THESIS

THE EFFECT OF MOUNTAIN PINE BEETLE CAUSED MORTALITY ON SUBALPINE FOREST STAND AND LANDSCAPE STRUCTURE IN ROCKY MOUNTAIN NATIONAL PARK, CO

Submitted by

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In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Fall 2009

COLORADO STATE UNIVERSITY

October 29, 2009

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY KELLEN NELSON ENTITLED "THE EFFECT OF MOUNTAIN PINE BEETLE CAUSED MORTALITY ON SUBALPINE FOREST STAND AND LANDSCAPE STRUCTURE IN ROCKY MOUNTAIN NATIONAL PARK, CO" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

THE EFFECT OF MOUNTAIN PINE BEETLE CAUSED MORTALITY ON SUBALPINE FOREST STAND AND LANDSCAPE STRUCTURE IN ROCKY MOUNTAIN NATIONAL PARK, CO

Mountain pine beetle (MPB) eruptions in lodgepole pine forests are a disturbance process that shape forest structure and successional trajectories. Chapter one examines the effect that MPB have on overstory stand and landscape forest structure. I distributed 46 randomly located clusters of three plots across the west side of Rocky Mountain National Park (RMNP), and characterized changes in stand structure and lodgepole pine mortality through three stages in the eruption. Across the landscape, diameter at breast height, basal area, and density decreased by 37%, 71%, and 34% respectively. Environmental factors (elevation and moisture) and tree size greatly influenced the early stage of the eruption; whereas later stages showed stronger relationships with stand structure factors (tree size, basal area, proportion of non-host trees, density and stand age). Changes in forest heterogeneity depended on spatial scales; at the local scale, heterogeneity increased among subplots within clusters, while heterogeneity among clusters declined over time.

In chapter two, I explored the effect of MPB-related mortality on aspen regeneration by examining whether suckering densities and growth rates increase with MPB-related mortality, and if ungulates utilize additional suckers through browsing. Conifer overstory mortality, aspen sucker density, stem elongation, total sucker height, and ungulate browsing rates were characterized in 48 plots over 8 stands. Heavy lodgepole pine

mortality decreased conifer basal area by 80% and stem density by 50% of pre-eruption levels. This appears to relieve competitive pressure on aspen in mixed conifer-aspen stands. Linear mixed-effects model results show that as weighted mortality increased, aspen sucker density increased three-fold, aspen stem elongation increases by 2.5-fold, and mean sucker height increases by two-thirds. Additionally, as sucker density increased, I did not find evidence to suggest that the rate of ungulate browsing increased. Mountain pine beetle related mortality relieves conifer pressure and may lead to successful aspen recruitment.

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ACKNOWLEDGEMENTS

My success on this thesis would not have been possible without the support of many individuals. I would like to thank Monique Rocca for her advice and encouragement during my studies at CSU. Thank you to Carissa Aoki, Matt Diskin, and Bill Romme for providing invaluable help with project setup and overall oversight. Many thanks to Brandon Corcoran, Jared Lyons, and Greg Pappas; great hiking companions and reliable field assistants. I am very much indebted to Dan Binkley, Phil Chapman, Emily Kachergis, Patrick Martin and Kate Cueno-Toy for providing useful comments on early versions of this manuscript. Thank you to Nathan Williamson and Judy Visty for their knowledge and support at Rocky Mountain National Park. Special thank you to Monique LaPerriere, my lover and best friend, for her help along the way. Without it, my time in graduate school would not have been such a joy and success. Finally, I would like to thank my parents Valerie and Steve Nelson, and my sister Annelise Nelson for their moral support and encouragement. This project was funded by McIntire-Stennis appropriations to Colorado State University and the National Park Service.

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Chapter 1: The effects of stand structure and environmental factors on lodgepole pine stand and landscape patterns through a mountain pine beetle eruption in Rocky Mountain National Park, CO

Abstract

An ongoing mountain pine beetle (MPB) outbreak has been dramatically changing Colorado's lodgepole pine forests since 1996. Warmer climate trends and extensive old forests facilitated this widespread outbreak. I distributed 46 randomly located clusters of three plots across the west side of Rocky Mountain National Park to examine the influence of environmental and stand structure factors on lodgepole pine mortality patterns, and to assess changes to stand and landscape structures through three stages in the eruption. Across the landscape, mean stem mortality reached 47%; however, 71% of basal area was killed. Surviving stand structure experienced large decreases in diameter at breast height (17.4 to 11.0 cm), basal area (29.3 to 8.5 m^2 ha^{-1}), and density (1393 to 915 stems ha^{-1}). Environmental factors (elevation and moisture) and tree size greatly influenced which stands saw high levels of mortality during the early stage of the eruption. In contrast, later stages of the eruption showed stronger relationships with stand structure factors (tree size, basal area, proportion of non-host trees, density and stand age). Changes in forest heterogeneity depended on spatial scale. At the local scale, heterogeneity increased among subplots within clusters, while heterogeneity among clusters on the landscape declined over time. The current mountain pine beetle outbreak has caused extensive changes to the subalpine forest landscape, but high densities of

surviving trees and increased stand-scale heterogeneity will allow forest recovery and increased resistance in the face of future outbreaks.

Introduction

Three quarters of Colorado's of lodgepole pine forest (600,000 ha) have been affected by the mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopk) since 1996 (Leatherman 2008). The Colorado outbreak is a subset of the larger sub-continental bark beetle eruption where over 47 million ha of Western North America has seen mortality in the last decade (Raffa et al. 2008). Broad-scale climatic forcing and widespread stands of susceptible host trees have been identified as causes for the initiation and development of positive feedbacks that maintain bark beetle population eruptions (Peters et al. 2004; Raffa et al. 2008). As an eruption progresses, tree demography, physiological stresses, and spatial patterns of living trees change, dictating which forest stands experience mortality during a particular year. We examined the influence of environmental and stand structure factors on lodgepole pine mortality patterns, and assessed changes to stand and landscape structures through multiple stages of a MPB eruption in Rocky Mountain National Park (RMNP), Colorado.

Mountain pine beetles are common in lodgepole pine (*Pinus contorta*) forests and eruptions are a natural disturbance process in the Rocky Mountains (Safranyik and Carroll 2006; Sibold et al. 2007). The size and duration of beetle activity vary from small endemic pockets of infestation that last one season to broad, landscape-scale events that can last for a decade or more (Amman and Cole 1983). Eruptions are initiated when broad-scale factors (e.g., drought, warm temperatures) intensify fine-scale processes (e.g., beetle reproductive success) that weaken host species and favor bark beetle reproduction

(Logan et al. 2003; Peters et al. 2004; Raffa et al. 2008). As broad-scale pressures increase, intermediate-scale stand and landscape patterns act to buffer the effects of beetle-tree interactions (Peters et al. 2007); the prevalence of stands of suitable host trees, the connectivity between those stands, and the severity of broad-scale pressures determine whether MPB populations will begin a positive feedback cycle and initiate an eruption (Raffa et al. 2008). The relative strengths of each of these factors also contribute to annual changes in stand-level susceptibility. For instance, if climatic forcing is the most important factor influencing host susceptibility, then I would expect stands on hot and dry sites to see the greatest beetle impact. Conversely, if stand structure contributes the greatest influence, then stands dominated by favorable host traits will be targeted. Lodgepole pine mortality is largely determined by the interaction of broad and fine-scale processes, but no studies have examined how these pressures change through an eruption.

Disturbance processes in subalpine forests influence the vulnerability of a region to bark beetle eruptions by affecting stand structure and landscape heterogeneity (Raffa et al. 2008; Safranyik and Carroll 2006). Infrequent, high-severity wildfires are recognized as the dominant disturbance process that structures lodgepole pine forests (Romme 1982). High-severity fire events result in nearly 100% mortality in the forest canopy, and new stands are commonly initiated following high-severity wildfire (Peet 2000). Species adaptations, namely serotinous cones that open and release seeds in response to heat pulses, allow for strong post-fire seedling recruitment (Peet 2000). Because of their fire regime and regeneration patterns, lodgepole pine forests are typically comprised of a complex mosaic of different even-aged patches with uniform stand structures (Romme

1982). Depending on the extent of previous wildfires and the age of regenerating stands, stand structure and the arrangement of patches on the landscapes may hinder or facilitate MPB eruptions.

This study examines how surviving stand and landscape structures change as an eruption progresses and identifies factors that influence lodgepole pine mortality at different stages in the eruption. Previous studies have identified stand-scale (Cole and Amman 1980) and broad-scale factors (Logan et al. 2003; Negron et al. 2009; van Mantgem et al. 2009) that are related to MPB-caused mortality, but no studies have compared the relative influence of these factors through an eruption. I place the MPB eruption in a temporal context to determine whether the influence of environmental and stand structure factors change as an eruption progresses. I quantify changes in mortality, surviving stand structure, and forest heterogeneity (at the stand and landscape scales) at early, middle, and late stages in the eruption. My sampling took place at what appeared to be the end of the eruption in this local area: extensive mortality had occurred in the previous five years but few or no trees were still being killed in most stands. (The eruption is continuing to expand into new areas to the north and east of my sampling area in 2009.) To address these objectives, I asked the following questions: (1) How did MPB-related mortality and stand structure change through multiple stages of a MPB eruption? (2) What are the relative influences of stand structure and environmental factors in determining lodgepole pine mortality at each stage of a MPB eruption? (3) Does stand and landscape heterogeneity change as a result of a MPB eruption?

Materials and Methods

Study Area

During the summer of 2008, I surveyed the lodgepole pine forest on the west side of RMNP, Colorado (Figure 1-1). The study area is situated at the northern end of the Front Range Mountains and southern end of the Mummy Range, west of the continental divide. Lodgepole pine forests in this portion of the park encompass 11,000 ha from 2500 to 3400 meters in elevation (USGS-NPS 2006). In nearby Grand Lake, Colorado, average precipitation is 484 mm per year, mean January minimum temperature is -16.5° C, and mean July maximum temperature is 24.6° C (http://www.wrcc.dri.edu/). Soils are typically rocky and infertile and follow a cryic temperature regime (NRCS 2007). Most of the lodgepole pine stands on the west side of the park regenerated following stand-replacing fires (Sibold et al. 2006) that have recurred on a 100 – 300 year return interval (Peet 2000; Sibold et al. 2006). Small-scale MPB eruptions and wind-throw events also occurred periodically during the 20th century (Sibold et al. 2007).

Native Americans began using RMNP during the archaic era and continued until the late 1800s; however, their impact on surrounding subalpine forests is believed to have been minor (Buchholtz 1983). Euro-American settlers arrived in the late 1860s and quickly began extracting the area's natural resources. During the 1870s and 1880s, localized logging supplied timber to an ephemeral mining boom and local tourist communities. These activities were banned after the establishment of the national park in 1915 (Buchholtz 1983; Hess 1993), but early management policies shaped park forests in their own way (Hess 1993). "Natural regulation" of elk herds has had long lasting

effects on park meadow (Hess 1993) and aspen systems (Binkley 2008; Hess 1993), and 20th century fire suppression may have affected the forest age mosaic (Sibold et al. 2006). Despite these impacts, lodgepole pine forests in RMNP are still within the historical range of variability for fire return interval and forest structure (Sibold et al. 2006).

I established 46 "clusters" of three sample plots using a spatially-balanced, random sampling design (Theobald et al. 2007) throughout the lodgepole pine cover type on the west side of RMNP (Figure 1-1). Clusters were considered suitable for sampling if plots were dominated by lodgepole pine and were not obviously manipulated by management (e.g., fuels reduction treatment). At each randomized point, three 0.04 ha fixed-area plots (20 X 20 m) were sampled, with the first plot at the random point and the second and third plots positioned 60 and 90 meters from the first in a triangular orientation along a random compass bearing (Figure 1-1). All trees taller than breast height (1.37 m) were measured and the following attributes were recorded: species, diameter at breast height (dbh), cone presence, serotiny, and "mortality category". Cone presence and serotiny were determined for each lodgepole pine by searching each tree with binoculars (Tinker et al. 1994). "Mortality category" was assessed for each lodgepole pine tree by classification into one of five qualitative categories representing mortality status and time-since-beetle attack (Table 1-1). Trees were classified as alive, one year since infestation: faded green to completely red foliage remaining on the tree, two years since infestation: ≥ 50% red/orange needles remaining, three or more years since infestation: ≤ 50% needles remaining on the tree, and died from causes other than the MPB (Keen 1955; Klutsch et al. 2009). Presence of MPB was identified using

characteristic signs of infestation including frass, pitch tubes, boring dust, galleries, or exit holes. Tree killed from agents other than MPB were removed from the analysis.

