MOUNTAIN PINE BEETLE IMPACTS ON TREE RESOURCES AND GROWTH RELEASE IN LODGEPOLE PINE DOMINATED SUBALPINE FOREST

By

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The final copy of this thesis has been examined by the signatories, and we Find that both the content and the form meet acceptable presentation standards Of scholarly work in the above mentioned discipline. Brayden, Benjamin Harlan (M.A., Geography) Mountain pine beetle impacts on tree resources and growth release in lodgepole pine dominated subalpine forest Thesis directed by Professor Susan W. Beatty

ABSTRACT

Over the past decade and a half Western North America has experienced a mountain pine beetle (Dendroctonus ponderosae Hopkins) (MPB) outbreak on a scale not previously recorded. Millions of hectares of lodgepole pine (Pinus contorta) in high elevation forests have been infested. Although bark beetles are an important part of the natural disturbance regime in this region, the current unprecedented level of tree mortality will have a significant impact on resources and light availability for the remaining live trees in the forest. In this thesis I investigated the impacts of extensive MPB-induced tree mortality on essential tree resources such as light, soil moisture, and soil nutrients, and how ensuing changes in these resources affect annual growth in surviving canopy-level trees. Using a decade-long chronosequence of mountain pine beetle disturbance in a lodgepole pine stand, I found that increased annual growth does occur in surviving canopy-level trees surrounded by high levels of neighboring tree mortality, but not in control plots representing a healthy intact forest. In infested plots where annual growth increase occurred in survivors, an increase in inorganic soil nutrients was observed, specifically, immediately after the transition from an intact canopy to one that has lost all needles and fine branches as a result of tree death. The spike in soil inorganic nitrogen that occurred during this period may have been taken up in part by surviving trees, as suggested by significantly lower leaf C:N. Other tree

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resources showed increase trends but lacked significance when compared to control plots. A confounding factor in the study site was a gradient of decreasing basal area (BA) with elevation, leading to differing initial BA in stands prior to infestation. Increased annual growth in surviving trees following bark beetle infestation is not simply a product of increased soil nutrients. Other resources likely limiting the post-infestation timing of growth increase may include available light, which can be restricted to low levels even after canopy deterioration due to initial stand density and BA encompassing the surviving tree. This study highlights the importance of understanding pre-infestation stand characteristics, and suggests promising areas for future research (light environment, fluxes in soil moisture, nutrients and stand carbon storage).

DEDICATION

To my amazing wife and parents who have all provided unconditional support.

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INTRODUCTION

The mountain pine beetle (Dendroctonus ponderosae Hopkins) (MPB) is a significant component of the natural disturbance regime in the subalpine and montane forest ecosystems of western North America. Historically, MPB has existed as more of a species-specific disturbance agent (Amman, 1977; Shore et al., 2006) when compared with other disturbances such as wildfire or blowdown. Beginning in the mid- to late-1990s MPB disturbance began to reach unprecedented levels in lodgepole pine (Pinus contorta) forests (Raffa et al., 2008). Changing climate is thought to be one of the main contributors to anomalous biologic disturbance events like that exhibited by MPB (Bale et al., 2002; Bentz et al., 2010; McDowell et al., 2011). Beginning in the 1970's temperatures have risen on average close to half a degree °C every decade in the West. Coupled with changes in precipitation (i.e. greater likelihood of drought), these two phenomena promote increased stress levels in individual trees (Van Mantgem et al., 2009; Wang et al., 2012) resulting in forests that are more susceptible to high intensity bark beetle infestation (Breshears et al., 2005; Raffa et al., 2008). Changing climate concomitant with other inciting factors (Wang et al., 2012), for example stand replacing fires that commonly occurred in the 19th century in north-central Colorado (Sibold et al. 2006), produce large areas of even-aged lodgepole pine dominated stands that are the age and size most susceptible to attack, supporting unprecedented levels of MPB infestation (Safranyik and Carroll, 2006; Chapman et al., 2012). Forests devastated by MPB cover an area approaching 53,000 km² in Western contiguous US states since the mid-1990s (Meddens et al., 2012). Some areas have experienced mortality rates approaching and even exceeding 70 percent (Hawkes et al., 2004; Klutsch et al., 2009; Wilkes, 2009; Collins et al., 2010), a level of canopy mortality that significantly alters forest dynamics.

Unlike other disturbance events that create drastic physical and biogeochemical changes almost immediately (Edburg et al., 2012), bark beetle disturbance progresses through marked stages or classes, each with distinct characteristics (Wulder et al., 2006; Klutsch et al., 2009) that impact the physical and biochemical microenvironment differently. Bark beetle disturbance and the consequent stages through which attacked trees progress are important components of the overall health of forests promoting forest heterogeneity by altering the microenvironment for extant community members and encouraging regeneration and succession (Romme et al., 1986; Veblen et al., 1991; Vyse, 2009; Collins et al., 2011). Mountain pine beetle is currently influencing these processes at a novel, magnified scale as epidemic levels of infestation have manifest across western North America.

Many of the amplified effects on microclimate, forest structure and biogeochemistry generated by MPB populations in recent years have been quantified. Surface litter greatly increases as affected canopies begin to deteriorate, losing needles and fine branches (Klutsch et al., 2009; Collins et al., 2011; Pugh and Small, 2011; Teste et al., 2011; Griffin et al., 2011; Bigler and Veblen 2011). Massive canopy deterioration also increases subcanopy light transmission (Pugh and Small, 2011), while extra litter creates cooler, wetter soils (Griffin et al., 2011) encouraging changes in understory density and community composition. Large infestations have increased watershed water yield (Potts, 1984; Pugh and Gordon, 2012) due to decreased snow retention and sublimation in the canopy that occurs in the grey and black classes, producing greater snowpack on the ground (Boon, 2011). Additionally, the reduction in living canopy level trees reduces transpiration (Knight et al. 1991), simultaneously increasing plant accessible soil moisture (Moorehouse et al., 2008; Clow et al., 2011).

In addition to physical property changes (i.e., changes in water quantity and subcanopy temperature), MPB-induced tree mortality also affects the nutrient content of subcanopy soil. Specifically, tree death influences essential nutrients like nitrogen (N) (Moorehouse et al., 2008; Clow et al., 2011; Griffin et al., 2011) and phosphorus (P). Moorehouse et al. (2008) showed that in ponderosa pine trees (*Pinus ponderosa*) attacked by MPB resorption of organic compounds from the needles is abandoned prior to senescence. The addition of this litter to the forest floor, combined with the decaying rhizosphere and reduction in stand uptake, has been shown to increase inorganic soil N (Moorhouse et al., 2008; Griffin et al., 2011; Edburg et al., 2012). Forest carbon (C) dynamics are also altered. Net ecosystem productivity is greatly reduced (Hicke et al., 2012) decreasing both system respiration and C sequestration; initially turning affected stands into C sources (Kurz et al., 2008; Brown et al., 2010). However, Brown et al. (2010) showed that affected stands did not become multi-decadal C sources as previously thought (Kurz et al., 2008) partly due to increased growth rates of surviving trees shown to potentially last upwards of 14 years (Alfaro et al., 2004). The increased growth rates described are known as growth release. Associated with growth release is competitive release, which is the increase in available resources due to the reduction in local competition with other trees, subsequently driving growth release.

