



Mountain pine beetle attack faster growing lodgepole pine at low elevations in western Montana, USA



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ABSTRACT

Global change has impacted forests through altered disturbance regimes. In the western US, climate change has resulted in extensive and severe mountain pine beetle outbreaks. These outbreaks have the potential to impact forest function through the selection of certain phenotypes. We investigated the potential for bark beetle-induced selection by way of measuring growth and climate response in mountain pine beetle-killed and surviving lodgepole pine in the Northern Rockies. We had three objectives: (1) investigate differences in growth between beetle-killed and surviving lodgepole pine prior to a recent outbreak, (2) compare the climate-growth relationships for beetle-killed and surviving lodgepole pine and how those relationships explain observed growth differences and predict mortality risk, and (3) investigate growth differences and growth-climate relationships across north- and south-facing aspects and over an elevation range representing local climate gradients. Significantly higher growth rates were observed in beetle-killed trees at low-elevation sites, but not at mid or high elevations. While aspect influenced overall growth, it did not have a significant influence on the difference in growth between beetle-killed and surviving trees. Growth showed significant relationships with several climate variables (i.e., previous-year August temperatures, October temperatures, annual precipitation, and summertime climatic water deficit), with slight differences in those relationships between beetle-killed and surviving trees. Mixed effects models demonstrated that higher growth rates and age increased the probability of mortality during the outbreak at all elevations, and also that climatic water deficit and previous-year August maximum temperatures were related to the magnitude of growth differences between beetle-killed and surviving trees. Overall, mountain pine beetles tended to attack large, fast-growing, lodgepole trees, especially at lower elevations where trees may be more susceptible to seasonal water stress.

1. Introduction

Forests are globally important due to the ecosystem services they provide (Trumbore et al., 2015). Recently, widespread mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks have occurred in the western United States and Canada, resulting in mass mortality across large areas of forest (Meddens et al., 2012). These outbreaks are driven in part by changes in regional climate, where temperatures have increased and precipitation patterns have shifted (IPCC, 2014). Warmer and drier conditions stress host trees and provide a longer period of temperatures suitable to beetles (Dale et al., 2001; Raffa et al., 2008; Bentz et al., 2010). Thus, beetles are both more capable of reproducing rapidly and can more easily overwhelm tree defenses (Mitton and Ferrenberg, 2012). As water stress is predicted to increase in many ecosystems in the western US (Seager et al., 2007; IPCC, 2014), the need to more fully understand the relationship between host trees, bark beetles, and climate is significant. Specifically, it is important to

understand how host trees interact with climate and to determine the impact of those interactions on host tree susceptibility to beetle attack.

Mountain pine beetles are a native, 'irruptive,' insect in western North America. Beetles attack trees by burrowing through the tree's bark and into the phloem. Successful attacks occur when sufficient numbers of beetles are recruited to attack the tree via the release of pheromones by the initial attackers (Raffa, 1988). These mass attacks succeed by overwhelming tree defenses, and result in mortality of the host tree. Beetles also introduce blue-stain fungus to trees during attacks, which helps to kill trees by blocking the xylem with fungal spores. Tree defenses include producing resins to physically expel beetles and producing defensive compounds, processes that require a substantial investment of resources (Raffa and Berryman, 1983). Trees become more susceptible to successful attack when climate conditions are stressful because their resources are already limited (Waring and Pitman, 1983). Additionally, climate conditions that are stressful to host trees are typically beneficial to the beetles, with warmer

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temperatures allowing some species to grow and mature faster (Bentz et al., 2010). While mountain pine beetles attack several species, their most common host is lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Raffa, 1988).

Numerous climatological variables have been linked to bark beetle outbreaks, including vapor pressure deficit (VPD) (Littell et al., 2010; Hart et al., 2014), climatic water deficit (CWD) (Millar et al., 2012), high previous-year summer and fall temperatures (Berg et al., 2006; Chapman et al., 2012), and multi-decadal oscillations such as the Atlantic Decadal Oscillation (Hart et al., 2014). Similar climate variables have been found to limit the growth of lodgepole pine (Chhin et al., 2008; Lo et al., 2010), reinforcing the link between climate and host tree resource limitation. All of these climate conditions decrease the availability of water to the host tree, inhibiting both its ability to grow and its ability to produce resin with which to pitch out attacking beetles (Kane and Kolb, 2010).