Within each plot, the following attributes were recorded: location (UTM coordinates), slope, aspect, elevation, and stand age. Stand age was determined by coring three of the oldest trees that appeared to have initiated in the last stand replacing fire. Increment cores were prepared using standard dendrochronological methods (Stokes and Smiley 1968) and annual rings were counted but not cross-dated. Tree ages were reported as ring counts and lumped into half-century groups defined by Sibold et al. (2006) to minimize dating errors.

Data Analysis

Changes in landscape mortality and stand structure

I tested for differences in lodgepole pine mortality and surviving stand structure among stages of the eruption to examine the rate of tree mortality and determine when surviving forest stand structure changed significantly from pre-eruption conditions. Cumulative lodgepole pine mortality was computed for each plot by dividing the total stems and basal area of trees that died after each stage by the number of living trees or basal area that preceded the eruption. "Stage mortality" was calculated by taking the difference in cumulative mortality between stages. Percent of landscape affected by each stage of the eruption is defined as the percent of clusters that had at least one MPB-infested tree. Surviving forest stand structure were estimated using surviving trees at the end of each stage. Differences between stages were tested using Tukey's HSD for the

following stand structure attributes: mean dbh, density, basal area, percent non-host species (density and basal area), percent of susceptible trees (PICO >15 cm dbh), and percent serotiny. The effect of MPB mortality on surviving diameter distribution was computed for surviving lodgepole pine trees at each stage of the eruption. Tukey's HSD was used to test for differences in the proportion of surviving trees in each size class (5 cm bins) between stages in the eruption. The number of surviving cone-bearing trees was also calculated. Tukey's HSD ($\alpha = 0.05$) was selected to control for comparison-wise and experiment-wise error rates.

Relative influence of stand structure and environmental factors in predicting lodgepole pine mortality

Linear mixed effects models were fit to predict lodgepole pine mortality (proportion stems killed) from z-score corrected stand structure and environmental factors using the nlme package within the R statistical framework (Pinheiro et al. 2009; R Development Core Team. 2009). The use of z-score corrected predictor variables allows the comparison of coefficients for determining the strength in which a particular stand structure or environmental factor influences lodgepole pine mortality. Cluster was used as the random effect due to my nested sampling design. Analysis was repeated using three sets of independent variables (stand structure attributes, environmental factors, and all attributes) for each stage of the eruption. Stage-specific mortality, defined as the proportion of trees greater than 1.4 m in height killed by MPB, was the response variable. Since all mortality values were below 0.5 (50%), a square root transformation was used to normalize the distribution. Predictor variables were converted to z-scores, and stand structure predictor attributes reflected surviving trees at the beginning of each stage.

Models exhibited linear predicted values and were homoscedastic. Each model was fitted using a structural modeling technique aimed at best describing the processes influencing lodgepole pine mortality. This included: (1) using stepwise bidirectional selection with the maximum likelihood method to minimize AIC, (2) refitting the optimal model in (1) using the REML method to produce unbiased estimates of random and fixed effects, and (3) dropping out insignificant terms ($\alpha = 0.05$) using backwards selection. The random effect, cluster, was tested to be significant (p-value < 0.0001) by fitting two intercept models – one with a random effect and the other without – and testing for differences using an analysis of variance (ANOVA). Coefficient of variation (R^2) relates directly to the explained variance of each fit model and was used to evaluate the relative ability of stand structure versus environmental factors to predict lodgepole pine mortality between stages of the eruption. R^2 was calculated using the likelihood ratio method (Magee 1990) as suggested by Kramer (2005). Plot-level stand structure parameters included plot age (years), mean dbh, density, basal area, proportion non-host species (density and basal area), and proportion of susceptible trees (PICO >15 cm dbh). Environmental parameters included elevation, slope, aspect, topographic convergence index, and equinox radiation (watt hrs/m^2). Aspect was transformed to a continuous distribution using Beers et al. (1966). Topographic convergence index provides an estimate of plot moisture (Beven and Kirkby 1979) and is a function of slope and the upslope contributing area. Equinox radiation is an estimate of solar exposure and includes topographic shading (ESRI ArcInfo 9.2 2006). Both TCI and equinox radiation were calculated using ESRI ArcGIS 9.2 with a USGS 10m DEM.

Changes in stand and landscape heterogeneity

My examination of spatial heterogeneity was conducted at the scale of individual clusters and at the landscape scale using three methods. (1) A variance component analysis was conducted differentiating variance within sample clusters and among sample clusters. A null linear mixed-effect model was fit (Pinheiro et al. 2009) to the dependent variable, stem mortality, to calculate the cluster (random effect) and residual variance for each stage. (2) Coefficient of variation (CV%) was computed and compared for stand structure attributes within each cluster at each stage in the eruption (citation). Differences in within-cluster CV% were compared using Tukey's HSD. (3) Semi-variograms were generated for dbh and basal area to assess changes in semi-variance and patch size prior to and late in the eruption. Theoretical curves (Legrende and Fortin 1989) were selected that best fit my field data using AIC (Reich 2008). The "Spherical model" was the optimal model in both cases and was bootstrapped (9999 iterations) with replacement to 75% of the field data. The median nugget, range, and sill are reported.

All analyses were conducted using the base, nlme (Pinheiro et al. 2009), and RSpatial (Reich 2008) packages within the R 2.9.1 statistical environment (R Development Core Team. 2009).

Results

Changes in landscape mortality and stand structure

Across the west side of RMNP, MPB-infested trees were wide spread and new trees were infested at increasing rates during each stage of the eruption. Early in the

eruption, 91% of clusters had at least one tree infested by the MPB (Table 1-2). This increased to 98% of clusters in the middle of the eruption, and 100% late in the eruption. The rate of stems killed per year increased during each stage of the eruption from 12% early in the eruption to 18% late in the eruption ($p = 0.0138$). Despite this increase, the rate of basal area killed did not change among stages ($p = 0.2948$), indicating that average size of killed trees declined as the outbreak progressed. Cumulative increases in percent of stems killed and basal area killed were found in all stages, increasing from 12% to 28% to 47%, and cumulative percent basal area killed grew similarly from 21%, to 46% to 71%.

The structure of the surviving forest changed considerably throughout the eruption (Table 1-3). Average diameter of lodgepole pines dbh was 17.4 cm before the eruption and decreased to 13.3 cm in the middle of the eruption, then 11.0 cm late in the eruption ($p < 0.0001$). Plot density decreased by late in the eruption from 1393 stem ha^{-1} to 915 stem ha^{-1} ($p = 0.0358$). Plot basal area decreased during each stage of the eruption from 29.31 m^2 ha^{-1} to 8.52 m^2 ha^{-1} ($p< 0.0001$). Percent of non-host species (stems/ha) did not change ($p = 0.2268$), but percent of non-host species (basal area/ha) increased from 10.6% before the eruption to 23.1% late in the eruption ($p = 0.0001$). The proportion of susceptible trees (dbh > 15 cm) was 58% before the eruption and decreased to 42% during the middle of the eruption. In the third year, nearly one-third of the susceptible trees remained alive. Percent of serotinous trees decreased from 50% before the eruption to 42% in the middle and 37% during the late stage of the eruption ($p < 0.0001$). The diameter distribution showed increases in the proportion of small diameter trees and decreases in the proportion of large diameter trees (Figure 1-2). The only size

class that did not change in proportion through the eruption is that between 16 and 20 cm dbh. Survival of cone-bearing trees decreased as the eruption progressed (Table 1-4) due to decreases in the proportion of serotinous trees and decreases in stand density. The percent of non-serotinous trees per plot did not change appreciably through the eruption.

Relative influence of stand structure and environmental factors on lodgepole pine mortality

Stand structure and environmental factors equally explained lodgepole pine mortality early in the eruption, but the relationship with environmental factors declined later (Table 1-5). R^2 for stand structure models increases from 0.38 early in the eruption to 0.66 late in the eruption. Conversely, R^2 for environmental models decrease from 0.37 early in the eruption to 0.24 late in the eruption.

Linear mixed effects models predicting lodgepole pine mortality that occurred during each individual stage identified changes in stand structure and environmental factors as the eruption progressed (Table 1-5). Lodgepole pine mortality during the early stage of the eruption was positively related to average lodgepole pine diameter ($p = 0.0001$) in the stand structure only model and negatively correlated with elevation ($p = 0.0077$) and topographic convergence index ($p = 0.0035$) in the environmental only model. When all attributes were used to predict lodgepole pine mortality, elevation had the greatest influence (coefficient = -0.0776; $p = 0.000$) while average lodgepole pine diameter (coefficient = 0.0771; $p = 0.0000$), and topographic convergence index (coefficient = -0.0498; $p = 0.0002$) had less impact on lodgepole pine mortality. During the middle stage of the eruption, stand structure attributes became solely important in predicting lodgepole pine mortality. These attributes did not change between the stand structure only model and the model that included all attributes. Ordered by the strength

of their relationship with lodgepole pine mortality, average lodgepole pine diameter (coefficient = 0.1135; p = 0.0000), basal area (coefficient = -0.0701; p = 0.0001), proportion of non-host species (coefficient = -0.0571; p = 0.0091), and plot age (coefficient = 0.0450; p = 0.0468) were all significant predictors. Lodgepole pine mortality in the late stage of the eruption was dominated by stand structure predictors; proportion of susceptible lodgepole pine trees (p = 0.0000), basal area (p = 0.0001), stand density (p = 0.0248), and proportion of non-host species (p = 0.0316) predicted lodgepole pine mortality in the stand structure only model. No environmental factors correlated in the environment-only model, but when the all attributes model were fit, equinox radiation became a significant predictor. In the all attributes model, susceptible lodgepole pine trees (coefficient = 0.1197; p = 0.0000) and basal area (coefficient = 0.0767; p = 0.0000) had the strongest influence on lodgepole pine mortality, but proportion of non-host species (coefficient = -0.0329; p = 0.0244), equinox radiation (coefficient = 0.0314; p = 0.0259), and stand density (coefficient = -0.0312; p = 0.0430) were also significant. R^2 improved only slightly with the inclusion of equinox radiation in the late, all attributes model from 0.66 in the stand structure only model to 0.67 in the all attributes model.

Changes in stand and landscape heterogeneity

Overall, forest heterogeneity increased at the cluster scale and patch heterogeneity decreased at the landscape scale. Using lodgepole pine mortality at each individual stage, I found that the majority of the variance in mortality occurred within clusters rather than among clusters (Table 1-1). Early in the eruption, 61% of the variance occurred within clusters compared with 38.7% among clusters. During the middle of the eruption, 67% of variance occurred within clusters and 33.5% among. The late stage of the eruption had

55% of the variance within the clusters and 45.1% among. Cluster-scale stand structure heterogeneity, measured as coefficient of variation (Figure 1-3; CV%), increased for stand density ($p = 0.0131$), stand basal area ($p < 0.0001$), susceptible lodgepole pine trees ($p = 0.0023$), and serotiny ($p = 0.0004$), but not in lodgepole pine diameter (dbh; $p = 0.1118$). Heterogeneity in cluster basal area increased earlier than other factors (Figure 1-3). Despite increases in cluster scale heterogeneity, lodgepole pine dbh and basal area patch heterogeneity decreased (Figure 1-4). Semi-variogram results for dbh indicate a slight decrease in patch semi-variance (44.85 to 38.96) and a large increase in patch size (4370 m to 8070 m). Basal area, on the other hand, had a large decrease in patch size (4866 m to 900 m) and a large decrease in semi-variance (0.17 to 0.10).

Discussion

Changes in landscape mortality and stand structure

The initiation of the MPB eruption on the west side of RMNP was synchronous and widespread. Mountain pine beetle infested trees were present in over 90% of study clusters early in the eruption; though, mortality did not rise in many stands until later. MPB populations during this period were elevated above endemic levels due to wind dispersal from other populations that erupted earlier in the region. These eruptions began in the late 1990s in the Routt National Forest (north), the area surrounding Willow Creek Pass, CO (west) and near Granby, CO (south). These surrounding eruptions provided a source of beetles that dispersed to RMNP forests and instigated an eruption in the broad expanses of suitable host trees.

The lack of severe MPB-related mortality despite widespread coverage of low numbers of MPB-infested trees indicates that beetles utilized the most susceptible sites and host trees in order to build populations to epidemic levels. As the eruption developed in my temporal framework, the percent of stems killed increased with stage, while the percent of basal area killed remained steady. This suggests that beetles selected nutritionally optimal (e.g., large diameter) trees early in the eruption, and became less selective in later stages, infesting more sub-optimal (smaller) trees. Supporting this, mean PICO dbh decreased by 37% as beetles utilized the largest trees, basal area decreased by 71% and stems ha^{-1} decreased by 34%.