Many studies have identified patterns of growth release occurring in saplings and understory as a result of changes in stand/canopy density produced by disturbance (Waring and Pitman, 1983; Wright et al., 1998; Williams et al., 1999; Coates, 2000; Brown et al., 2010; Kayes and Tinker, 2012). Dendrochronological studies examining patterns of historic beetle outbreak use growth release found in the annual ring record of surviving trees to identify the occurrence of past disturbance events (Heath and Alfaro, 1990; Veblen et al., 1991; Alfaro et al., 2004, Smith

et al., 2012). However, very little research has been conducted describing the response of surviving mature lodgepole pine trees in the context of the specific drivers of the observed change after bark beetle disturbance. Bebber et al. (2004) examined managed eastern white pine (Pinus strobus) forests under thinning treatments and found increased diameter increments in the boles of trees that were left standing. However, these findings were not tied to specific drivers of growth release and the experiment was conducted under circumstances in which biomass was removed from the forest, differing from biologic disturbance. Heath and Alfaro (1990) investigated growth release in a lodgepole pine forest as a result of MPB disturbance, finding increased growth rates in mature trees, but similar to other studies examining growth release they did not directly relate their findings to specific drivers (i.e. resources). To our knowledge, no studies have explicitly quantified growth release in subalpine, canopy-level trees relative to the specific biotic and abiotic changes that are produced by bark-beetle disturbance. The major objective pursued herein was to investigate how changes in forest structure and plant resources caused by MPB-induced tree mortality affect the growth of surviving canopy level trees at the tree scale. Specifically, surviving trees will likely experience growth release as a result of competitive release. In this study, we use various methods to investigate how MPB-induced mortality (and the associated reductions in competition with neighboring trees as well as potential resource augmentation) affects primary productivity and growth in mature surviving lodgepole pine trees. We tested two null hypotheses. 1) The growth rate of mature surviving canopy trees does not significantly increase after high levels of MPB-induced mortality occurs at the stand level. 2) Resources essential for tree growth and survival including, but not limited to, light, soil nutrients, and soil moisture will not significantly change as high levels of MPBinduced mortality occurs at the stand level. Finally, based on the refutability of these null

hypotheses, determine the relationship, if any, between modified resources (independently and collectively) and any observed change in surviving tree growth rates.

METHODS

Site Description

The study took place in the Fraser Experimental Forest (FEF), a 93 km² research forest located west of the continental divide in the Arapaho National Forest in north-central Colorado (Figure 1). The site is located at 39.9075 N, 105.8528 W at an elevation of 2913 m in lodgpole pine (Pinus contorta Dougl. Ex Loud.) dominated subalpine forest. Engelmann spruce (Picea engelmannii), subalpine fir (Abies lasicarpa), and quaking aspen (Populus tremuloides) are interspersed throughout the site and compose $\sim 25\%$ of the canopy. Lower elevations, including our site, were selectively clear-cut from the beginning to the middle of the 20th century. Vegetation ground cover is dominated by *Vaccinium* spp. with small patches of *Arnica* spp. and other forbs. The site has a consistent, gently sloping N-NE aspect. Mineral soils are a sandy-loam to sandy-clay-loam, mostly derived from gneiss and schist. The organic soil horizon is \sim 2-10 cm deep and is a loam. The soils are highly permeable, but are capable of storing a considerable amount of water, the majority of which is derived from snowmelt. The climate at FEF consists of long, cold winters and short, cool summers. The local mean annual temperature is 0.5 °C at 2745 m. Average annual precipitation is 737 mm with almost two thirds falling as snow between the months of October and May. Mountain pine beetle populations started escalating in the Fraser Valley beginning around 2001, reaching epidemic levels less than five years later (Figure 2) and continuing through 2011, when mortality rates approached 70% in lodgepole pine (Wilkes 2009).





Figure 1. A) Location of Fraser Experimental Research Forest in Colorado. B) Location of site and plots at FEF.



Figure 2. Change in MPB infestation between 2000 and 2006 in the Fraser Valley (Wilkes 2009).

Experimental Design

We designed a space-for-time study to capture the extended temporal scale of the outbreak. Twenty-5 m radial plots were selected representing a decade long chronosequence of beetle disturbance in *P. contorta* dominated subalpine forest. The plots were grouped into four "classes" of tree mortality: three consecutively older experimental classes defined by time since beetle (TSB) infestation (Griffin et al., 2011) and a control class (0 yrs TSB) representing no infestation (n=5) (Figure 3). The control class (also referred to as the green class) describes uninfested trees. The red-class (~2-4 yrs TSB) is marked by the desiccation of the still attached needles, turning them red/orange. The grey class (~5-7 yrs TSB) is characterized by the abscission of needles and fine branches, as well as the preliminary loss of bark (late grey class). The black class (~7+ yrs TSB), not previously discussed by Wulder et al. (2006) or Klutsch et al. (2009), was important to identify in this analysis of disturbance progression because of the continued potential for changes to the physical and biochemical environment. The black class describes trees with no needles or branches < 0.5 cm, and severe degradation of bole bark; it is essentially a standing snag. The black class has been referred to as the "silver stage"



Figure 3. A visual representation of trees from the four age classes described: green (control), red (2-4 yrs TSB), grey (5-7 yrs TSB), black (7+ yrs TSB).

(Donato et al., in press) in the literature when TSB is greater than 25 years, however this is beyond the scope of this study.

A healthy non-infested *P.contorta* tree, henceforth referred to as the "focal tree," was located at the center of each of the twenty plots (Figure 4). At a *minimum*, the focal tree's three nearest mature neighbors had to be *P. contorta* trees having the crown degradation characteristic of the TSB class for that plot. Mature was defined as having a DBH > 6 cm and a height that placed it in the canopy. Plots were classified by crown degradation as described by Klutsch et al. 2009.

During the decade of infestation, the beetles progressively moved from the bottom of the slope to the top. This phenomenon influenced the location of the selected chronosequence classes. The black class plots were located at the lower elevations and the red class plots were higher up on the slope. The grey and control plots were interspersed among all elevations (Figure 5).



Figure 4. A diagram depicting plot design and requirements for plot classification. The starred trees represent the minimum number and proximity of mature trees required to classify the plot (red in this case).



Figure 5. Map of plots and their distribution on the slope at the FEF site.

Tree Measurements and Increment Cores

The diameter at breast height (DBH) (1.4 m) was measured for every tree, alive and dead, in each plot. The respective DBH measurements were used to calculate the basal area (BA) of each tree. All individual tree BAs in each plot were summed and divided by the plot area (0.0079 ha) to determine total BA for each plot (given m² ha⁻¹). In addition to total BA, living and dead BA were calculated and recorded for each plot by using the above process, but only including trees from the respective categories. The heights of all the trees in each plot were measured using a clinometer and the distances between the focal tree and every other tree in the plot were measured at breast height and recorded.

Two increment cores were taken from each of the 20 focal trees, one from the downhill side (north aspect) and one from the side hill face (east aspect) of the tree bole, using a 12 mm diameter increment borer (Haglöf Sweden, Långsele, Sweden). The respective annual rings from the North and East cores were averaged for each year to control for the circumferential variation (Stokes and Smiley, 1968) in annuli widths inherent in trees growing on a slope. The twenty most recent annual ring-widths (1992-2011) were individually measured to the nearest hundredth of a mm using digital calipers and a microscope. The latter ten rings (2002-2011) represent the period of beetle infestation at the site beginning with initial infestation in 2001-2002. The former ten rings (1992-2001) represent tree growth from the decade prior to infestation at the site. The pre-infestation rings recorded for each focal tree represent annual focal tree growth rates previous to any infestation at the site and were used to control for variation in focal tree DBH and plot BA and density that may have confounded growth release produced by MPB disturbance. This was done by examining the percent change of each annual focal tree ring from 2002-2011 relative to that focal trees mean ring width from 1992-2001.

$$\frac{RW_A - RW_M}{RW_M} \times 100$$

Where RW_A is each ring-width from 2002-2011 and RW_M is the mean ring-width from 1992-2001.