Mountain pine beetle outbreaks have the potential to influence the characteristics of host stands through beetle preference for certain host tree characteristics, as well as through differential success of beetle attacks based on tree traits. Resistance to mountain pine beetles may vary among stands and individuals due to environmental or genetic variation (Raffa and Berryman, 1983; Alberto et al., 2013), such that in the right outbreak conditions, trees with lower resistance may be killed more readily than trees with naturally higher resistance (Ferrenberg et al., 2014). During severe outbreaks, it is therefore possible that the phenotypic traits of host stands may shift due to extensive mortality within one resistance group (de la Mata et al., 2017).

The results of previous studies on selection for certain phenotypes, both in lodgepole pine and other pine species, are highly variable. High levels of mortality in ponderosa pine were found to primarily affect slower-growing individuals, leading towards selection for faster-growing trees (Knapp et al., 2013). Similarly, Millar et al. (2012) found evidence for selection towards faster-growing whitebark pine in the eastern Sierra Nevada, CA due to higher mortality among slower-growing individuals from mountain pine beetle. However, a separate study on ponderosa pine found that a greater number of individuals from fast-growing families were killed during an intense bark beetle outbreak, resulting in selection towards slower growth in the population (de la Mata et al., 2017). Results from a study in British Columbia, Canada on lodgepole pine also found that faster-growing families within populations were more susceptible to mountain pine beetle attack (Yanchuk et al., 2008). In an Aleppo pine (*Pinus halepensis* Mill.) plantation in Spain, high bark beetle mortality was observed in both fast- and slow-growing individuals. However, individuals that were more responsive to annual climate variations were less likely to have been killed (Sanguesa-Barreda et al., 2015). The ages of the stands in these studies differed substantially, with the Knapp et al. (2013) and Millar et al. (2012) studies focusing on relatively old (> 150 years) stands, and the de la Mata et al. (2017), Yanchuk et al. (2008), and Sanguesa-Barreda et al. (2015) studies focusing on a younger (< 50 years) stands. These studies suggest high variability in the impacts of bark beetles on pine stands, potentially due to variations in local climate, host species, stand age, and topographic variables. Studies have consistently found that water deficit plays a role in regulating annual tree growth and pine susceptibility to attack, and that climate-related growth differences may exist between trees that succumbed to pine beetles and trees that survived outbreaks. Further research is therefore necessary to illuminate the relationship between climate (e.g., water deficit) impacts on growth and how that relationship translates into mountain pine beetle susceptibility.

Differences in growth between beetle-killed and surviving trees may suggest a difference in the allocation of resources (Ruel and Whitham, 2002; Bigler and Veblen, 2009). Trees may differ in the amount of carbon allocated towards growth versus defensive compounds (Hermes and Mattson, 1992), or carbon compounds used for growth and maintenance when drought limits photosynthetic activity. Trees that are

affected more by drought may also have a higher chance of successful beetle attack (Hanks et al., 1999). If an outbreak occurs with sufficient severity, this could push the local host tree population towards having lower growth, but higher defenses. However, this has not been demonstrated consistently (Lahr and Krokene, 2013; Hood and Sala, 2015), suggesting that differences in growth may instead be explained by environmental context. Trees growing in more or less favorable environments may naturally react differently to climate stress, resulting in differential mortality during bark beetle outbreaks. While the trees may appear phenotypically different when examining growth and growth-climate responses, they may not have any natural differences in allocation strategies. In this scenario, trees with higher growth might also have greater natural resistance to pine beetles (Mitchell et al., 1983) due to greater access to resources (Christiansen et al., 1987).

For this study, we had three objectives: (1) investigate differences in growth between beetle-killed and surviving lodgepole pine prior to a recent outbreak, (2) determine and compare the climate-growth relationships for beetle-killed and surviving lodgepole pine and how those relationships explain observed growth differences and predict mortality risk, and (3) investigate growth differences and growth-climate relationships across north- and south-facing aspects and over an elevation range representing a local gradient in climate stress.