Mountain pine beetle eruptions in lodgepole pine forests accelerate forest successional trajectories in the interim between stand replacing fire events. Lodgepole pine is both a seral and climax species, depending on site conditions (Pfister and Daubenmire 1975). The synergistic effect between MPB and competition-based mortality contributes to the replacement of lodgepole pine on a site or facilitates the development of late-successional stand structures. This is evident in the increase in non-host basal area and the development of a diameter distribution reminiscent of an inverse-J shaped curve as the eruption progresses. Stands late in the eruption contain high proportions of small diameter trees and small proportions of large diameter trees, traits that are characteristic of late successional forests. This indicates a transition in forest succession from a post-fire stand initiation phase to a late-successional stage where multiple cohorts of trees persist together and shade-tolerant species occur in higher proportions. Previously-studied MPB- affected stands in RMNP have been characterized by bimodal age distributions, where an even-aged cohort establishes following a stand-

replacing fire, and a second, younger, even-aged cohort regenerates after MPB eruption (Sibold et al. 2007). If current post-eruption stands develop without being reinitiated by wildfire, diameter distributions may cease to resemble that of a stand-replacing disturbance regime and may take on traits of late-successional forests where perpetual rates of initiation and mortality occur through time.

Mountain pine beetle eruptions leave high numbers of surviving trees and an ample seed source to regenerate forest stands. Cumulatively, 53% of lodgepole pine stems greater than breast height survived the eruption at the time of sampling. Most of these trees are small diameter, but significant proportions of them bear cones (60%). To my surprise, trees with serotinous cones were killed disproportionately to trees with open or no cones. This may be the result of advanced regeneration occupying smaller size classes (not yet susceptible to MPB) that established from trees with open cones in the initial post-fire cohort. If this is the case, MPB may exert selective pressure on non-serotinous trees that can maintain high tree densities after eruptions and regenerate at lower stocking levels after fire, maximizing growth to achieve susceptible size classes. Both cases facilitate the regeneration of susceptible forests. In any case, proportions of serotinous cones found on the west side of RMNP were higher than other regions such as Yellowstone and Montana (Muir and Lotan 1985; Tinker et al. 1994). Surviving lodgepole pines have ample seeds for regeneration after the current MPB eruption or stand replacing fire.

My study took place near the end of the epidemic stage of the eruption (Amman 1984), when optimal food sources decreased in availability causing beetles to infest sub-optimal trees. Mountain pine beetle eruptions rarely cause 100% mortality of trees over

breast height (Amman and Cole 1983; Rocca and Romme 2009), and often, when beetles reach epidemic populations, 85% of host basal area is killed. Other studies have demonstrated that MPBs favor host trees greater than 20 cm in dbh, and reduce basal area more effectively than density (Cole and Amman 1980; Klutsch et al. 2009; Safranyik and Carroll 2006). In the case of this study, over 70% of basal area had been utilized by the late stage of the eruption. This indicates that a small amount of additional mortality is to be expected following this study. Continued low levels of mortality are common until suitable host trees have diminished on the landscape.

Relative influence of stand structure and environmental factors in predicting lodgepole pine mortality

Broad-scale, climatic forcing initiated the eruption in RMNP, and environmental factors played a key role in MPB population development. Synchronous, low-severity infestations across the landscape indicate that mountain pine beetles were not limited in these systems, but were selecting highly susceptible sites with host trees that could increase brood success and allow low populations to increase. This was illustrated in my LME models where during the early stage of the eruption, MPB populations developed in lower-elevation forests, utilizing large trees on dry sites. This stage corresponded to regional drought between 2000 and 2004 (Bigler et al. 2007) which weakened host trees and permitted the MPB to overcome the defenses of otherwise healthy lodgepole pines. Once beetles make the transition to stressed but otherwise healthy host trees, brood success increases and rising populations employ a mass attack strategy to utilize all mature trees within a stand (Raffa et al. 2008).

On the west side of RMNP, after populations increased and stand and landscape thresholds were breached, broad-scale forcing subsided in the middle stage of the eruption but this did not suppress populations because a positive feedback cycle had begun and beetles were able to overcome the defenses of healthy trees. During this stage, large trees in older stands were favored. Because of their age, these stands had already experienced competition-based mortality and possibly even previous MPB mortality. Consequently, they tended to have moderate or low basal area due more to low densities preceding the eruption than the sizes of trees available. Stands with high proportions of non-host species were less susceptible to MPB attack. After this stage, the highest-quality stands became scarce and beetles attacked trees in any stand that had significant proportions of susceptible trees. Late-stage MPB-caused mortality was focused on moderate to high basal area sites that had remaining moderate-sized trees. Again, late in the eruption high proportions of non-host species inhibited MPB-caused mortality, but warmer sites were disposed to mortality.

The roles of stand structure and environmental factors in predicting lodgepole pine mortality changed as the eruption progressed. Where environmental factors were important for the initiation of the MPB eruption, prime stand conditions characterized mortality during the middle stage, and sheer numbers of moderately sized (15 – 25 cm dbh) trees were attacked only after prime stands had experienced mortality. Decoupling exogenous initiation factors and endogenous sustaining factors may be a particular challenge for those developing risk or forecast models and for forest managers implementing preventative treatments on the ground.

Changes in stand and landscape heterogeneity

Forest heterogeneity occurs at multiple spatial scales and is closely linked to the development of contagious ecosystem processes such as MPB eruptions. Often defined as the variability of a system property over space (Li and Reynolds 1995), high heterogeneity can suppress a population's ability to surpass eruptive thresholds (Raffa et al. 2008) and may expedite recovery after an eruption occurs. Mortality during the eruption in RMNP was explained by both within-cluster (stand-scale) variance and among-cluster (landscape-scale) variance. Stand-scale variance characterizes lodgepole pine mortality slightly more than landscape-scale variance. Hence, stand-level heterogeneity and landscape-level heterogeneity both influence the susceptibility of stands and landscapes to MPB eruptions.

The MPB eruption on the west side of RMNP increased stand-level heterogeneity but decreased landscape-level heterogeneity. Forest structure, in part, regulates MPB population growth, which is limited by a stand's supply of large-diameter host trees and environmental stress (Safranyik and Carroll 2006). Uniform stands of susceptible trees (low cluster heterogeneity) allow MPB populations to grow quickly and facilitate a population's ability to overcome stand-level thresholds, allowing an eruption to transfer to surrounding forest stands (Raffa et al. 2008). High variability within a stand is uncommon in lodgepole pine forests that regenerated following stand-replacing fire. Increases in the variability of stand structure attributes can impede MPB population development by restricting the density of suitable host trees, creating barriers of non-host and unsusceptible host trees, and slowing population development. High stand structure variance can allow favorable phases of environmental stress to expire without requisite

MPB population levels to surpass stand-level thresholds. If MPB populations do surpass within-stand thresholds, patch size and variability among patches of lodgepole pine affects the ability of contagious processes to spread across a landscape (Peters et al. 2007).

To assess changes in patch size and variability that are linked to landscape MPB susceptibility, I chose to characterize average lodgepole pine dbh and stand basal area because of their high correlation with MPB mortality. Lodgepole pine dbh experienced a moderate decrease in variability that was accompanied by a large increase in patch size. Basal area experienced a dramatic decrease in both variability and patch size as a result of MPB-related mortality. In each case, patches across the landscape are larger and/or more similar to one another than prior to the eruption, and I conclude that landscape heterogeneity decreased following the MPB eruption.

Lodgepole pine forests are currently in a successional stage with few suitable host trees and have a low risk of infestation. As forests recover and regain stocking levels that were present before the eruption, heterogeneous lodgepole pine stands and non-uniform stand structure are anticipated to persist. Despite the fact that endemic populations of MPB are common in these forests, these stand structures may make it difficult for beetle populations to become self-perpetuating within forest stands and erupt at increasing scales. In the case that future MPB populations surpass stand-level thresholds, high contiguity and low among-stand variability of dbh and basal area may increase the ability of MPB to transfer across a landscape and incite a new landscape level eruption.

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Table 1-1: Mortality stage classification system.

Mortality Stage	Estimated years since trees were killed	Tree characteristics
Early	3 +	Dead, characteristic signs† with ≤ 50% needles remaining
Middle	2	Dead, characteristic signs† with ≥ 50% red/orange needles remaining
Late	1	Dead, characteristic signs† with all needles remaining
Surviving	-	Alive with no characteristic signs† of mountain pine beetle infestation
Other causes	-	Dead, cause of death not related to the mountain pine beetle

† Characteristic signs of mountain pine beetle infestation include frass, pitch tubes, boring dust, galleries or exit holes.

Table 1-2: Mean (standard error) landscape mortality for each stage of the eruption and cumulative mortality since the beginning of the eruption. The percent of landscape affected equals the percent of clusters that had at least one MPB infested tree. Significant differences (Tukey's HSD) within rows are denoted with different letters.

Mortality	Early	Middle	Late
Percent of landscape affected (% clusters)	91%	98%	100%
Percent stems killed	12.1% (1.30)[a]	16.7% (1.67)[a,b]	18.3% (1.58)[b]
Percent basal area killed	21.1% (2.04)[a]	25.0% (2.07)[a]	25.2% (2.09)[a]
Cumulative percent stems dead	12.1% (1.30)	28.8% (2.4)	47.1% (2.29)
Cumulative percent basal area dead	21.1% (2.04)	46.1% (2.99)	71.3% (2.16)

Table 1-3: Mean (standard error) surviving forest structure attributes at the end of each stage of the eruption. Significant differences (Tukey's HSD) within rows are denoted with different letters.

	Stand Attributes by Stage of Eruption			
Stand Structure Variable	Pre-eruption	Early	Middle	Late
Mean surviving DBH (cm)	17.39 (0.59)[a]	16.37 (0.61)[a]	13.27 (0.59)[b]	10.96 (0.53)[c]
Mean lodgepole pine density (stems ha^{-1})	1393 (121.2)[a]	1274 (121.6)[a,b]	1125 (123.2)[a,b]	915 (119.9)[b]
Mean basal area (m^2 ha^{-1})	29.31 (0.90)[a]	23.51 (0.98)[b]	16.23 (1.08)[c]	8.52 (0.69)[d]
Percent of non-host species (stems ha^{-1})	18.8% (2.34)[a]	19.7% (2.42)[a]	22.5% (2.65)[a]	25.7% (2.86)[a]
Percent of non-host species (m^2 ha^{-1})	10.6% (1.59)[a]	11.7% (1.74)[a]	17.2% (2.38)[a,b]	23.1% (2.78)[b]
Percent of PICO stems greater than 15 cm DBH	58.0% (2.47)[a]	53.9% (2.63)[a]	41.8% (2.67)[b]	30.6% (5.54)[c]
Percent serotinous trees	50.4% (1.79)[a]	48.8% (1.80)[a,b]	42.0% (1.97)[b,c]	36.6% (2.02)[c]

Table 1-4: Surviving cone-bearing trees at the end of each stage of the eruption. Percent serotinous and non-serotinous cones do not sum to 100 as many trees did not bear cones. Four plots had no remaining lodgepole pine trees greater than dbh after the latest measured stage of the eruption.

Stage of Eruption	Percent Serotinous Trees	Percent Non-Serotinous Trees	Mean Living lodgepole pine Stems ha^{-1}	Mean Living Cone Bearing Trees ha^{-1}
Pre-Eruption	50.4%	27.8%	1393	1089
Early	48.8%	28.2%	1274	981
Middle	42.0%	27.0%	1125	776
Late	36.6%	26.3%	915	576

Table 1-5: The relative influence of stand structure and environmental factors in predicting lodgepole pine mortality (proportion stems dead). Linear mixed-effects model, 137 plots in 46 clusters. Rocky Mountain National Park, CO.