Focal Tree Leaf C:N

Needles were collected from focal trees on July 28th. The needles were dried at 60 °C for 72 hours and then ground into a powder with a mortar and pestle. Small amounts of liquid nitrogen were occasionally added to the mortar to aid in pulverizing the more recalcitrant cellulose to ensure a homogenous sample. The ground samples were stored in a desiccator at room temperature until analysis. Approximately 2-3 mg of sample was analyzed with a Costech, ECS 4010 Carbon and Nitrogen analyzer (Costech Analytical Technologies Incorporated, Valencia, CA, U.S.A.), which employs combustion/gas chromatography to determine the ratio of component elements.

Focal Tree Photosynthetic Rate (Light Curves)

Light response curves are the non-linear photosynthetic response of plants to increasing levels of light and are used to determine photosynthetic rates of trees (Ogren and Evans, 1993). We constructed light curves for the twenty focal trees between July 26th and July 28th 2011 during the middle of the growing season. Samples of sun-exposed (when possible) south facing branches were cut using a pole pruner and ladder. The cut end of the samples were submerged in water and cut again to simultaneously remove and prevent embolism during analysis. The

branches remained submerged while light curves were measured for each sample using a LI-COR LI-6400 equipped with the LI-6400XT console and 6400-02B LED Light Source (LI-COR Incorporated, Lincoln, NE, U.S.A.). The needles were exposed to 9 incremental increases in Photosynthetically Active Radiation (PAR) ranging in photosynthetic photon flux densities (PPFD) from 0 μ mol m⁻² s⁻¹ to 2000 μ mol m⁻² s⁻¹. Light levels remained at each PPFD until photosynthetic flux rates (μ mol CO₂ m⁻² s⁻¹) stabilized. Once a stable photosynthetic rate had been recorded the PPFD was increased. We examined the photosynthetic rate for each focal tree at the maximum PPFD value of 2000 μ mol m⁻² s⁻¹ (A_{max}). This represents the photosynthetic rate of the tree at or above the maximum light level that the tree would experience naturally and is a good indication of photosynthetic capacity.

Focal Tree Leaf Water Potential

Leaf pre-dawn (ψ_p) water potentials were sampled the night of July 27th and 28th between 11pm and 4am. Due to light limitation during sampling, branch samples were selected from the southern aspect as high as possible on the focal tree to ensure the greatest likelihood of sunexposure during the day. After harvesting, each sample was immediately fit into a model 1000 plant water status console (PMS Instrument Company, Albany, OR, U.S.A) where positive pressure from N₂ was forced into the chamber. The value when *xylem water* began to exude from the cut stem was recorded. These pressure values are representative of the negative pressure held by the stem and used as a proxy for soil matric potential (plant available water) (Richie and Hinckley, 1975; Hinckley et al., 1978). LAI'

Hemispherical photos were taken of the forest canopy in September 2011 at four locations within each study plot, one in each cardinal direction surrounding and approximately 5 m away from the focal tree. Photos were acquired using a Nikon D700 camera with a Sigma EX Fisheye 8 mm lens. The camera was positioned 1 m above the ground, leveled to gravity, and oriented to true north. The hemispherical photos were analyzed to calculate percent canopy openness and LAI' using the Gap Light Analyzer 2.0 software (GLA; Frazer et al. 1999). LAI' is defined as the product of a clumping factor (Nilson 1971) and the leaf area index (Black et al. 1991) and is a measure of total plant area, including both leaves and woody material. Canopy density is calculated from these data by subtracting percent canopy openness from complete (100%) canopy cover. Reported LAI' was integrated over the zenith angles 0° to 60° (Stenberg et al. 1994). Gap Light Analyzer software was also used to model transmitted light flux through the canopy for the interval of July 1 - July 31. The percent total light transmitted is the ratio of radiation incident on the plot surface when there is blockage of light from the surrounding topography and overlying forest canopy. Total transmitted light (%) was calculated using a 2minute solar step, a cloudiness index of 0.5, a spectral fraction (0.25–25 mm) of 1.0 MJ m⁻² d⁻¹, a beam fraction of 0.5, a clear-sky transmission coefficient of 0.7, and an assumed solar constant of 1367 W m⁻² (Hardy et al., 2004).

Ground Cover

Percent ground cover was determined in the plots for vegetation (defined as any forb, shrub, grass, sedge, or small sapling), as well as woody debris including non-beetle killed logs, stumps and snags 10 cm or greater (Harmon et al. 1986). The radial plots were quartered and the

percent ground cover of both vegetation and woody debris was visually estimated by three people, three separate times, and subsequently averaged.

Soil Sampling and Analysis

Soils were sampled in July 2011 in the middle of the growing season. Approximately 100 g of organic soil and 100 g of mineral soil were collected 1m from the focal tree bole at each of the four primary intercardinal directions (NE, SE, SW, and NW) and stored on ice until processing. All subsequent soil assay procedures were completed for both organic and mineral soil samples. Pits exposed by soil sampling were used to record organic layer and litter layer depths. Within twelve hours we sieved and homogenized soils, removing coarse plant litter, debris, and >1mm roots. Soil samples were then immediately extracted for dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorous using the potassium sulfate (K2SO4) extraction method described by Weintraub et al. 2007. Dissolved inorganic N and P extracts were analyzed spectrophotometrically on a Bio-Tek Synergy HT microplate reader (Bio-Tek Inc., Winooski, VT, U.S.A.) using vanadium chloride/sulfanilamide reduction chemistry and colorimetric determination of nitrite for nitrate (Doane and Horwath 2003), ammonium using a modified Berlethot reaction following the protocol of Rhine et al. (1998), and dissolved inorganic phosphorous by the malachite green colorimetric procedure (D'angelo et al. 2001).

The remaining four organic and four mineral samples from each plot were homogenized, generating one sample for each of the two respective soil types for each plot. These soil samples were sent to the Colorado State University soil lab for analysis of additional plant nutrients as well as percent soil organic matter.

Immediately after snow melt, ion-exchange resin bags (Castle and Neff, 2009, modified method) were installed at the interface of the organic and mineral soils, 1 m from the focal tree bole at each of the four cardinal directions (N, E, S, and W). The resin bags were used to quantify 2011 growing season time-integrated pools of inorganic nitrogen and phosphorous. Ion-exchange resin bags were removed from the soil at the end of September 2011 and frozen at - 20°C until extraction. Resin beads were removed from the bags, added to 40 mL of 2 M potassium chloride (KCl), churned for 1 hour in an orbital shaker and incubated at 4°C overnight. KCl extractions were vacuum filtered and frozen at -20°C until analysis. Samples were spectrophotometrically analyzed for dissolved inorganic nitrate, ammonium, and phosphorous using the same chemistry protocol for soil inorganic nitrogen and phosphorous in the K2SO4 extracts described above.

In addition to plant nutrient pools, we assessed soils for pH, bulk density, texture and moisture using the soil samples collected from each plot. Soil pH was determined with an Oakton pH Testr 3 digital pH meter (Oakton Instruments, Vernon Hills, IL, USA) with a resolution of 0.01 and accuracy of +/- 0.02. A 1:1 solution of 30g soil to 30 mL of deionized water was homogenized and then allowed to sit for 5 minutes before being measured. We assessed bulk density by coring plot soils using a standard soil corer with a known diameter (1.42 cm), which was ideally too small for rocks of significant size to enter and induce error. The length of each core was measured with digital calipers and used to calculate the volume. The samples were oven dried at 110 °C for 48 hours and then weighed. Bulk density was calculated as dry mass (g)/core volume (cm³). Soil texture was established using a modified hydrometer method described by Day (1965), which is based on Stokes's Law. Gravimetric soil moisture was determined for both organic and mineral soils by weighing and then drying 5g of

wet soil at 60 °C for a minimum of 48 hours and then re-weighing the sample and calculating it as (g wet-g dry)/g dry. Soil temperature (integrated over 0-15 cm depth) was sampled throughout the growing season 1 m from the focal tree-bole in each cardinal direction using a temperature probe attached to a LI-COR LI-6400 infrared gas analyzer (LI-COR Incorporated, Lincoln, NE, U.S.A.).