2. Methods

2.1. Study area

Our study sites occur within the Boulder Mountains of the Beaverhead-Deerlodge National Forest (Fig. 1), where elevation ranges from ~1400 m to ~3100 m. The area experienced a severe mountain pine beetle outbreak in the mid-2000s. Primary tree species in the area are lodgepole pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt), and whitebark pine (*Pinus albicaulis* Engelm.). Douglas-fir and lodgepole pine are dominant species at low to mid elevations, and whitebark pine, subalpine fir, and lodgepole pine are dominant species at higher elevations. According to the nearest climate station, located ~34 km away in Boulder, MT, January was the coldest month between 1949 and 2015, with an average temperature of -12.4°C . July was the warmest month with an average temperature of 28.2°C [<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?mt1008>]. Within this period, annual precipitation averaged 279 mm, with most precipitation falling in June. The actual study site temperature and precipitation are likely slightly colder and wetter, as Boulder, MT is located just outside the forested area at a lower elevation (1521 m).

2.2. Plot selection and design

Twelve plots were selected for the study from the Thunderbolt Creek and Boulder River drainages. The plots span both north and south aspects, and three elevational bands across a 600 m gradient. Potential plot locations were selected based on apparent lodgepole pine dominance, significant mortality due to mountain pine beetle, and stand access (Montana Natural Heritage Program, 2017; USDA Forest Service, 2000–2014). Actual plots were selected upon visiting the sites, with selection determined by (1) dominance of lodgepole pine in the canopy, (2) substantial mountain pine beetle-caused mortality in the stand (> 40%), and (3) survival of at least 10 trees in the plot and immediate vicinity. In order to capture more of the variability in stand dynamics, two plots were chosen within each aspect-elevation combination (e.g., south – low #1 = SL1, south – mid #2 = SM2, etc.). Plots were required to be a minimum of 100 m from one another so as to limit spatial autocorrelation.

Ten beetle-killed trees were selected within a 10 m radius circular plot, and two increment cores were taken at 1.37 m height on opposite sides of the tree, perpendicular to the slope. Beetle-killed trees were randomly