Predictor Set	Stage	df	R^2	Parameter	Coefficient	SE	t-value	p-value
Stand Structure	Early	90	0.38	Intercept	0.3058	0.0252	12.15	0.0000
				Mean lodgepole pine DBH	0.0665	0.0157	4.25	0.0001
	Middle	87	0.54	Intercept	0.3554	0.0238	14.89	0.0000
				Mean lodgepole pine DBH	0.1135	0.0185	6.13	0.0000
				Basal area	-0.0701	0.0173	-4.05	0.0001
				Proportion of non-host species	-0.0571	0.0214	-2.67	0.0091
				Plot age	0.0450	0.0223	2.01	0.0468
	Late	87	0.66	Intercept	0.3870	0.0151	25.62	0.0000
				Susceptible lodgepole pine stems (>15 cm DBH)	0.1183	0.0167	7.09	0.0000
				Basal area	0.0736	0.0175	4.20	0.0001
				Density	-0.0349	0.0153	-2.28	0.0248
				Proportion of non-host species	-0.0320	0.0146	-2.18	0.0316
Environmental	Early	89	0.37	Intercept	0.3054	0.0230	13.27	0.0000
				Elevation	-0.6281	0.0230	-2.72	0.0077
				Topographic convergence index	-0.0422	0.0141	-3.00	0.0035
	Middle	91	0.35	Intercept	0.3551	0.0293	12.10	0.0000
	Late	91	0.24	Intercept	0.3867	0.0259	14.95	0.0000
All Predictors	Early	88	0.48	Intercept	1.7103	0.3785	4.52	0.0000
				Elevation	-0.0776	0.0224	-3.46	0.0008
				Mean lodgepole pine DBH	0.0771	0.0147	5.23	0.0000
				Topgraphic Convergence Index	-0.0498	0.0128	-3.90	0.0002
	Middle	87	0.54	Intercept	0.3554	0.0238	14.89	0.0000
				Mean lodgepole pine DBH	0.1135	0.0185	6.13	0.0000
				Basal area	-0.0701	0.0173	-4.05	0.0001
				Proportion of non-host species	-0.0571	0.0214	-2.67	0.0091
				Plot age	0.0450	0.0223	2.01	0.0468
	Late	86	0.67	Intercept	0.3868	0.0147	26.33	0.0000
				Susceptible lodgepole pine stems (>15 cm DBH)	0.1197	0.0164	7.29	0.0000
				Basal area	0.0767	0.0173	4.44	0.0000
				Proportion of non-host species	-0.0329	0.0144	-2.29	0.0244
				Equinox radiation	0.0314	0.0139	2.26	0.0259
				Density	-0.0312	0.0152	-2.05	0.0430

Table 1-6 Components of variance analysis for proportion of stems killed at each stage of the eruption. Variance and percent of total variance within and among the random term, cluster.

Stage	df	Within Cluster Variance	Among Cluster Variance
Early	91	0.154 (61.3%)	0.122 (38.7%)
Middle	91	0.184 (66.5%)	0.131 (33.5%)
Late	91	0.155 (54.9%)	0.141 (45.1%)

Figure Captions

Figure 1-1: (a) The west side of Rocky Mountain National Park, Colorado. (b) Spatially balanced, random clusters in the lodgepole pine cover type. (c) Three 20 X 20 meter sub-plots were located in a triangular structure at each random cluster. Plot A is located at the random point and a random azimuth was used to locate Plot B. Plot C was positioned 90° clockwise from the random azimuth.

Figure 1-2: Diameter distribution of surviving lodgepole pine trees changed as the eruption progressed. Percent of surviving large trees decreased while the percent of surviving small trees increased. By the late stage of the eruption, diameter distribution resembles an inverse J-shaped curve reminiscent of late successional forest stands. Error bars signify one standard error from the mean.

Figure 1-3: Coefficient of variation (CV%) for each stand structure attribute within each cluster by stage of the eruption. CV% increases for density, basal area, percent susceptible PICO stems, and percent serotiny but did not for average dbh. Error bars signify one standard error, and different letters denote significant differences from Tukey's HSD test.

Figure 1-4: (a) Semi-variogram for surviving mean lodgepole pine diameter shows a doubling of patch size and a small decrease in semivariance from before to late in the eruption. (b) Semi-variogram for surviving PICO basal area shows a fivefold decrease in patch size and a large decrease in semivariance from before to late in the eruption.

Figure 1-1

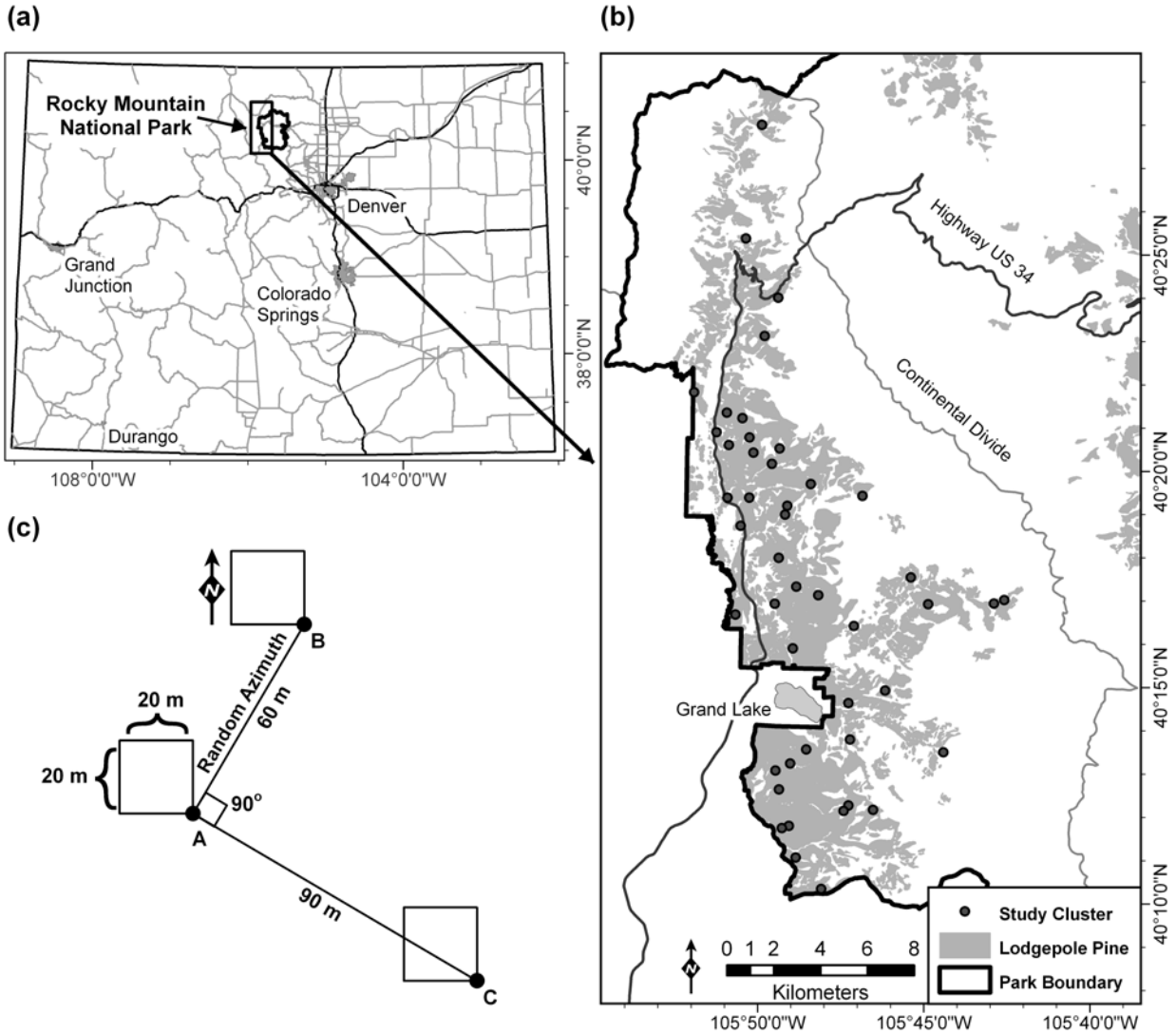

(a)
Rocky Mountain National Park
Denver
Grand Junction
Colorado Springs
Durango
40°0'0"N
38°0'0"N
108°0'0"W
104°0'0"W
(b)
Highway US 34
Continental Divide
Grand Lake
40°25'0"N
40°20'0"N
40°15'0"N
40°10'0"N
105°50'0"W
105°45'0"W
105°40'0"W
0 1 2 4 6 8
Kilometers
Study Cluster
Lodgepole Pine
Park Boundary
(c)
B
20 m
Random Azimuth
60 m
20 m
90°
A
90 m
C

Figure 1-2

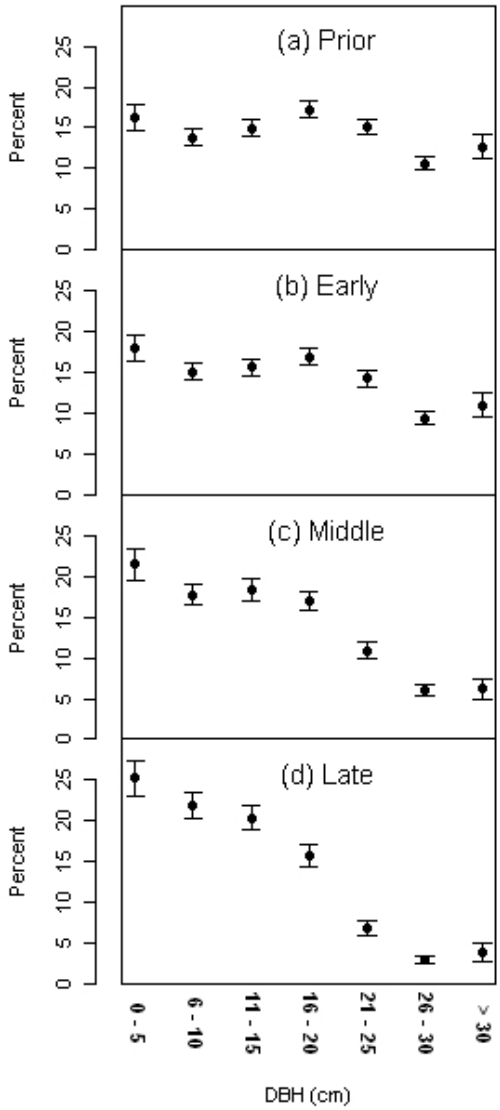

(a) Prior
(b) Early
(c) Middle
(d) Late
Percent
0
5
10
15
20
25
0 - 5
6 - 10
11 - 15
16 - 20
21 - 25
26 - 30
> 30
DBH (cm)