Statistical Analysis

Data were analyzed using non-parametric statistical tests. The Mann-Whitney U test (Wilcoxon rank-sum test) was employed for testing significant differences between the means of two groups. We used a Kruskal-Wallis test, which is an expansion of the Mann-Whitney test used for three or more groups, to compare the means of different variables across all of the TSB classes. Initially, we applied parametric analytical methods (e.g. t-tests) to determine differences between the means of two groups. Likewise, we used ANOVA to test for differences among the TSB classes. Ultimately, we decided to use non-parametric methods because a large portion of the variables we collected did not meet the assumptions of the t-test or ANOVA (i.e. normal distribution and/or equal variance). The Mann-Whitney U test was a simple replacement for the t-test and required no further modification or considerations. Contrary to this, using the Kruskal-Wallis test in place of ANOVA required more deliberation. Once a significant difference was determined among TSB classes using the Kruskal-Wallis test, post-hoc analysis differs somewhat from the ANOVA Tukey HSD test. Rather, the more suitable multiple comparison post-hoc test described by Siegel & Castellan (1988) was used if the Kruskal-Wallis test revealed a significant difference among the classes ($\alpha = 0.05$). We justified both the Mann-Whitney and Kruskal-Wallis tests due to their more robust outcomes compared with the t-test and ANOVA.

Forest ecology variables are often not normally distributed; skewed distributions were consistent in a large portion of the variables and were identified as such using a Shapiro test for normality. Unequal variance was also a common issue in the data. Due to the inconsistency in meeting the assumptions of parametric tests we decided to use the more robust non-parametric methods rather than a combination of parametric and non-parametric tests based on equal variance and Shapiro test outcomes for each variable.

RESULTS

Basal Area

As elevation at the site increased, site BA decreased ($R^2 = -0.68$, p < 0.01) (Figure 6). The progression of beetle infestation followed this gradient; older TSB plots were located lower on the slope becoming progressively younger with greater elevation.





A.

Figure 6. Hemispherical photographs showing how BA progressively decreases with elevation at the site. Photograph A was taken at the bottom of the slope and Photograph B was taken at the top.

Despite the significant correlation between elevation and BA among the 20 plots, no significant difference existed among the class means for total BA. Class total BA means ranged from

 $41.24\pm2.38 \text{ m}^2 \text{ ha}^{-1}$ in the black class to $22.7\pm6.22 \text{ m}^2 \text{ ha}^{-1}$ in the red class (Table 1). Control plots were located throughout the BA gradient and are reflective of this with a mean total BA of $30.25\pm8.62 \text{ m}^2 \text{ ha}^{-1}$.

	Control	Red	Grey	Black	Chi-squared, p- value
Total Basal Area (m ² ha ⁻¹)	30.25±8.62	22.7±6.22	38.19±3.33	41.24±2.38	3.4, 0.33, n.s.
Area (m ² ha ⁻¹) Dead Basal Area	21.37±5.35 a	0.58±0.52 b	4.91±1.89 ab	9.61±3.95 ab	14.02, 0.0029
(m ² ha ⁻¹) Percent of Total	8.75±4.43 a	22.11±6.24 ab	33.24±2.83 b	31.56±2.47 b	10.47, 0.01
BA Living (%) Percent of Total	77.53±8.29 a	2.61±2.15 b	12.39±4.74 ab	22.0±7.59 ab	14.20, 0.0026
BA Dead (%)	22.07±8.26 a	97.37±2.16 b	87.52±4.77 ab	77.85±7.64 ab	14.20, 0.0026

Table 1. Mean values and Kruskal-Wallis coefficients describing different plot basal area variables.

Contrary to this, mean living basal areas did significantly differ among the four TSB classes (Table 1), which was expected as a result of the experimental design. Living BA ranged from $21.37\pm5.35 \text{ m}^2 \text{ ha}^{-1}$ in the control class to $0.58\pm0.52 \text{ m}^2 \text{ ha}^{-1}$ in the red class. Dead BA was also significantly different among the TSB classes (Table 1); grey plots represented the greatest dead BA with $33.24\pm2.83 \text{ m}^2 \text{ ha}^{-1}$ and control the lowest $8.75\pm4.43 \text{ m}^2 \text{ ha}^{-1}$.

Ring Width

Focal tree ring-widths for the 2011 growing season were significantly different among classes. The smallest mean ring-widths were found in the control class $(1.0\pm0.1 \text{ mm})$ and the largest in the red class $(3.6\pm0.3 \text{ mm})$ (Figure 7); however, all infested classes (i.e. red, grey, and black) displayed much larger ring-widths than the control. One exception was the focal tree in plot 15 of the grey class, which was host to a large infestation of dwarf mistletoe (*Arceuthobium* Sp.).



Figure 7. Increment cores from focal trees in the red class (top) and control class (bottom) illustrating different annual growth between healthy trees in a beetle-killed stand and healthy trees in an unaffected stand.

The growth rings found in tree 15 were much smaller than even the control focal trees, and likely a product of stress caused by the resource siphoning of the parasite. We did not notice the mistletoe until fieldwork was completed and therefore removed plot 15 from all analyses.

Actual ring-width during 2011 was heavily influenced by the BA/elevation gradient that occurred at the site. The three infestation classes displayed a progressive increase in actual ring-width that was the inverse of TSB class age (i.e. the largest rings were in red and smallest in black). Reviewing the ring-widths prior to the beetle outbreak revealed that the inequity among the plots existed independently of any competitive release effect and could be attributed almost entirely to plot BA. To control for the effects of BA we attempted two methods to compare post infestation ring-widths to the mean ring-width from the decade prior to infestation: 1) Actual change from the prior decade mean (mm), and 2) percent change in ring-width from the prior

decade mean. Actual change compared to the mean of the decade prior to infestation was deemed ineffective for removing the effects caused by inequity in initial plot BAs. Focal trees with larger pre-infestation annual rings showed larger actual increases that were proportionate to pre-infestation growth. As a result, percent change in ring-width over the mean from the decade prior to infestation proved to be the most effective control for unequal plot BAs and is shown for the entire period of infestation in Figure 8. Once the BA effect had been accounted for, growth

Percent Change in Focal Tree Annual Ring-Widths



Figure 8. The percent change in post-infestation focal tree annual ring-width relative to the focal trees own mean ring-width from the decade prior to infestation. The means of each infested class were compared to the mean of the control class for each year starting in 2002.

release in each class as a function of TSB became readily discernible, displaying relative annual increases corresponding to length of exposure to greater resources. This was most evident in the experimental groups during the two most recent years (2010 and 2011), with values ranging from $132.6\pm23.2\%$ to $176.9\pm54.2\%$ in 2010 and $191.4\pm23.5\%$ to $269.5\pm88.9\%$ in 2011, both years represented by red and black respectively. A significant difference in ring-width percent increase first appeared in 2009 when infested classes began to deviate from the control class. Smaller increases in ring-width were present in the control group ($5.3\pm16.3\%$ and $26.6\pm21.1\%$ in 2010 and 2011) during the decade of infestation.