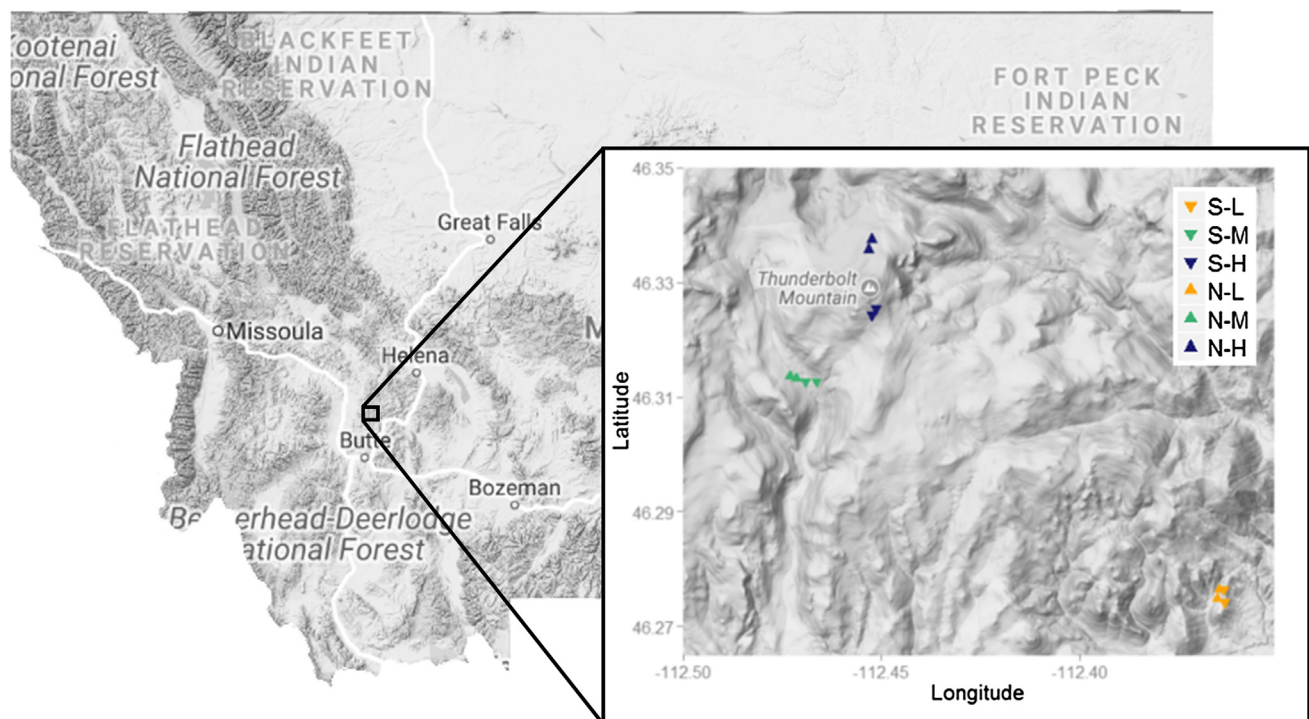


Fig. 1. Study location in Montana, USA. Low-elevation plots (-L) are in yellow, mid-elevation plots (-M) are in green, and high-elevation plots (-H) are in blue. South (S-) and North (N-) aspects are designated by the direction of the arrow symbol.

Table 1

Characteristics of chosen study sites. Plot names are determined by aspect (North/South), elevation (Low/Mid/High), and plot number within the aspect-elevation combination. *n* indicates number of trees sampled. If surviving *n* is higher than the surviving trees within the plot, additional surviving trees were sampled within 1 m of the plot boundary. The surviving trees within plot column indicates the total number of surviving trees > 5in DBH in the plot, not just those sampled. Median age represents the age of the trees in 2005, when the outbreak began. The median BAI values were calculated for 1950–2005 with units of mm²/year. Plot density and percent mortality at each plot were measured in September 2017. All other plot variables were measured in July 2016. Median mortality year was rounded to the nearest year. PICO indicates measurements of lodgepole pine (*Pinus contorta*).

Plot	Surviving <i>n</i>	Beetle-kill <i>n</i>	Surviving median age	Beetle-kill median age	Median BAI (S)	Median BAI (BK)	Elevation (m)	Aspect (°)	Slope (°)	PICO Plot density (trees/m ²)	Total plot density (trees/m ²)	% PICO mortality	Median mortality year	Surviving trees within plot
SL1	9	10	108	107	145.3	235.4	1873	160	20	0.11	0.12	62	2008	13
SL2	11	13	100	101	136.0	198.0	1859	116	18	0.11	0.13	73	2007	9
NL1	11	12	94	96	214.7	336.4	1861	270	18	0.10	0.11	74	2007	8
NL2	9	9	120	110	137.7	246.6	1854	302	14	0.10	0.13	69	2006	10
SM1	10	10	115	140	226.7	186.2	2132	184	15	0.11	0.12	49	2007	18
SM2	10	10	114	120	285.6	379.1	2152	184	20	0.06	0.06	63	2006	7
NM1	10	8	124	163	139.0	169.4	2152	58	20	0.13	0.14	71	2007	12
NM2	10	11	124	124	129.6	151.0	2173	38	12	0.14	0.15	74	2008	11
SH1	10	10	100	126	205.4	283.5	2505	138	14	0.12	0.13	82	2007	7
SH2	10	10	131	138	189.1	209.8	2481	182	24	0.08	0.09	68	2007	8
NH1	10	11	212	225	154.9	168.3	2504	328	12	0.12	0.12	56	2008	17
NH2	10	10	208	215	160.3	171.8	2482	328	6	0.13	0.15	86	2008	6

selected across the plot to obtain an even distribution of samples. Ten surviving trees of similar diameter to the beetle-killed trees were selected and cored within the plot. If ten surviving trees were not found within the plot, additional surviving trees close to the boundary of the plot (i.e., within 1 m) were used. Non-random sampling of surviving trees was used in order to minimize the difference in ages between surviving and beetle-killed trees. Six of the plots did not have sufficient surviving trees within the plot radius, necessitating that trees outside the plot be sampled (Table 1). No plots required more than 40% of surviving trees to be sampled outside the plot radius. A total of 482 tree cores were collected for the study. Of the 482 tree cores collected, 444 were included in the analysis. Thirty-eight cores were discarded from the analysis due to poor correlations with the master chronologies (see Section 2.4). Additionally, age, DBH, and the coefficient of variation for annual growth within trees were assessed in order to provide context for other results.