Figure 1-3

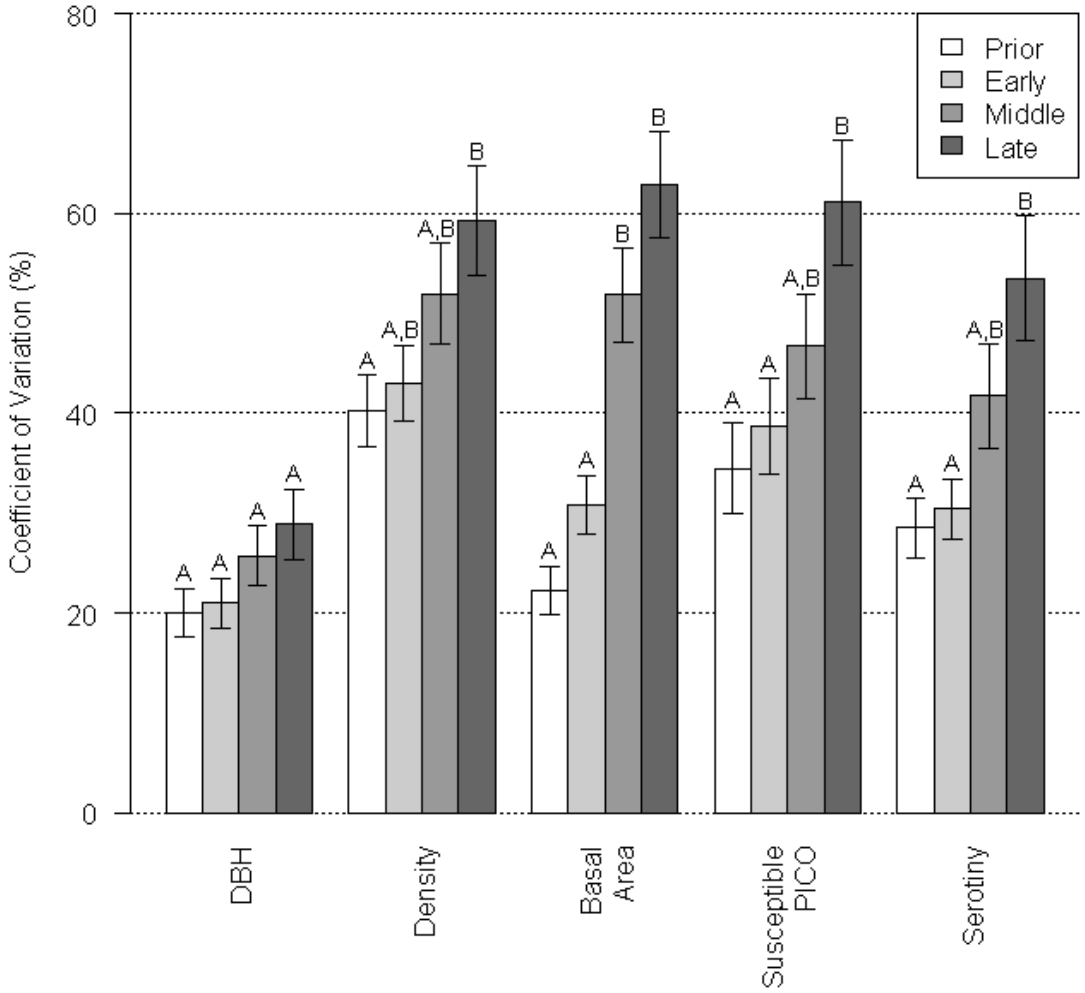
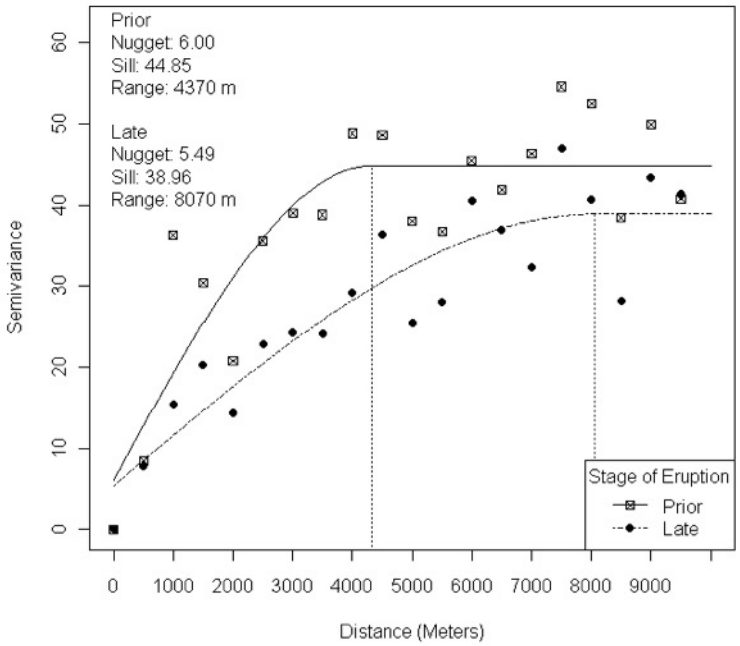
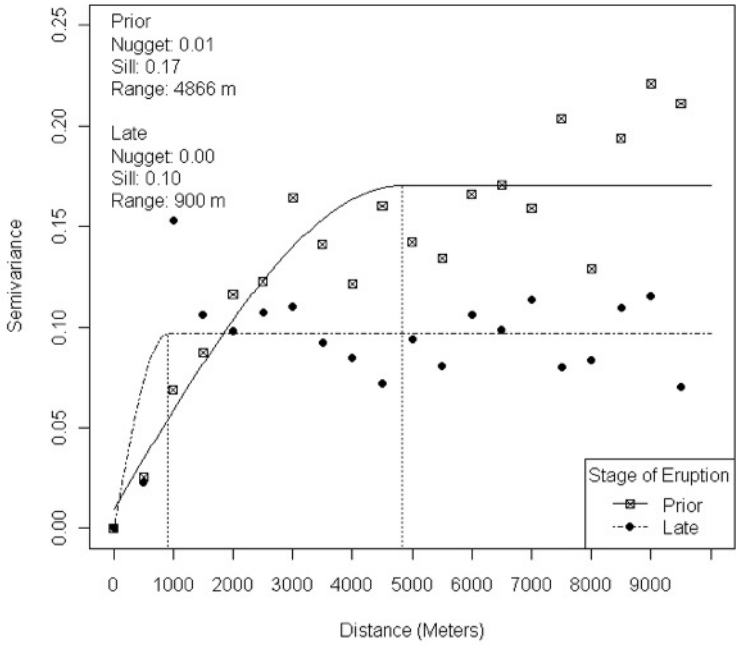

Prior
Early
Middle
Late
Coefficient of Variation (%)
80
60
40
20
0
A
A
A
A
A
A,B
A,B
B
A
A
B
B
A
A
A,B
B
A
A
A,B
B
DBH
Density
Basal Area
Susceptible PICO
Serotiny

Figure 1-4

(a)


Prior
Nugget: 6.00
Sill: 44.85
Range: 4370 m
Late
Nugget: 5.49
Sill: 38.96
Range: 8070 m
Semivariance
0
10
20
30
40
50
60
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
Distance (Meters)
Stage of Eruption
Prior
Late

(b)


Prior
Nugget: 0.01
Sill: 0.17
Range: 4866 m
Late
Nugget: 0.00
Sill: 0.10
Range: 900 m
Semivariance
0.00
0.05
0.10
0.15
0.20
0.25
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
Distance (Meters)
Stage of Eruption
Prior
Late

Chapter 2: Aspen suckering density and growth increases following mountain pine beetle-related mortality in Rocky Mountain National Park, CO

Abstract

The mountain pine beetle (MPB) eruption in Rocky Mountain National Park is causing extensive mortality of lodgepole pines and may reduce competitive pressure on aspen. I assessed the effect of MPB-related mortality on aspen regeneration by examining whether suckering densities and growth rates increase with MPB-related mortality, and if ungulates utilize additional suckers through browsing. Conifer overstory mortality, aspen sucker density, stem elongation, total sucker height, and ungulate browsing rates were characterized in 48 plots over 8 stands. At the time of sampling, heavy lodgepole pine mortality had decreased conifer basal area by 80% and stem density by 50% of pre-eruption levels. This appears to relieve competitive pressure on aspen in mixed conifer-aspen stands. Linear mixed-effects model results show that as weighted mortality increases, aspen sucker density increases three-fold, aspen stem elongation increases by 2.5 times, and mean sucker height increases by two-thirds. Additionally, as sucker density increased, I did not find evidence to suggest that the rate of ungulate browsing increased. Mountain pine beetle related mortality relieves conifer pressure and may lead to successful aspen recruitment.

Introduction

Successful regeneration of aspen in Rocky Mountain National Park (RMNP) is constrained by competition from conifers and facilitated by escape from ungulate browsing (1997; Binkley 2008; Kaye et al. 2005; Suzuki et al. 1999). Stands showing reduced regeneration are often considered to be "declining" as a result of one of these two factors (Kashian et al. 2007). Although the effect of elk browsing may suppress regeneration in low elevation stands on the east side of RMNP (Baker et al. 1997; Binkley 2008; Suzuki et al. 1999), reduced regeneration in mixed conifer-aspen stands at higher elevations is due to infrequent disturbance events (Kashian et al. 2007), and the high conifer component present in late-successional forests (Kaye et al. 2005). The recent mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) eruption in RMNP is causing extensive mortality of lodgepole pine (See Chapter 1) and may reduce competitive pressure exerted on aspen. In this study, I examine the effects of MPB-related mortality on aspen regeneration densities and growth.

Aspen stands in subalpine forests take many forms and can persist in low abundance during the interim between stand replacing fires. Long distance transects established throughout the park estimated aspen cover to be more than twice as high as previously reported estimates using aerial-photo methods (Kaye et al. 2003; Suzuki et al. 1999). This indicates that more than 3% of the park contains aspen cover below a conifer overstory (Kaye et al. 2003). Species succession in these forests often begins after stand-replacing fire. Subalpine aspen abundance and regeneration rates can fluctuate greatly over temporal scales (Kashian et al. 2007), and their form is largely dependent on the duration of time since the last stand-replacing disturbance. Surviving aspen rootstocks

facilitate rapid growth after fire and outcompete conifer species that must regenerate from seeds and have slow growth rates (Shepperd et al. 2001; Shepperd and Smith 1993). In the case of mixed aspen-lodgepole pine forests, pines rarely invade sites after aspen establishment. Rather, lodgepole pines co-establish with aspen on a site, then become dominant due to differing life history traits such as longer life (Kaye et al. 2005). High proportions of conifers in the overstory do not influence the mortality rate of established aspen trees but do suppress aspen suckers (Kaye et al. 2005).

Long periods between fire events are often punctuated with secondary disturbances such as MPB eruptions. Eruptions can vary greatly in severity and extent depending on host tree availability and climatic conditions (Raffa et al. 2008). If beetle populations rise to epidemic levels, an eruption becomes self-perpetuating and up to 85% of healthy host basal area may be killed (Cole and Amman 1980). Lodgepole pine forests on the west side of RMNP and elsewhere in the Rocky Mountain region have been affected by extensive mortality from the MPB. For mixed conifer-aspen forests in the park, the death of large portions of lodgepole pine may mark a reduction in competitive pressure inhibiting aspen regeneration. No studies have directly explored the effect of MPB-related mortality on aspen regeneration and I addressed the following questions: (1) Do losses in lodgepole pine cover resulting from MPB attack initiate a suckering response in aspen? (2) Do aspen suckering densities and growth rates increase with MPB-related mortality in the overstory? (3) If aspen suckering does increase, will elk utilize additional suckers through browsing?

Materials and Methods

Study Area

This study was conducted on the west side of Rocky Mountain National Park in north-central Colorado (Figure 2-1; 40°15'N, 105°48'W). Aspen (*Populus tremuloides* Michx.) populations in this portion of the park exist on mesic forest sites in both pure and mixed stands. Mixed stands are largely shared with lodgepole pine (*Pinus contorta* var. latifolia), although Englemann Spruce (*Picea englemannii*) and Subalpine Fir (*Abies lasiocarpa*) also occupy sites at higher elevations and on north facing slopes. Elevation of these stands range from 2550 to 3250 meters above sea level. Using climate station data from Grand Lake, CO, mean minimum and maximum temperatures are -16.5° C in January and 24.6° C in July. Average annual precipitation is 484 mm per year. (http://www.wrcc.dri.edu/)

Field Sampling

In August 2008, I sampled eight stands in the "Mixed Conifer with Aspen" and "Montane Aspen" cover types (USGS-NPS 2006). Six 0.04 ha fixed-area plots (20 X 20 m) were located in each stand (Figure 2-1). Eight to ten candidate plot locations within each stand were identified prior to visiting field sites as having a mixture of conifers and aspen. This was done using ESRI ArcGIS 9.2 by overlaying a cover type map on a 2005 color aerial photo. Plots were spaced a minimum of 75 meters and a maximum of 400 meters from one another. Stands were separated by a minimum of 1500 meters. Upon arriving in a stand, plots were randomly oriented at each candidate location and assessed

for suitability for sampling. Suitable sites were dominated by lodgepole pine, had MPB-affected trees, and at least one overstory aspen tree. In the case of the "Upper Montane Aspen" cover-type, plots were often located near the perimeter of the stand where overstory aspen shared lodgepole pine cover.

Site characteristics, overstory stand structure, conifer regeneration, and aspen sucker density and growth were measured and recorded at each plot. Site characteristics included geographic location, elevation, aspect, and slope. All trees taller than breast height (1.37 m) were measured, and species, diameter at breast height (dbh) and, for MPB-killed lodgepole pines, time-since-death was recorded. Tree species other than lodgepole pines were noted as live or dead. Lodgepole pine was classified into 6 qualitative categories estimating the year in which they were infested. Trees were classified as alive, one year since infestation: faded green to completely red foliage remaining on the tree, two years since infestation: ≥ 50% red/orange needles remaining, three years since infestation: ≤ 50% needles remaining on the tree, four or more years since infestation: ≤ 5% of needles remaining on the tree, and died from causes other than the mountain pine beetle (Keen 1955; Klutsch et al. 2009). Characteristic signs of MPB infestation (e.g., frass, pitch tubes, boring dust, galleries, and exit holes) were used to determine the cause of death.

Conifer and aspen understory trees were measured by delineating four 5 X 20 m sub-plots in each 20 X 20 plot (Figure 2-1). Trees shorter than breast height were tallied in the two center sub-plots by species. Aspen suckers were aged using bud scars and tallied in one-year age classes up to an age of 10 years. Clumps of aspen suckers were aged by the tallest sucker and tallied as one individual, since only one sucker from the

group is likely to become a tree (Romme et al. 1995). Aspen growth was measured on 30 randomly selected aspen suckers. The closest sucker to the transect tape was selected at 2-meter intervals along the center three sub-plot boundaries (Figure 2-1). At each 2-meter mark, total age, total height, and the last two years of stem elongation (cm) was measured on the nearest sucker. Elongation is reported from the top of the current growth to the top of the previous bud scar. Presence or absence of browsing was noted (yes or no) for each year's growth. If 30 aspen suckers did not exist within the plot then all available suckers were measured.