Leaf C:N

Carbon to nitrogen ratio sampled from focal tree leaves revealed no difference among classes. The grey class was found to have the lowest C:N (42.49 ± 2.37) followed by the black class (49.43 ± 4.34). The control and red classes had ratios similar to each other and higher than the grey and black classes (56.69 ± 6.22 and 57.54 ± 4.89 , respectively). The higher ratios found in the control and red classes were primarily the product of lower nitrogen content (Table 2). Diverging from the chronosequence and examining the pre-needle drop and post-needle drop status of neighboring trees by binning control with red, and grey with black did expose a difference in C:N (Mann-Whitney W = 72, p < 0.05) (Figure 9). In this case, C:N of focal tree needles in a post-needle drop environment are significantly lower. Additionally, if we examine the C:N in each of the four classes with regard to DIN in the soil, a clear difference across the chronosequence was revealed (Chi-squared = 10.11, p = 0.01).

	Control	Red	Grey	Black
Leaf Carbon (%)	50.9±0.2	50.7±0.36	50.1±0.2	50.3±0.3
Leaf Nitrogen (%)	0.93±0.09	0.91±0.07	1.2 ± 0.06	1.05 ± 0.09

Table 2. TSB class means for C and N content extracted from focal tree needles.



Needle Carbon/Nitrogen Ratio

Figure 9. Comparison of mean focal tree C:N between plots containing neighbors with needles (green and red classes) on the tree, and plots containing neighbors post-needle abscission (grey and black classes).

Photosynthetic Rates

Values for A_{max} were highest in the red class (11.33±0.7 µmol m⁻² s⁻¹) and lowest in the black (9.78±0.38 µmol m⁻² s⁻¹) with control and grey class values nearly identical to black (Figure 10). Despite the range in values, no significant difference in A_{max} photosynthetic rates was found.



Figure 10. Mean photosynthetic light curves for each TSB class. Grey is brown and Black is yellow so that

the different classes can be more easily distinguished.

Leaf Water Potential

Leaf pre-dawn water potential is generally considered to represent soil water potential (Richie and Hinckley, 1975) providing a good proxy for plant available soil moisture, and consequently the level of water stress the tree is experiencing. Leaf water potentials were sampled after a period of multiple heavy rain events producing ψ_p that were relatively high across the chronosequence. Despite this, a significant difference was present in ψ_p (Figure 11). The lowest levels were found in the control class (-0.32±0.09 MPa), but were still well above the wilting point of -1.5 MPa. Both grey and black classes constituted ψ_p levels less negative than

those found in the control class with values of -0.24±0.05 MPa and -0.22±0.02 MPa respectively. The least negative ψ_p existed in the red class (-0.13±0.01 MPa). Pre-dawn water potential also showed a very strong negative linear relationship (R² = -0.74, p < 0.001) with living BA, which suggests competition for soil water. We also examined the difference in mean ψ_p between focal trees with either living or dead neighbors (i.e. control plots compared to all infestation classes) (Figure 12).



Focal Tree Pre-Dawn Water Potential

Figure 11. ψ_p means for all classes.

A significant difference (Mann-Whitney W = 13, p < 0.05) was also present between focal trees surrounded by dead neighbors and those surrounded by healthy neighbors.



Focal Tree Pre-Dawn Water Potential

Figure 12. ψ_p mean comparison between focal trees with dead neighbors and living neighbors.

Transmission and Canopy Density

Effective leaf area index (LAI') values from each TSB class were well coupled to total BA from that class. However, unlike total BA, significant differences were present in LAI' among classes (Table 3). The highest LAI' value belonged to the black class at 1.258±0.04 and the lowest to the red class with 0.898±0.06. Canopy density differed as well, with the grey class actually having the highest canopy density (72.277±1.46%), and the red having the lowest (63.27±1.53%). However, due to the BA gradient that exists at the site a more appropriate metric to examine canopy dynamics is the ratio of canopy density to total BA. Despite this, the class means for canopy density/BA ratio did not differ across TSB plots either, although the highest

values occurred in the red class (3.531 ± 0.75) and the lowest in black (1.737 ± 0.08) and were more representative of the canopy degradation that occurs with TSB.

					Chi-squared,
	Control	Red	Grey	Black	p-value
LAI' Canony Density	1.232±0.09 ab	0.898±0.06 a	1.235±0.10 ab	1.258±0.04 b	8.5, 0.03
(%) % Capopy	69.982±2.25 ab	63.276±1.53 a	72.277±1.46 b	70.89±1.04 ab	9.99, 0.01
Density/BA	3.164±0.8	3.531±0.75	1.941±0.19	1.737±0.08	3.1, 0.37, n.s.

Table 3. Mean class values and Kruskal-Wallis coefficients describing canopy characteristics.

Vegetation Ground Cover

Using LAI' and canopy density values, transmission levels can be calculated, and

represent a proxy for incident radiation at the forest floor. Although the highest levels of forest



Percent Vegetation Ground Cover

Chronosequence Class



floor radiation occurred in the red class, percent vegetation ground cover (PVGC) was lowest (24.978±5.42%), with the highest PVGC represented in the black class (51.9±11.25%). The approximate doubling of PVGC progressively from the control class to the oldest class was significant (Figure 13). Contrary to its relationship with radiation, PVGC showed positive trends with some of edaphic variables like mineral soil moisture and organic soil depth ($R^2 = 0.52$, p = 0.02; $R^2 = 0.46$, p < 0.05).

Soil Analyses

Soil temperature was highest in the red class $(9.93\pm0.31^{\circ}C)$ and lowest in grev $(8.90\pm0.15^{\circ}C)$ (Table 4) and showed a strong negative relationship with canopy density (R² = -.50, p < 0.05). In contrast to temperature, organic soil moisture showed relatively strong positive linear relationships with representative measures of ground-level radiation such as canopy density and LAI' and was lowest in the red class (34.22±3.14%). Relatively similar levels of soil moisture were found in the other three classes (the mean of all three was 43.53±0.40%) (Table 4). Organic soil moisture had a very strong positive relationship with soil organic matter (SOM) $(R^2 = 0.71, p < 0.001)$, both variables showing a similar pattern across classes; a dip in SOM occurred in the red class $(21.9\pm3.58\%)$ while remaining relatively stable across the other classes, but highest in the control group (34.33±3.74%). Mineral soil moisture was not different across the chronosequence, but did show a progressive increase with TSB class. It was lowest in the control $(13.13\pm1.7\%)$ and highest in the black $(17.76\pm1.96\%)$. Soil moisture was sampled two days after a rain event and was a single point measurement; a more thorough analysis of moisture flux should be done. Litter layer and organic soil depths were similar across all groups, although there was quite a large range in organic soil depth and reflective of TSB (Table 4). Bulk