2.3. Climate data

Climate data were obtained from the Boulder, MT climate station [<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?mt1008>]. Monthly maximum temperature, minimum temperature, and precipitation were prepared for the analysis. Vapor pressure deficit (VPD) was calculated from climate station data (Buck et al., 1981), using the equations

$$e_s = 0.6108e^{\frac{17.27T}{237.3+T}}$$

$$VPD = \frac{100-RH}{100}e_s$$

where e_s is saturated vapor pressure, T is temperature in degrees Celsius, and RH is relative humidity as measured at the climate station. Hydrologic year (annual) precipitation was calculated from the

monthly data, and previous-year values of all variables were determined. RH data came from the Helena, MT climate station [<https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?mthele>] because the Boulder station did not record the variable. Monthly climatic water deficit (CWD) (Dobrowski et al., 2013) was also included in the analysis as a variable representative of drought, and because it has been demonstrated to have significant relationships with growth in other study locations (Millar et al., 2012). All data preparation was completed in R (R Core Team, 2013).

2.4. Tree core preparation

Increment cores were prepared according to standard dendrochronological techniques (Stokes and Smiley, 1968). Master chronologies for each aspect-elevation combination were created using approximately ten cores from surviving trees at each location. Cores were cross-dated, then scanned at 2400 dpi. Annual ring widths were measured using CooRecorder 7.8 (Cybis Elektronik, 2014), and final chronologies quantitatively validated in COFECHA (Holmes, 1983).

Basal area increment (BAI), a measure of growth, was calculated using ring widths and estimated distance to pith with the *dplR* package (Bunn et al., 2015) in R. Distance to pith was estimated based on growth and curvature of the earliest observed rings if the pith was not present in the core (Larsson, 2014). Converting annual ring widths to BAI overcomes the decrease in ring width that occurs as a function of increasing tree size (Biondi and Qeadan, 2008).

2.5. Statistical analyses

2.5.1. Climate correlations

In order to determine which climate variables to include in models of mortality risk and growth differences, correlations between BAI and climate variables were tested using Pearson correlations. Correlations were considered significant if p -values were ≤ 0.05 . Climate variables were tested for correlations with zero (current-year) and one year (previous-year) lag times.

2.5.2. Mortality models

A binomial mixed effects model was used to model mortality risk as a function of elevation, aspect, tree age, mean 1950–2005 BAI, and growth resistance to extreme values of correlated climate variables. Stress resistance was calculated for each tree as the BAI during stressful years relative to the BAI during ‘normal’ years. Stressful years were determined as years in which the value of the variable exceeded the 75th percentile of its distribution over the 1950–2005 period. All years in which the variable did not exceed the 75th percentile were designated as ‘normal.’ None of the variables included in the binomial mortality model showed signs of collinearity. Models were fit according to protocols in Zuur et al. (2009). Both plot and tree were considered as random effects in the model.

2.5.3. BAI-climate models

General linear mixed effects models (GLMMs) were used to model BAI as a function of climate variables, mortality, and tree age (Fernández-de-Uña et al., 2016). Climate variables shown to be significant in the BAI-climate correlation analysis were considered for the models. Potential climate variables were checked for collinearity and the variable deemed most ecologically important was chosen if two variables were collinear. Variables were considered sufficiently independent with variance inflation factors less than 10.

One model was created for each aspect-elevation combination in order to determine the growth controls at each site, and whether pre-outbreak growth differed significantly between beetle-killed and surviving trees. Both plot and tree were considered as random effects in each model, and autocorrelation was modeled between years. Residual heterogeneity was allowed to vary by plot for the mid- and high-

elevation models. Residual heterogeneity did not vary significantly between plots at low elevations and was not included in those models.

2.5.4. Growth difference models

Plot-level differences in BAI between beetle-killed and surviving trees were also modeled using GLMMs. These models predicted BAI differences as a function of aspect, elevation, and climate variables. Plot was considered as a random effect. Residual heterogeneity was allowed to vary by plot and autocorrelation was again modeled between years.

