rocky Mountains: Regulators of primary productivity? *The American Naturalist*, *127*(4), 484-494.

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. *In Proceedings of a Symposium: Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests*. April 25–27, 1978. Pullman, Washington. *Edited by* Kibbee, D. L.,Berryman, A. A., Amman, G.D., and Stark, R. W. University of Idaho, Moscow, Idaho pp. 77–84.

Safranyik, L., & Carroll, A. L. (2006). The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. *In The mountain pine beetle: a synthesis of its biology, management and impacts on lodgepole pine*. *Edited by* Safranyik, L. and Wilson, B. Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, Victoria, British Columbia. pp. 3-66.

Safranyik, L., Carroll, A. L., Régnière, J., Langor, D. W., Riel, W. G., Shore, T. L., Peter, B., Cooke, B. J., Nealis, V. G., & Taylor, S. W. (2010). Potential for range expansion of mountain pine beetle into the boreal forest of North America. *The Canadian Entomologist*, *142*(5), 415-442.

Taylor, S. W., & Carroll, A. L. (2003, October). Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. In *Mountain pine beetle symposium: Challenges and solutions* (pp. 41-51). Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC.

Turner, M. G., Hargrove, W. W., Gardner, R. H., & Romme, W. H. (1994). Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science*, *5*(5), 731-742.

Whitehead, R. J., & Russo, G. L. (2005). *Beetle-proofed lodgepole pine stands in interior British Columbia have less damage from mountain pine beetle* (Vol. 402). Pacific Forestry Centre.

Williams, H., Hood, S. M., Keyes, C. R., Egan, J. M., & Negrón, J. (2018). Subwatershed-level lodgepole pine attributes associated with a mountain pine beetle outbreak. *Forests*, *9*(9), 552.