	Control	Red	Grey	Black	Chi-squared, p- value
PVGC (%)	27.55±3.33	24.978±5.42	47.875±5.33	51.9±11.25	8.83, 0.03*
Litter Depth (cm)	1.6±0.18	1.7±0.08	1.812±0.08	1.675±0.07	1.27, 0.74, n.s.
Organic soil Depth (cm)	3.05±0.56	1.97±0.42	4.34±0.9	3.22±0.3	6.9, 0.075, n.s.
Organic Soil Organic Matter (%)	34.33±3.74	21.9±3.58	32.89±3.78	29.09±1.7	5.1, 0.17, n.s.
Organic Soil Gravimetric Moisture (%)	43.76±3.86	34.22±3.14	44.09±2.95	42.75±1.84	6.37, 0.09, n.s.
Organic Soil Bulk Density (g cm ⁻³)	0.493±0.05 ab	0.692±0.08 a	0.354±0.07 b	0.461±0.04 ab	7.3, 0.06, n.s.
Mineral Soil Gravimetric Moisture (%)	13.13±1.7	16.63±1.61	17.34±1.66	17.76±1.96	2.98, 0.39, n.s.
Mineral Soil Bulk Density (g cm ⁻³)	1.20±0.07	1.16±0.10	1.35±0.01	1.16±0.15	3.94, 0.27, n.s.
Soil Temperature (°C)	9.67±0.31 ab	9.93±0.15 a	8.90±0.15 b	9.46±0.13 ab	8.65, 0.03
		0.10 0		5120 00	
Growing Season DIN (μg N g ⁻¹ resin)	4.56±0.53 ab	3.99±0.72 a	11.07±1.9 b	7.61±1.32 ab	9.24, 0.026
Growing Season NH4 (µg N g ⁻¹ resin)	2.61±0.79 a	2.31±0.58 a	6.85±1.47 b	3.73±0.18 ab	10.56, 0.01
Growing Season NO3 (µg N g ⁻¹ resin)	1.95±0.82	1.68±0.16	4.22±1.49	3.87±1.31	3.4, 0.33, n.s.
Growing Season PO4 (µg P g ⁻¹ resin)	21.52±8.78	24.50±8.05	42.96±7.97	41.47±7.77	4.3, 0.23, n.s.
Organic pH	4.634±0.09	4.884±0.06	4.515±0.12	4.762±0.12	5.9. 0.11. n.s.
Organic NH4 (ug N g^{-1} soil)	7 81+1 1	7 81+1 28	9 35+1 87	8 40+1 16	0.76.0.86 n.s
	0+0 -	0.216+0.11 h	0.168±0.12 ab	0.055+0.02 ch	8.2.0.04
	0±0 a	0.316±0.11 D	0.168±0.12 ab	0.055±0.05 ab	8.2, 0.04
Organic PO4 (µg P g⁻¹ soil)	10.90±3.29 ab	2.50±0.65 a	12.74±3.54 b	9.62±3.95 ab	9.35, 0.025
Organic P (ppm)	16.58±3.98	9.92±1.33	18.8±7.26	16.2±1.97	3.06, 0.38, n.s.
Organic K (ppm)	379.14±60.63	244.04±20.63	346.475±42.12	263.62±36.81	5.46, 0.14, n.s.
Organic Zn (ppm)	10.20±1.17 ab	8.42±1.22 ab	11.65±1.15 a	6.4212±0.97 b	7.26, 0.06, n.s.
Organic Mn (ppm)	168.62±25.06 a	65.294±13.98 b	158.475±12.57 a	97.638±8.85 ab	13.72, 0.003
Organic Cu (ppm)	3.54±0.45	3.16±0.66	4.90±0.20	3.55±0.76	5.39, 0.14, n.s.
Organic Fe (ppm)	272.6±15.81	233.28±25.26	243.85±22.07	230.06±20.95	2.9, 0.41, n.s.
Mineral pH	4.69±0.08 ab	4.91±0.06 a	4.42±0.13 b	4.74±0.13 ab	8.24, 0.04
Mineral NH4 (µg N g⁻¹ soil)	1.83±0.13	2.214±0.35	1.61±0.14	1.93±0.38	2.3, 0.51, n.s.
Mineral NO3 (µg N g ⁻¹ soil)	0.010±0.01 a	0.297±0.08 b	0.167±0.04 ab	0.086±0.02 ab	10.75, 0.01
Mineral PO4 (µg P g⁻¹ soil)	0.624±0.1	0.378±0.03	0.742±0.23	0.558±0.18	3.47, 0.32, n.s.
Mineral P (ppm)	7.64±1.14 a	8.08±1.20 a	22.75±7.15 b	8.6±2.05 a	5.01, 0.17, n.s.
Mineral K (ppm)	117.2±14.53	118.15±10.79	108.12±11.43	111.49±7.23	0.6, 0.89, n.s.
Mineral Zn (ppm)	0.81±0.24	1.05±0.18	1.06±0.18	0.56±0.12	5.85, 0.12, n.s.
Mineral Mn (ppm)	21.97±3.7	10.73±2.24	21.06±2.37	11.30±1.94	9.69, 0.02*
Mineral Cu (ppm)	1.33±0.11	1.30±0.28	1.86±0.38	1.05±0.13	3.69, 0.3, n.s.
Mineral Fe (ppm)	235.08±34.32	222.66±20.55	317.85±45.66	197.44±22.10	5.78, 0.12, n.s.
Kruskal-Wallis (post-hoc multiple comparison (a=0.05))				

* = Kruskal-Wallis significant but multiple comparison (g=0.05))
* = Kruskal-Wallis significant but multiple comparison test showed no significant difference
n.s. = Not Significant
ab = Outcome of Kruskal-Wallis post-hoc test

Tale 4. Mean class values and Kruskal-Wallis coefficients for soil variables.

densities for both soil types did not differ among TSB classes, although there was quite a large difference in the organic soil ranging from 0.692 ± 0.08 g cm⁻³ in the red class to 0.354 ± 0.07 g cm⁻³ in the grey class (p = 0.06). Soil texture (data not shown) at the site was consistently a loam in the organic soil and sandy-loam to sandy-clay-loam in the mineral soil. Organic soil pH was the same throughout the chronosequence, ranging from 4.884 ± 0.06 to 4.515 ± 0.12 in red and grey respectively, however, a strong linear relationship with soil moisture existed (R² = -0.53, p = 0.02). Mineral pH did differ among classes (Table 4), becoming more acidic post-needle drop in the transition from the red class to the grey (4.91 ± 0.06 to 4.42 ± 0.13 , high and low respectively), and returning to higher levels in the black class.

Single point growing season soil assays for primary inorganic nutrients NH_4^+ , NO_3^- , and PO_4^{3-} revealed significant class differences for NO_3^- in both organic soil (Figure 14) and mineral soil (Figure 15), as well as for PO_4^{3-} in organic soil (Figure 16). Although very low levels of NO_3^- were present in the soil samples, both soil types showed significant increases between the control class and the red class (Table 4), before progressively dropping back to pre-infestation levels in the two older TSB classes. Some notable, albeit not significant, changes were an increase in NH_4^+ , observed between the red and grey classes in the organic soil (7.81 ± 1.28 to $9.35\pm1.87 \ \mu g \ N g \ dry \ soil^{-1}$) and a decrease in PO_4^{3-} ($10.90\pm3.29 \ to \ 2.50\pm0.65 \ \mu g \ P g \ dry \ soil^{-1}$) between the control class and the red class. Manganese (Mn) was the only ancillary plant nutrient showing a significant difference among classes. Both organic and mineral soil showed a large drop in Mn between the control and red classes ($168.62\pm25.06 \ to \ 65.294\pm13.98$ in the organic and $21.97\pm3.7 \ to \ 10.73\pm2.24$ in the mineral) before returning to higher levels in the two older classes (Table 4).

Organic Soil Single Point NO3

Figure 14. TSB class means for mid-growing season organic soil NO₃⁻ assay.



Mineral Soil Single Point NO3

Figure 15. TSB class means for mid-growing season mineral soil NO₃⁻ assay.



Organic Soil Single Point PO4

Figure 16. TSB class means for mid-growing season organic soil PO_4^{3-} assay.