3. Results

3.1. Site characteristics

All plots showed high levels of mortality ranging from 49 to 86% (Table 1), with most mortality occurring between 2006 and 2008. Stands were similar in density, with no discernable pattern across elevations and aspects, although the diameter and age of trees did increase with elevation (Table 1; Figs. A.2 and A.5). While it was possible to locate stands spaced evenly along the elevation gradient, the exact aspect of stands varied slightly from north-south alignment.

3.2. Climate correlations

Correlations between BAI and maximum temperature, minimum temperature, precipitation, and VPD were significant ($p \leq 0.05$) for several months, with similar correlation patterns between aspects (Table A.1). Beetle-killed trees generally showed slightly stronger correlations with climate variables, and while the coefficient of variation for BAI was slightly lower over the study period in beetle-killed trees relative to surviving trees, this was not related to climate variation (Fig. A.3) nor significant across plots. In general, late-summer maximum temperatures and VPD of the previous growing season were negatively related to growth across elevations and aspects, with only a few exceptions. Additionally, current-year October temperatures and VPD were generally positively related to growth across high-, and sometimes mid-elevation sites. Annual precipitation was positively correlated with BAI at both aspects of low elevations for both beetle-killed and surviving trees. Summertime CWD was correlated with BAI at low-elevation sites across both aspects for both beetle-killed and surviving trees.

3.3. Mortality model

Mortality risk was explained by both mean 1950–2005 BAI and tree age (Table 2). Growth rate was the most significant predictor of mortality ($p < 0.001$) followed by age. Resistance to instances of high previous-year August temperatures and high CWD were both tested as potential variables due to their high and consistent correlations with BAI, but neither were found to be significant predictors in the model. The differences in growth rate found in the model were also clearly seen when comparing overall BAI time series for each elevation-aspect

Table 2

Results of the binomial mixed effects model predicting mortality risk. Coefficient β is the coefficient of the predictor variable, $SE(\beta)$ is the standard error of that coefficient, z is the z -score of the coefficient, and p is the p -value of the coefficient. The χ^2 metrics show the significance of each predictor variable by way of comparing the model with and without the variable. Measures of model fit are reported for scaled values of the predictor variables in order to provide more context for their relative influence on mortality risk.

Predictor	Coef. β	$SE(\beta)$	z	p	χ^2	df	p_{χ^2}
Intercept	−0.04	0.14	−0.25	0.8			
Growth rate (1950–2005)	−0.54	0.15	−3.48	< 0.001	13.4	1	< 0.001
Age in 2005	−0.29	0.14	−2.03	0.04	4.2	1	0.04

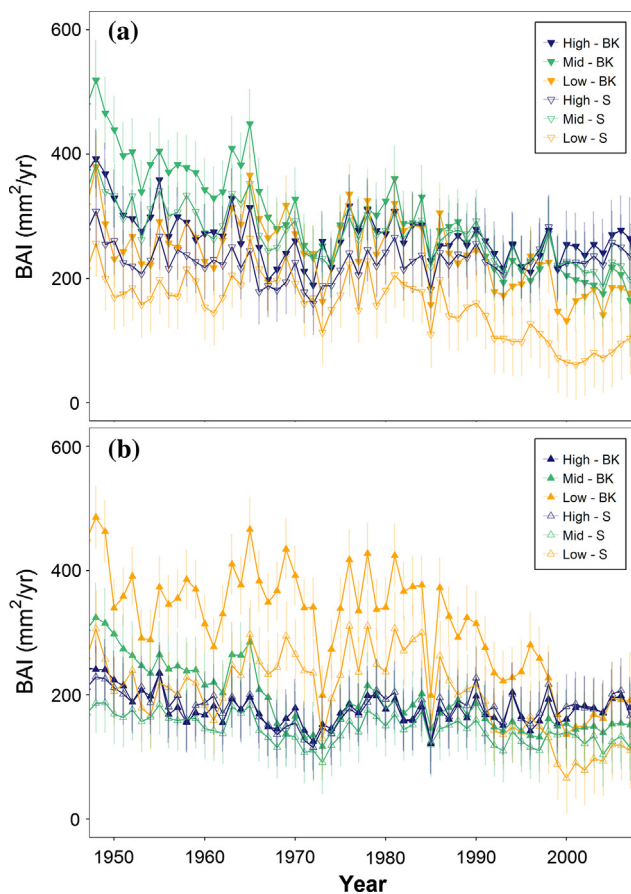


Fig. 2. Basal area increment (i.e., BAI) over time on (a) south-facing, and (b) north-facing slopes. Open symbols represent mean annual BAI values of surviving trees and filled symbols represent mean annual BAI values of beetle-killed trees.

combination (Fig. 2), especially at low-elevation sites. The final model did not include either elevation or aspect as being important for overall mortality risk.