Data Analysis

Mean basal area (m^2 ha^{-1}) and density (stems ha^{-1}) was calculated for conifer trees preceding the eruption and for surviving conifers at the time of sampling. Aspen basal area (m^2 ha^{-1}) and density (stems ha^{-1}) is reported for the time of sampling. To document the severity of the outbreak in the overstory, I created an index of mountain pine beetle mortality, in which I weighed the proportion of basal area killed by the year of mortality. Large trees were given heavier weights because they use more resources and reduced overstory competition the most. Weighted mortality was calculated for each plot by weighting each time-since-death class (1-4) with its respective proportion of plot basal area, then computing a weighted average.

Regenerating aspen and conifer understory trees were characterized at each stand. Aspen sucker density (ha^{-1}), average sucker age, and conifer seedling density (stems < dbh ha^{-1}) were calculated from tallies taken from the two center sub-plots. The random sub-sample of 30 suckers was used to calculate mean aspen sucker height, mean 2008 elongation, and percent ungulate browsing. Elongation for the 2008 growing season was

calculated from the mean elongation of unbrowsed individuals. The 2007 sucker growth record was used to calculate the percent of browsed suckers because significant elk browsing is believed to take place in the fall and my 2008 mid-summer sampling did not capture a full season of browsing. My estimate of 2007 browsing may be conservative because some sucker attrition may have occurred during the winter of 2007/2008. Aspen and conifer saplings were defined as taller than dbh but less than 3 cm dbh. Sapling density (ha^{-1}) was calculated from trees sampled across the entire plot.

To determine if aspen suckers respond to conifer mortality, I fit linear mixed-effects models (LME) to predict total sucker density, 2008 stem elongation, total sucker height, and mean sucker age from weighted mortality, and browsing intensity from aspen sprout density. Stand was used as the random effect. Square-root transformation was necessary to satisfy model assumptions of homoscedacity and linear predictor values for total sucker density, total sucker height, and mean sucker age. A natural log transformation was necessary for 2008 elongation, and an arcsine (square-root(%)) transformation was used to satisfy model assumptions on proportion suckers browsed. Traditional coefficient of variation (R^2) is not accurate when using LME models due to the separate calculation of fixed and random-effect error terms. For this study, R^2 is calculated using the likelihood ratio method (Magee 1990) as suggested by Kramer (2005).

All data analyses were done using the base and nlme (Pinheiro et al. 2009) packages within the R 2.9.1 statistical environment (R Development Core Team. 2009).

Results

Overstory tree cover was substantially reduced as a result of MPB-related lodgepole pine mortality (Table 2-1). Conifer basal area decreased by nearly 80% and conifer density (ha^{-1}) was reduced to one half of its pre-eruption level. The proportion of overstory aspen in these stands increased from 8% to 31% of basal area (m^2 ha^{-1}) and 13% to 23% of stems ha^{-1}. Mean weighted stand mortality of 1.7 indicates that most stands had significant needle fall at the time of sampling. Weighted stand mortality ranged from 1.1 to 2.2 in individual stands. Additional mortality of suitable host trees is expected to have occurred following the sampling for this study.

Density of aspen suckers and conifer seedlings varied widely among stands, and the two tended to be inversely related (Table 2-2). Mean aspen sucker density across all stands was 3464 and ranged from 2233 to 5167 suckers ha^{-1}. Conifer seedlings ranged from 108 to 1508 with a mean of 597 seedlings ha^{-1}. Aspen saplings were rare, occurring in only two stands, but conifer saplings were present in all stands and often comprised a significant proportion of pre-eruption (20%) and surviving (39%) overstory density. LME model results show that as weighted mortality increases, aspen sucker density also increases ($p=0.0273$; $R^2 = 0.04$). My model predicts a three-fold increase in aspen sucker density ha^{-1} between no mortality and high mortality plots (Figure 2-2). As would be expected with an increase in sucker density, my LME model shows mean sucker age decreasing to nearly one-half of low mortality levels as weighted mortality increases and new suckers establish with increased mortality ($p = 0.0053$; $R^2 = 0.06$), demonstrating heavy recruitment of aspen suckers as conifer mortality increases (Figure 2-3).

Not only does conifer mortality influence aspen suckering density, it increases sucker growth and total sucker height (Figure 2-4; Figure 2-5). Model results show 2008 sucker elongation increasing by 2.5 times from low to high mortality (p-value = 0.0001; $R^2 = 0.15$), and total sucker height increasing by two-thirds with mortality (p-value = 0.0131; $R^2 = 0.28$). Ungulates did not browse additional proportions of aspen suckers ha^{-1} in 2007, although, the intensity of browsing often changes each year. The LME model predicting proportion of browsed suckers showed no change as aspen sucker density increased (p-value = 0.1106). In individual stands, ungulate browsing ranged from 48% to 87% with a mean of 73%.

Discussion

The decline in aspen that results from rising proportions of conifers in aspen systems is a topic of concern among land managers and the focus of recent research (Kashian et al. 2007; Kaye et al. 2005; Magee 1990; Shepperd et al. 2001; Smith and Smith 2005). It is well documented that aspen can dominate post-fire stands due to suckering from surviving rootstocks and rapid growth rates. Aspen is also recognized as a seral species on many sites, giving way to slower growing and shade tolerant conifers as stands mature. In a study in Utah, Shepherd et al. (2001) demonstrated that conifers reach the aspen canopy in approximately 100 years and continue increasing in site dominance thereafter. Stand-replacing fires occurred across the west side of Rocky Mountain National Park during the second half of the 19th century (Sibold et al. 2006). Consequently, the age of my conifer-aspen stands suggests that conifers reached an aspen dominated overstory in the last 20 – 50 years, and overstory aspen are beginning their gradual decline in dominance due to their natural life expectancy and lack of shade

tolerance (Kaye et al. 2005). No studies to my knowledge have concluded that aspen disappears from late successional stands; however, many studies point out that aspen will continue to decrease in mixed conifer-aspen stands until the next stand-replacing disturbance (Kashian et al. 2007; Kaye et al. 2005; Kaye et al. 2003; Shepperd et al. 2001; Smith and Smith 2005). Post-fire lodgepole pine stands develop size classes that are highly susceptible to MPB eruptions in roughly the same timeframe (Safranyik and Carroll 2006).

My study documents large decreases of conifer overstory in late successional mixed conifer-aspen stands as a result of MPB-related lodgepole pine mortality. Overstory aspen now occupy higher proportions of stand basal area and density. Despite these increases, aspen stands included in this study have few saplings available to grow into the overstory (aspen saplings are absent in 75% of conifer-aspen stands), and the ability of newly regenerated aspen suckers to reach the overstory is unclear. This density of aspen saplings is lower than other local studies that quantified aspen saplings in the elk summer range of RMNP (Binkley 2008; Kashian et al. 2007; Suzuki et al. 1999). These differences can be attributed to my focus on conifer-dominated aspen stands, and fit findings from studies examining stands with similar mixes of species (Smith and Smith 2005). Shade tolerant conifer saplings that were found in relatively high numbers are likely to utilize new canopy openings. Still, post-disturbance aspen suckers protected from browsing can grow in excess of 1 meter per year, and higher soil temperatures resulting from an open forest canopy may influence levels of the plant growth hormone, auxin, stimulating a suckering response (Landhausser et al. 2006).

Aspen sucker density in low mortality stands reflect those found by other authors who have examined mixed conifer-aspen systems in the Southern Rocky Mountains (Kashian et al. 2007; Kaye et al. 2005; Kurzel et al. 2007; Smith and Smith 2005). As MPB-related mortality increases, however, sucker densities surpass background levels. I attribute this change to large decreases in conifer basal area and density. Sucker densities in stands with high MPB-related mortality were not similar to pure aspen stand background-suckering densities documented in some studies (Barnett and Stohlgren 2001; Kashian et al. 2007; Romme et al. 1995; Sankey 2008; Smith and Smith 2005). Additionally, sucker densities even in my stands of high-conifer mortality did not approach densities present after more severe disturbances such as clear-cutting treatments (Bartos and Mueggler 1982), fire (Bartos and Mueggler 1981; Hessl and Graumlich 2002; Keyser et al. 2005; Romme et al. 1995), and heavy livestock grazing (Sankey 2008). Nevertheless, the measured increase in aspen suckering density may increase the chance of suckers reaching sapling height classes where they can escape elk browsing pressure.

The negative effect that high elk numbers have had on aspen regeneration is well documented in RMNP (Baker et al. 1997; Binkley 2008; Packard 1942). The extermination of natural predators at the turn of the 20th century and the "natural regulation" policy imposed by the National Park Service in 1968 (Hess 1993) have contributed to unprecedented elk population levels. Past studies in RMNP have used 2.5 meters (Baker et al. 1997) to signify the tree height necessary to escape elk browsing. Significant proportions of stands across the RMNP region do not have regenerating aspen reaching this height (Suzuki et al. 1999). Approximately 80% of aspen forests in the elk

winter range in the Estes Park Valley have no successful regeneration (Baker et al. 1997; Binkley 2008; Suzuki et al. 1999). Suzuki (1999) estimates that only 30% of stands outside of the elk winter range (elevation > 2800 m) are in this condition. At higher elevations and on the west side of RMNP, aspen stands have maintained expected levels of recruitment during the latter half of the 20th century (Binkley 2008). This does not appear to be the case in stands included in this study that were targeted for their high proportions of conifers. Total aspen sprout heights in my stands were found to be less than 1 meter, but are similar to those found in Yellowstone (Romme et al. 1995) and Utah (Keyser et al. 2005). Only one stand, Mt. Cairns, contained an appreciable number of saplings. This is likely due to the low rate of elk browsing as a consequence of the talus/boulder fields and cliffs surrounding this site. Mean sucker browsing over all stands was in agreement with Kaye et al. (2003). I believe that the combination of intense conifer competition and extensive elk browsing has suppressed successful aspen regeneration in these stands.

This study took place near the end of the epidemic stage of the MPB eruption in RMNP (See Chapter 1). Heavy lodgepole pine mortality appears to have relieved competitive pressure on aspen in mixed conifer-aspen stands. Sucker density increased by three times, 2008 sucker elongation increase by a factor of 2.5, and average sucker height increased by two-thirds in plots with increasing mortality. Elk browsing rates did not increase with higher sucker densities in the most recent year documented (2007), and this alone may permit substantial increases in suckers ha^{-1} to escape ungulate browsing. High number of attacked trees still held needles and fine twigs at the time of sampling, and mortality is expected to persist at lower levels until susceptible host trees have been

exhausted from the landscape. Additional research is needed to determine if increases in aspen density and growth are sustained after additional affected lodgepole pines lose their needles, and whether suckers surpass the 2.5-meter height threshold that regulates successful regeneration. This study lays the ground-work for future investigation related to the effects of MPB on aspen populations, and indicates that aspen may respond when conifer competition is reduced.

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Table 2-1: Summary of aspen and conifer basal area and density (>3 cm dbh) in six plots at each of eight study locations demonstrating large decreases in conifer basal area and density. Values are Mean (Standard Error).

Stand	Elevation	Overstory Conifer BA (m^2 ha^{-1})		Aspen BA (m^2 ha^{-1})	Overstory Conifer density (ha^{-1})		Aspen density (ha^{-1})
		Pre-Eruption	Post-Eruption		Pre-Eruption	Post-Eruption	
Mt. Acoma	2748 (12.6)	15.9 (2.8)	2.2 (0.7)	0.5 (0.2)	575 (98.3)	283 (59.0)	54 (16.4)
Bowen-Baker	2822 (15.2)	36.6 (5.6)	12.6 (3.1)	3.9 (1.3)	804 (137.0)	529 (100.7)	142 (53.9)
Mt. Cairns	2844 (22.1)	25.6 (3.9)	5.1 (2.9)	1.2 (0.4)	767 (158.9)	342 (153.4)	275 (80.1)
Mt. Patterson	2999 (28.3)	24.8 (1.5)	4.7 (0.7)	2.0 (0.3)	563 (50.7)	308 (42.7)	100 (19.4)
Nisa Mountain	2827 (3.3)	28.8 (3.1)	5.1 (1.8)	3.2 (1.3)	733 (96.8)	375 (123.8)	83 (25.6)
Pontiac Pit	2862 (13.5)	33.1 (4.8)	2.8 (1.2)	3.5 (0.7)	517 (52.8)	192 (49.0)	96 (21.8)
Tonahutu Spur	2711 (4.3)	34.5 (4.6)	7.8 (1.6)	1.7 (0.4)	1096 (210.0)	538 (124.5)	46 (7.7)
West Valley	2655 (5.87)	28.8 (2.7)	6.5 (2.2)	4.7 (0.9)	1108 (276.7)	558 (212.7)	125 (9.1)
Average	2809 (15.0)	28.5 (1.5)	5.8 (0.8)	2.6 (0.3)	770 (59.1)	391 (43.7)	115 (15.7)

Table 2-2: Comparison of the degree of conifer mortality and understory aspen and conifer trees at each mixed lodgepole-aspen stand included in this study. Values are mean (Standard Error).