The ion exchange resin captured a significant difference across the chronosequence in timeintegrated dissolved inorganic nitrogen (DIN) representing the entire growing season (F = 7.43, p < 0.01) (Figure 17). TSB classes varied from $3.99\pm0.72 \ \mu g \ N g \ resin^{-1}$ prior to needle drop, in the red class, to $11.07\pm1.9 \ \mu g \ N g \ resin^{-1}$ post-needle drop in the grey class. It was primarily NH₄⁺ driving the difference in DIN among classes, as it also represented a significant difference among them (Table 4). Nitrate showed the same pattern as NH₄⁺ across the chronosequence, and although there was no statistical difference found, the fluctuations of NO₃⁻, which mirrored those seen in NH₄⁺, bolstered the difference in DIN among the TSB classes. Time integrated PO₄³⁻ ranged from $21.52\pm8.78 \ \mu g \ g^{-1}$ resin in the control plots to $42.96\pm7.97 \ \mu g \ g^{-1}$ resin in the grey plots but was not significantly different among the classes. The pattern in PO₄³⁻ to some degree resembled that of N, increasing between red and grey classes. However, PO₄³⁻ values did not decrease between grey and black classes like was observed for both types of DIN. Instead, the quantity of growing season PO_4^{3-} reached in the grey class was maintained in the black class.



Time Integrated Dissolved Inorganic Nitrogen

Figure 17. TSB class means for growing season time-integrated dissolved inorganic N.

2011 Ring-width

After observing growth release in the focal trees we examined actual 2011 ring-width as a function of the levels of various tree resources that we sampled. Stepwise regression was used to generate general linear models (GLM) and ordinary least squares (OLS) multiple regression models. The independent variable that most effectively predicted 2011 ring-width was the ratio of remaining living BA (potential focal tree competition) to total BA (potential competition prior to beetle disturbance), which we designated Δ LBA (Table 5). We log transformed Δ LBA (Figure

18) providing a better fit for the exponential decay exhibited by the original function. This model explains 85% of the variation in actual ring-width at the site at FEF (Adj $R^2 = 0.85$, p < 0.0001):

$$\Delta LBA = BA_{Living}/BA_{Total}$$

$$R_{2011} = \Delta LBA$$

	Estimate	SE	t-value	p-value		
Intercept	3.915	0.199	19.64	<0.0001		
Log(ΔLBA)	-1.572	0.155	-10.12	<0.0001		
F-statistic: 102.4 on 1 and 17 DF, Adj. R²=0.85						

Table 5. Actual 2011 ring-width GLM regression coefficients.

Where R_{2011} is the actual 2011 ring-width and ΔLBA is the ratio of living BA to total BA within 5m of the focal tree.



2011 Ring Width as a Function of Log(ΔLBA)

Figure 18. 2011 actual ring-width as a function of the log of Δ LBA. The GLM shows the power of the ratio of remaining living BA to total BA within 5m of trees that survive beetle disturbance to predict the actual annual growth of surviving trees at the site.

DISCUSSION

This study demonstrates that as MPB-induced mortality rates approach or exceed 70% in a lodgepole pine dominated subalpine forest, surviving mature P. contorta trees experience a significant increase in annual growth (growth release). Within 3-7 years TSB, trees that have survived a stand level infestation can increase their annual incremental growth by up to 100%. After a period of 4-10 years, it is possible that some surviving trees will have tripled their annual incremental growth (200%), relative to their own mean annual ring width prior to stand infestation. This large increase in annual biomass production that occurs in surviving trees is generated by competitive release. Neighboring trees, that once constrained the resources available to focal trees, have been removed from competing in plot level resource allocation. As a corollary to increased growth rates, we show that various resources essential to tree growth also change as the forest stand progresses through TSB. Soil nutrients represent the majority of significant differences in resource availability across TSB classes found in this experiment, particularly between red and grey/black phases. Soil moisture and light transmission did represent patterns that increased with TSB, but neither was significant. The fact that no difference was identified in these multidimensional variables is likely a product of sample size, and more importantly, the presence of the aforementioned BA/elevation gradient.

The BA gradient that existed at the site, which may have influenced the progression of beetle infestation, posed some potential confounding interactions. We therefore controlled for stand BA gradient, after which the percent ring-width increase was related to infestation class (i.e. a positive correlating between percent increase and TSB) in the two most recent years (Figure 8, 2010 and 2011). The pre-beetle BA gradient may have delayed the timing of postbeetle response. The black and grey classes may have experienced a release from competition for

resources sooner than the red class, however it wasn't seen in growth release likely because of the higher initial BA values. More specifically, the BA gradient created conditions where dead BA and LAI' in both of the older classes was greater than total BA and LAI' in the red class. Despite the increase in availability for some soil resources in the older classes, standing dead trees probably continued to limit light access for focal trees. It is likely that only when needles, fine twigs and some larger branches in the canopy deteriorate enough to increase light exposure did focal trees in the older classes respond to the increase in soil resources. Drever and Lertzman (2001) showed that in young Douglas-fir (Psuedotsuga menziesii) trees, site quality (i.e. soil nutrients and moisture) had little effect on growth response in low light levels. This effect may be what is seen in the grey and black classes in Figure 8, where both classes show delayed growth release occurring for a number of years after the year of initial plot infestation. Using the method described by Klutsch et al. 2009, we estimated that neighboring trees in the black class experienced initial infestation in 2001-2002, but they show no noticeable increase in percent change until after 2004, and no significant increases were recorded until 2009. In contrast to this, we estimated initial infestation in the red class to have taken place only 4 years prior to 2011 and, contrary to the older classes, an almost immediate large increase in ring-width percent change occurred (Figure 8). We propose that the immediate growth response in the red class was because, in addition to a reduction in close proximity neighbors, the lower initial BA created an environment where light may not have been as much of a limiting factor, before or after neighboring tree mortality. The seemingly greater historic light access likely experienced in red class plots is suggested by the ring record; the red class exhibits the largest actual annual ringwidths before and after infestation and studies have shown this to be a result of low BA

(McDowell et al., 2007). This initial BA environment may have allowed the red class to exploit the increased availability of other resources as a result of infestation.

The control TSB class exhibits a minor increase in ring-width percent change beginning in 2006. This led us to consider that the increase in the control and the other classes might also be influenced by climate variation. For example, our subalpine site is a snow driven system (Elder et al., 2006); anomalies in annual snowfall (i.e. snowfall far above average), generally give rise to greater snow water equivalent (SWE) and groundwater recharge, extending moisture availability further into the growing season, potentially producing favorable conditions which could lead to larger ring-widths. However, we found no correlation between ring-width and SWE (Figure 19). Annual snowfall was relatively consistent from 2005 to 2011 during the major period of release seen in the focal trees. In fact, 2010 was actually the lowest SWE year since 2004, and 2011 was lower than 2007, 2008, and 2009.

It is reasonable to assume that moisture was affected by the BA gradient. Other studies have shown increased soil moisture (Griffin et al., 2011) and water yield (Potts, 1984; Pugh and Gordon, 2012) from decreased transpiration (Knight et al., 1991). Although we expected to see differences corresponding to TSB class, no significant difference in either organic or mineral soil moisture was found across classes. The pattern seen in the organic soil moisture (i.e. the driest organic soil moisture in the red class) may be the result of greater direct insolation higher on the slope with lower BA and reduced canopy cover. In the absence of a BA gradient we might expect to see changes in organic soil moisture that coincide with TSB, and are the product of changes in canopy density/LAI' (Pugh and Small, 2011), litter layer (Griffin et al., 2011), and



Ring–Width as a Function of Max SWE for 10 Years

Figure 19. Class mean ring-widths for each year for the ten years since initial infestation showing no correlation with snow water equivalent.

perhaps vegetation ground cover. Despite this, organic soil moisture would not generally be indicative of changes to tree accessible soil moisture, as the organic soil layer at the site was extremely shallow. Mineral soil moisture would probably be more representative of changes to soil moisture due to reduced uptake and transpiration by canopy trees (Knight et al., 1991). Greater total BA (and stand density) in the older classes located lower on the slope inherently led to higher *remaining* living BA in the post disturbance environment. Although living BA in these plots was less than the control group, values were still greater than plots higher on the slope (red). The slightly higher remaining living BA in the older classes likely affected the mineral soil moisture values by maintaining higher local transpiration. This is supported by the ψ_p found in each class (Figure 11). Leaf pre-dawn water potential is generally considered to represent soil water potential (Richie and Hinckley, 1975) providing a good proxy for plant available soil moisture, which can be reduced by drought and/or competition. Although gravimetric mineral soil moisture showed an anecdotal increase with TSB class, only the red class showed significantly less negative ψ_p than the control indicating that the somewhat higher remaining living BA in the older classes might be affecting water relations for the focal tree.