3.4. BAI-climate models

The fixed effects components of the GLMMs demonstrated that climate influences on growth at each site differed across elevations, and also differed slightly by aspect (Table 3, Fig. A.6). Notably, mortality was only a factor in determining growth at low elevations and tree age was not important in any of the models. Low-elevation models showed significantly higher pre-outbreak growth rates in beetle-killed trees than surviving trees. All elevations and aspects showed previous-year August maximum temperatures to be important for growth. October maximum temperatures negatively impacted growth for low-elevation sites and south-facing sites across elevations. Annual precipitation positively influenced growth at low elevations and the north-facing mid-elevation sites. CWD had a negative impact on growth at high-elevation sites and at south-facing mid-elevation sites.

3.5. Growth difference model

Differences between beetle-killed and surviving tree BAI were explained by CWD, previous-year August maximum temperature, and elevation (Table 3, Fig. A.7). The model results found that beetle-killed trees were typically faster growing than surviving trees, with elevation strongly determining the value of that difference. Low-elevation sites had significantly larger growth differences than mid and high sites,

whereas the mid and high site growth difference results were indistinguishable from one another and were not significantly different from 0. The overall difference between beetle-killed and surviving tree BAI decreased with increasing CWD as well as with increasing previous-year August maximum temperature. However, the sites with the largest growth differences also coincided with the highest CWD and August temperature values (Reed et al., 2018).

4. Discussion

4.1. Growth differences across elevations and aspects

We found that beetle-killed trees grew consistently faster than surviving trees in the half century prior to a severe mountain pine beetle outbreak at low-elevation sites, while there were no significant differences in growth rate at the mid- and high-elevation sites. This finding is consistent with results from some studies on lodgepole, ponderosa, and limber pine from similar locales (Yanchuk et al., 2008; de la Mata et al., 2017), but contrasts with others (Millar et al., 2012; Knapp et al., 2013; Ferrenberg et al., 2014). Our results provide further evidence that observed differences in growth between beetle-killed and surviving trees vary substantially across host species and climate regions, as well as with stand age and along gradients of bark beetle population densities. Additionally, we found evidence that growth differences vary by elevation, which may explain some of the variation seen in results from previous studies.

There are a number of possibilities as to why we observed faster growth in beetle killed trees. Beetle outbreak pressure may have a strong influence on host selection, with particularly large epidemics having the ability to override the defenses of host trees, regardless of their relative resistance to attack (Boone et al., 2011). As beetle populations increase in density, host trees that are naturally more resistant (i.e., larger or faster growing) (Christiansen et al., 1987) to beetle invasion may become more susceptible than less resistant trees because they provide more resources to beetles (Boone et al., 2011). Similarly, trees with thicker phloem also tend to have higher growth rates (Shrimpton and Thomson, 1985). As trees with thicker phloem can support more beetles (Amman and Baker, 1972; Safranyik and Carroll, 2006), it follows that the faster-growing trees are more likely to be attacked during a severe outbreak. The high stand mortality rates seen in this study (\bar{x} = 70%) may therefore explain the observed patterns of growth differences (Boone et al., 2011).

Growth differences between surviving and beetle-killed trees appear to diminish with increasing elevation, with significant differences only observed at low-elevation, more water-limited sites. Growth at low elevations was indeed positively correlated with precipitation (Table 3; Table A.1), demonstrating some control of moisture on growth. This implies that there may be some difference in resource allocation strategy between mortality groups, which is shown best when trees are under high water stress and competing for very limited resources. Specifically, trees that are fast-growing might allocate fewer carbon resources to defenses and therefore suffer more in water-limited conditions, resulting in higher susceptibility to beetle-related mortality. However, stress due to water limitation does not prove that there were differences in allocation strategy between mortality groups. At dry, low-elevation sites, the larger, faster-growing, trees may have simply been more water-stressed than the smaller trees within the plot due to higher water requirements, resulting in their defenses being more easily overcome by the beetles than equivalent trees at higher elevations. Additionally, while climate was related to the magnitude of growth differences at low-elevation sites, resistance to high CWD and late summer temperatures was not a significant predictor of mortality risk in our models as would be expected if trees occupied sites with substantially different microclimates.