Stand	Weighted Mortality	Aspen Sucker Density	Aspen Sapling Density	Average Sucker Age	Aspen Sucker Height	Percent Browsed	Conifer Seedling density	Conifer Sapling Density
Mt. Acoma	2.2 (0.1)	3642 (559)	21 (20.8)	3.5 (0.4)	60.2 (3.4)	65.6% (9.1)	375 (129.6)	213 (97.2)
Bowen-Baker	1.2 (0.2)	2233 (663)	0.0 (0.0)	3.2 (0.3)	31.0 (2.1)	62.4% (7.9)	1508 (526.9)	113 (29.4)
Mt. Cairns	2.0 (0.2)	5167 (1708)	604 (97.1)	4.8 (0.3)	79.7 (6.0)	48.4% (4.8)	142 (50.7)	75 (45.6)
Mt. Patterson	1.5 (0.1)	3588 (975)	0.0 (0.0)	3.3 (0.2)	32.7 (1.3)	76.4% (3.4)	500 (187.5)	79 (25.3)
Nisa Mountain	2.0 (0.2)	3704 (1886)	0.0 (0.0)	3.3 (0.5)	24.9 (4.4)	77.4% (5.1)	575 (209.7)	292 (97.6)
Pontiac Pit	1.1 (0.2)	2967 (1026)	0.0 (0.0)	2.9 (0.3)	37.5 (1.4)	86.9% (4.5)	500 (278.1)	117 (47.3)
Tonahutu Spur	1.8 (0.1)	2325 (525)	0.0 (0.0)	3.6 (0.4)	44.7 (2.8)	82.1% (2.9)	1067 (408.4)	263 (123.3)
West Valley	1.8 (0.2)	4090 (1004)	0.0 (0.0)	3.8 (0.2)	46.0 (5.2)	83.9% (2.8)	108 (56.9)	63 (43.2)
Average	1.7 (0.1)	3464 (397)	78.1 (31.2)	3.6 (0.1)	44.6 (2.7)	72.9 % (2.5)	597 (111.6)	152 (26.6)

Figure Captions

Figure 2-1: (a) The geographic location of Rocky Mountain National Park, Colorado. (b) Mixed lodgepole-aspen stands included in this study on the west side of Rocky Mountain National Park. (c) Six sub-plots were established in each stand to assess lodgepole pine mortality and aspen sprouting density and vigor. Dots along the center sub-plot boundaries indicate the locations of random aspen sucker growth and browsing measurements.

Figure 2-2: The influence of mountain pine beetle–related conifer mortality on aspen sucker density. Regression line reflects back-transformed LME model results that were fit using data from 48 plots in 8 mixed lodgepole-aspen stands.

Figure 2-3: The influence of mountain pine beetle–related conifer mortality on mean aspen sucker age. Regression line reflects back-transformed LME model results that were fit using data from 48 plots in 8 mixed lodgepole-aspen stands.

Figure 2-4: The influence of mountain pine beetle–related conifer mortality on 2008 sucker elongation. Regression line reflects back-transformed LME model results that were fit using data from 48 plots in 8 mixed lodgepole-aspen stands.

Figure 2-5: The influence of mountain pine beetle–related conifer mortality on total aspen sucker height. Regression line reflects back-transformed LME model results that were fit using data from 48 plots in 8 mixed lodgepole-aspen stands.

Figure 2-1

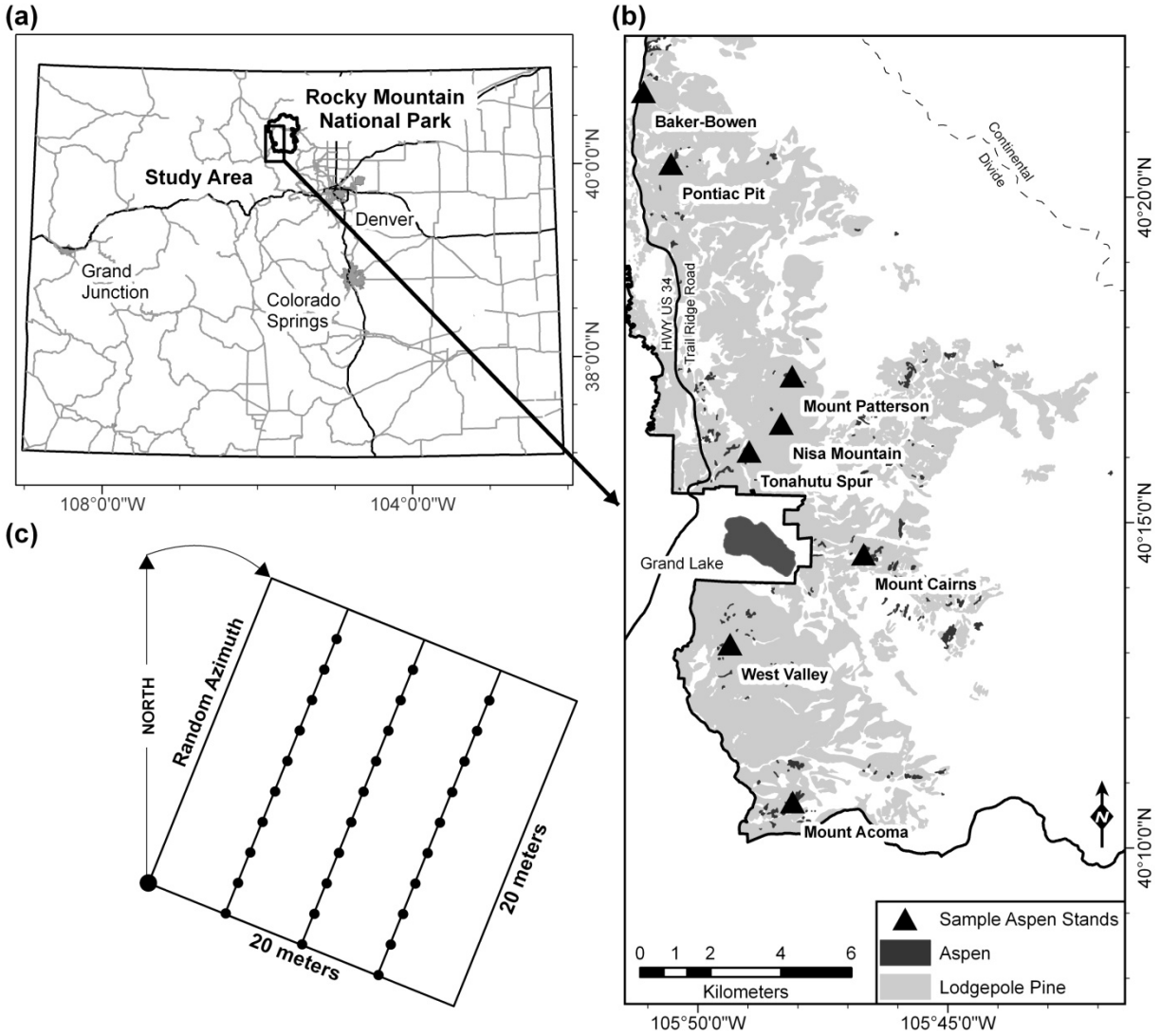

(a)
Rocky Mountain National Park
Study Area
Denver
Grand Junction
Colorado Springs
40°0'0"N
38°0'0"N
108°0'0"W
104°0'0"W
(b)
Baker-Bowen
Pontiac Pit
Continental Divide
HWY US 34
Trail Ridge Road
Mount Patterson
Nisa Mountain
Tonahutu Spur
Grand Lake
Mount Cairns
West Valley
Mount Acoma
40°20'0"N
40°15'0"N
40°10'0"N
Sample Aspen Stands
Aspen
Lodgepole Pine
0 1 2 4 6
Kilometers
105°50'0"W
105°45'0"W
(c)
NORTH
Random Azimuth
20 meters
20 meters

Figure 2-2

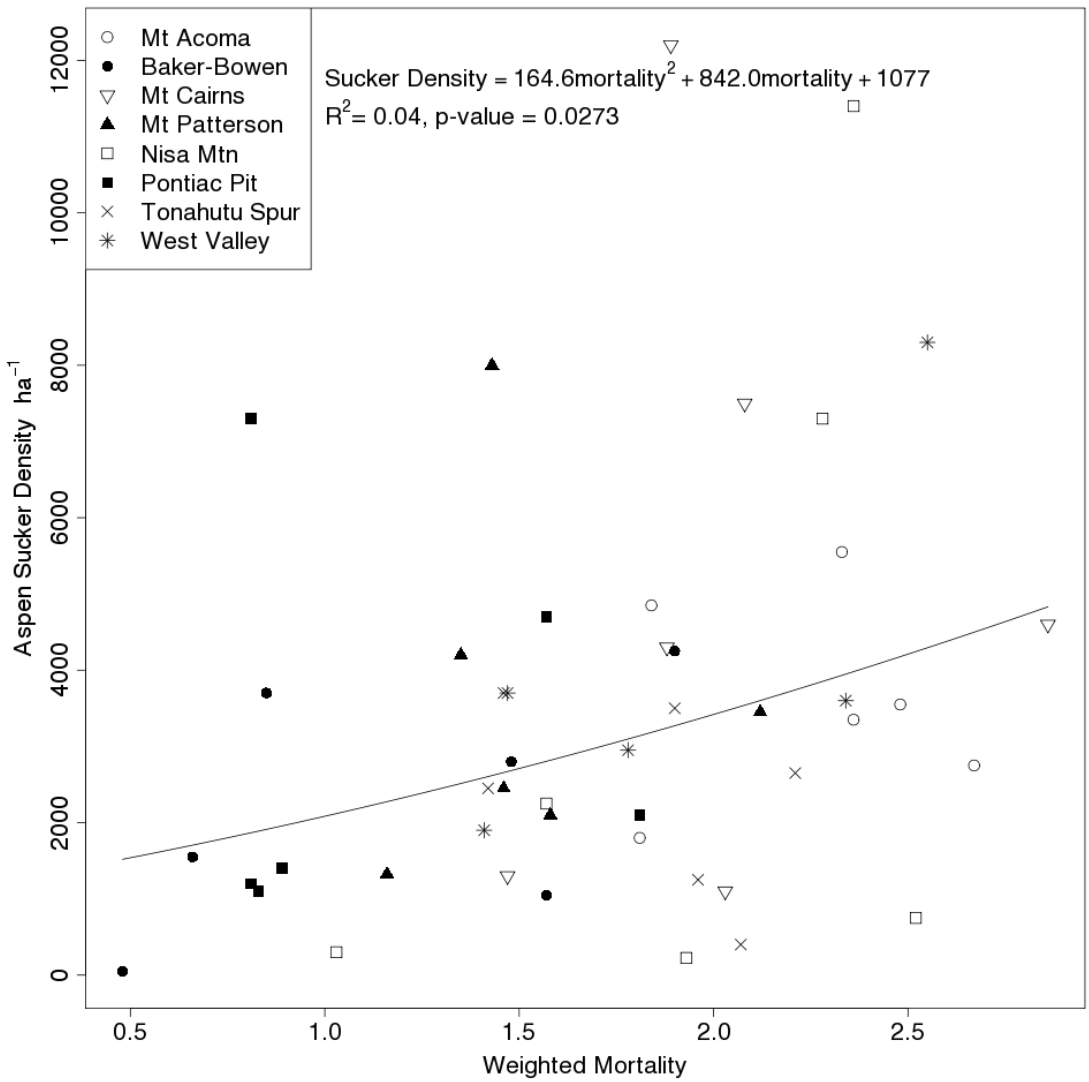

Mt Acoma
Baker-Bowen
Mt Cairns
Mt Patterson
Nisa Mtn
Pontiac Pit
Tonahutu Spur
West Valley
Sucker Density = 164.6mortality^2 + 842.0mortality + 1077
R^2= 0.04, p-value = 0.0273
Aspen Sucker Density ha^{-1}
0
2000
4000
6000
8000
10000
12000
0.5
1.0
1.5
2.0
2.5
Weighted Mortality