Although the BA gradient affected plot canopy density and most likely soil moisture, it is unlikely that the general pattern in soil ions was greatly influenced. The chronosequence shows very similar increases in soil N and P to previous studies (Moorhouse et al., 2008; Griffin et al., 2011; Edburg et al., 2012) conducted in similar forest systems experiencing bark beetle disturbance. The significant increase in time-integrated growing season DIN, and the noticeable increase in PO₄³⁻ that occurred between the red and grey classes (pre- and post- needle drop) can be attributed to two phenomena which represent relative changes, and are not *directly* effected by discrepancies in local BA: 1) Tree uptake of soil nutrients at the stand scale is drastically decreased with large-scale mortality. A decrease in overall demand from the stand increases potential inorganic nutrient totals in the soil. 2) Needles and fine twigs that fall to the ground after MPB induced mortality, and fine roots all increase the substrate available for decomposition and mineralization. The reduction in uptake and eventual augmentation of the soil described in the two processes above affect the timing and content of inorganic nutrients in the soil in different ways. The significant spike in single point organic and mineral NO₃⁻ seen immediately in the red class (figures 14 and 15) is likely the result of reduced uptake. The red class represents the point during beetle infestation when a majority of the stand no longer demands soil resources suggesting why we see the spike in NO_3^- . The high levels of available single point N due to

reduced uptake tapers off in the older classes probably as a result of the significant increase in understory that both we and the literature describe (Stone and Wolfe, 1996), the increasing role of saplings and the mid-canopy (Yang, 1998), and perhaps efficiency adjustments made by the focal trees. On the contrary, we see a different pattern when looking at entire growing season inorganic nutrients like DIN. The significantly higher cumulative N found in older classes is probably due to the increase in substrate available for decomposition (Griffin et al., 2011). Although a single point measurement during the growing season may indicate higher N in the red class relative to the control because of the reduced uptake, cumulative N is higher in the older classes because needles and fine roots are decomposing over the course of the growing season, generating continuous inorganic N inputs (Pearson et al., 1987; Clow et al., 2011). Furthermore, trees attacked by bark beetle show reduced or no resorption of nutrients prior to abscission (Moorhouse et al., 2008). This potentially provides higher levels of mineralizable organic compounds in the litter that does fall. Although previous research (Schimel and Bennet, 2004) has shown that an increase in soil inorganic N does not necessarily reflect greater mineralization rates, Tranhan (dissertation, 2012) showed a strong correlation between soil NH4⁺ and soil moisture and temperature at our exact site, which suggests the potential for increased mineralization rates.

In line with the discussion on substrate, we did not see significant differences in litter layer across the chronosequence, however, we did observe slightly larger amounts of litter as TSB progressed and many studies support a significant increase between pre- and post-needle drop (Klutsch et al., 2009; Collins et al., 2011; Pugh and Small, 2011; Teste et al., 2011; Griffin et al. 2011; Bigler and Veblen 2011).

Within a few years of stand infestation, large changes to nutrient (more specifically N) cycling are occurring as a result of beetle disturbance. With reduced uptake and increased substrate in the soil it would be reasonable to assume that greater nutrient export rates in forest stands and watersheds would occur, resulting in increased N content in streams. However, this has not been found to be the case in other studies. Clow et al. (2011) demonstrated that streams in beetle-infested watersheds did not show any increase in N levels, attributing their findings to uptake by understory growth and maturing saplings, among other things, but not mature tree growth release. Lodgepole pine dominated subalpine forests, specifically those hosting a biologic disturbance, appear to show very tight cycling of N; increased inputs to the soil are rapidly used by remaining individuals before N has a chance to leach out of the system (Vitousek and Melillo, 1979). We found support for this in the needle C:N of the focal trees. Focal trees that experienced greater growing season soil N (i.e. trees in a post-needle drop environment) showed significantly lower C:N ratios (Figure 9) than those that had low growing season N. This also appears to substantiate that the increase in substrate, and subsequent potential for decomposition and mineralization may hold more influence over changes to the local N-cycle than reduction in uptake.

CONCLUSION

No one resource could be specifically identified as having the greatest impact on growth release in the focal trees. Although light seems to be a limiting factor, moderating when focal trees are able to exploit enhanced soil resource pools, it cannot be pointed to as the single factor controlling growth release. Instead, we found that the ratio of living BA to total BA, a proxy that includes light and is also representative of soil resource status in terms of remaining potential

competition, was the best predictor of actual annual ring-width in the focal trees. This one variable was able to significantly explain well over three quarters of the annual ring-width variation.

Understanding this relationship should aid in improving applied forestry practices as well as having potential implications for forecasting and modeling future forest dynamics. Lodgepole pine is an important timber species in western North America. Studies have shown that lodgepole pine responds well to thinning at an early age (Cole, 1975), but that mature stands show little to no increase following thinning, actually producing a negative net volume (Hatch, 1967) due to the removal of mature tree biomass. However, the rules of structured thinning treatments do not apply to the anatomy and magnitude of MPB disturbance. Inadvertent largescale timber loss in commercial stands of mature lodgepole pine *produced by high levels of MPB infestation* will generate increased productivity in surviving trees over a relatively short period of time, potentially offsetting much of the net loss. If this knowledge is considered in long-term planning for commercial timber stands affected by MPB then better mitigation of economic losses might be achieved in the long-term.

Additionally, forest carbon (C) sinks are becoming increasingly important as atmospheric levels of CO_2 are increasing. Forests are the greatest component of the terrestrial land sink and have been shown to absorb about one third of anthropogenic sources of CO_2 (Manning and Keeling, 2006). In western North America mountain forests are the largest C sink, nearing 2/5 of the total uptake in the contiguous US (Schimel and Braswell, 2005). As the MPB epidemic has rapidly changed the role of western subalpine forests in the C balance, some models, like that of Kurz et al. (2008), have estimated that these forests will transition from a small C sink to a large C source spanning more than two decades. We found that in most cases infested trees remained

standing for a minimum of 10 years and the literature reports greater than 20 years (Bigler et al., 2007; Bigler and Veblen, 2011). Thus, limiting the substrate for decomposition and subsequent release of C to the atmosphere through microbial respiration. At the same time we show surviving trees increase their growth by up to 200%, often in less than 10 years. In doing so they may be sequestering more C than they did previously. Although some more recent models (Pfeifer et al., 2011) do account for the increase in aboveground C stocks in surviving trees, we feel that including high-resolution empirical measurements of mature tree growth release at a stand level can only improve carbon models post biologic disturbance. Furthermore, models that predict C dynamics and regeneration at much larger scales may benefit from using the simple and relatively accessible predictor of annual ring-width (LBA:TBA) that we have introduced. Remote sensing can easily determine this ratio with pre- and post- infestation infrared imaging. Of course more empirical measurements are needed across many geographic areas before this ratio can be broadly applied, but it may be a start to better resolving the C future of forests affected by beetle disturbance.

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