Figure 2-3

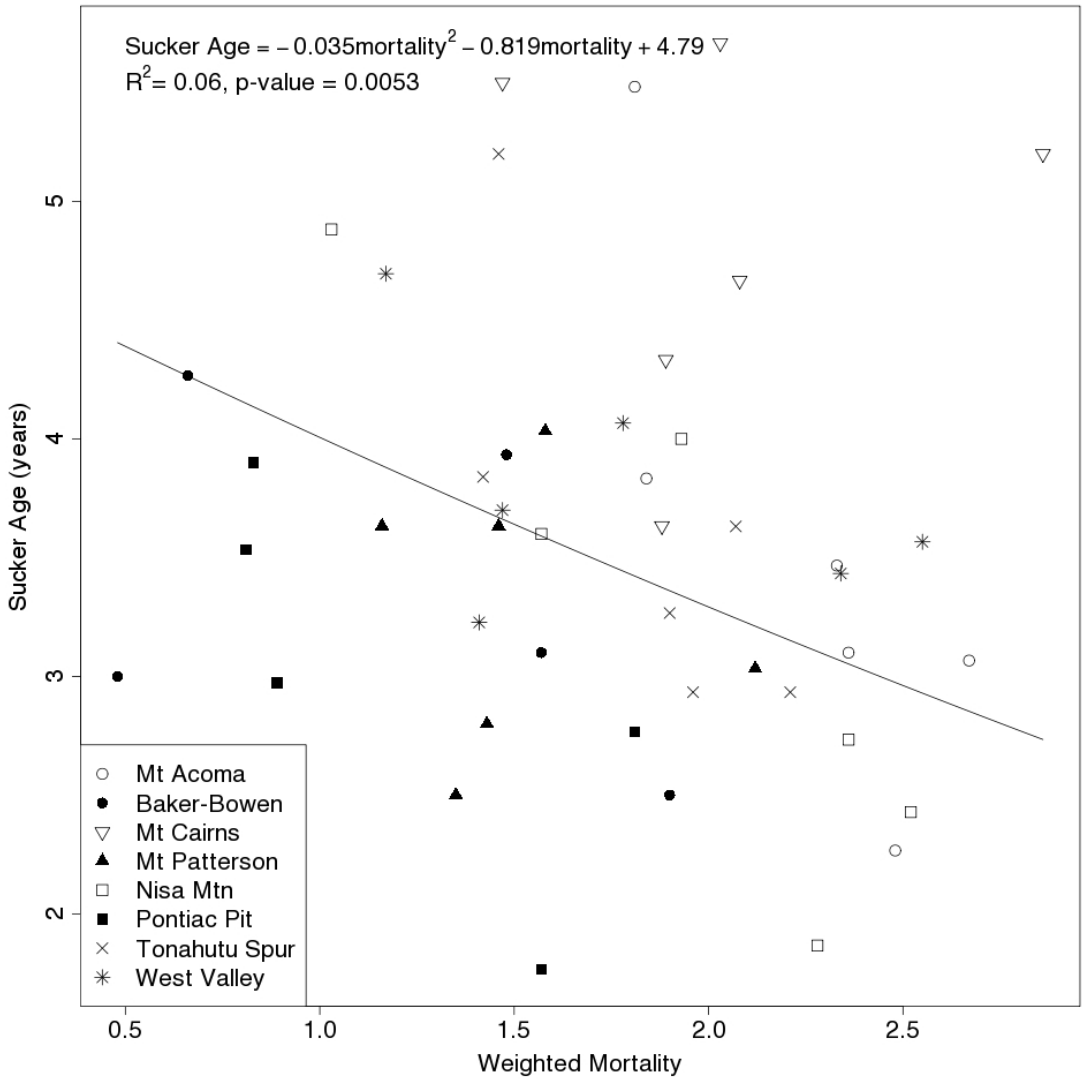

Sucker Age = – 0.035mortality^2 – 0.819mortality + 4.79
R^2= 0.06, p-value = 0.0053
Sucker Age (years)
Weighted Mortality
2
3
4
5
0.5
1.0
1.5
2.0
2.5
Mt Acoma
Baker-Bowen
Mt Cairns
Mt Patterson
Nisa Mtn
Pontiac Pit
Tonahutu Spur
West Valley

Figure 2-4

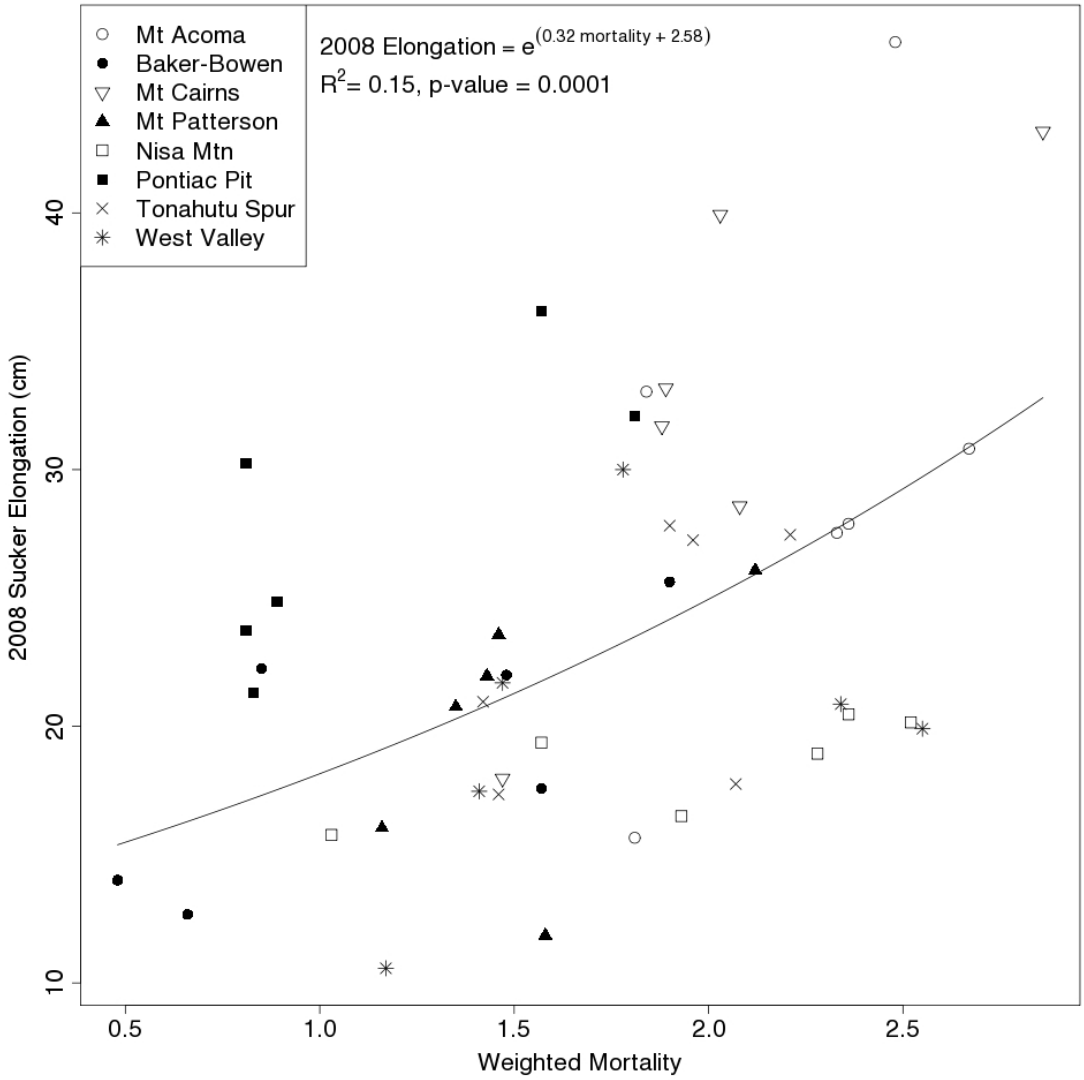
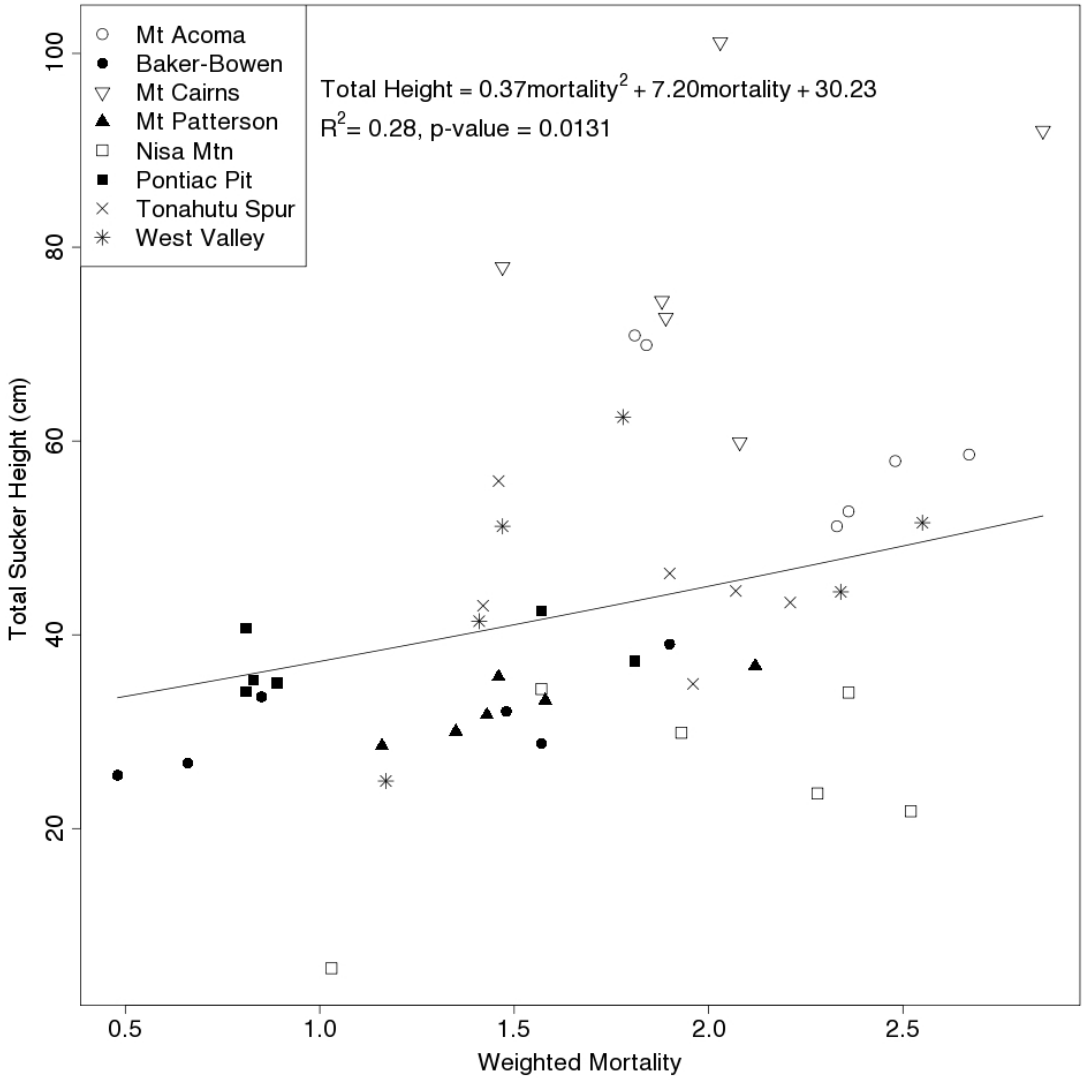

Mt Acoma
Baker-Bowen
Mt Cairns
Mt Patterson
Nisa Mtn
Pontiac Pit
Tonahutu Spur
West Valley
2008 Elongation = e^(0.32 mortality + 2.58)
R^2= 0.15, p-value = 0.0001
2008 Sucker Elongation (cm)
10
20
30
40
0.5
1.0
1.5
2.0
2.5
Weighted Mortality

Figure 2-5


Mt Acoma
Baker-Bowen
Mt Cairns
Mt Patterson
Nisa Mtn
Pontiac Pit
Tonahutu Spur
West Valley
Total Height = 0.37mortality^2 + 7.20mortality + 30.23
R^2= 0.28, p-value = 0.0131
Total Sucker Height (cm)
20
40
60
80
100
0.5
1.0
1.5
2.0
2.5
Weighted Mortality