While growth differences between beetle-killed and surviving trees changed along an elevational gradient, there were no significant

Table 3

Model results for BAI-climate relationships and BAI difference-climate relationships. Coefficient β is the coefficient of the predictor variable, $SE(\beta)$ is the standard error of that coefficient, z is the z-score of the coefficient, and p is the p-value of the coefficient. The AIC metrics show the AIC of the final model (AIC_{final}) relative to that of a model without a variable (AIC_{drop}). p_L is the p-value for the likelihood that the models are different from one another.

Model	Predictor	Coef. β	$SE(\beta)$	t	p	AIC_{final}	df_{final}	AIC_{drop}	df_{drop}	p_L
South Low BAI	Intercept	14.74	0.63	23.51	< 0.001	8168.9	9	8176.2	8	0.002
	Mortality (S)	−3.02	0.92	−3.26	0.003					
	Previous-year August Tmax	−0.14	0.01	−9.62	< 0.001					
	October Tmax	−0.05	0.01	−3.58	< 0.001					
	Annual Prcp	0.007	0	14.3	< 0.001					
North Low BAI	Intercept	16.76	1.19	14.11	< 0.001	8943.3	9	8949.7	8	0.004
	Mortality (S)	−3.23	1.05	−3.08	0.004					
	Previous-year August Tmax	−0.14	0.02	−7.97	< 0.001					
	October Tmax	−0.05	0.02	−3.22	0.001					
	Annual Prcp	0.007	0	12.1	< 0.001					
South Mid BAI	Intercept	16.44	1.52	10.82	< 0.001	7879.2	8	8066.5	7	< 0.001
	Previous-year August Tmax	−0.18	0.01	−14.14	< 0.001					
	CWD	−0.002	0	−5.41	< 0.001					
	October Tmax	−0.07	0.01	−5.74	< 0.001					
North Mid BAI	Intercept	12.3	0.45	27.34	< 0.001	7066.9	7	7215.3	6	< 0.001
	Previous-year August Tmax	−0.14	0.01	−12.54	< 0.001					
	Annual prcp	0.001	0	2.96	0.003					
South High BAI	Intercept	15.42	0.51	30.5	< 0.001	7671.7	8	7985.5	7	< 0.001
	Previous-year August Tmax	−0.24	0.01	−18.6	< 0.001					
	CWD	−0.002	0	−5.54	< 0.001					
	October Tmax	−0.07	0.01	−6.18	< 0.001					
North High BAI	Intercept	13.35	0.32	41.39	< 0.001	7327.3	7	7732.8	6	< 0.001
	Previous-year August Tmax	−0.25	0.01	−21.49	< 0.001					
	CWD	−0.002	0	−3.84	< 0.001					
Growth Difference	Intercept	17.57	13.29	1.32	0.19	5954.28	19	5969.29	18	< 0.001
	CWD	−0.03	0.01	−4.29	< 0.001					
	Previous-year Aug. Tmax	−0.78	0.28	−2.81	0.005					
	Elevation (Low)	80.91	19.18	4.22	0.002					
	Elevation (High)	24.27	18.78	1.29	0.23					

differences between aspects. We had expected that the growth differences would be smaller on less water-limited, north-facing aspects, and the lack of significant differences suggests that the changes in climate along an elevational transect are greater than those across aspects. Alternatively, the similarity in results among aspects may be due to the larger range of size classes on north-facing slopes (Fig. A.5), with beetles being able to choose larger, faster-growing, trees on north-facing slopes.

4.2. Variation in mortality across elevations

Beetle pressure, as measured by stand level mortality, may vary across elevations and can influence growth differences between beetle-killed and surviving trees. Simard et al. (2012) found that beetle-related lodgepole pine mortality increased with elevation in the Greater Yellowstone ecosystem, although this may have been due to increased basal area in stands at higher elevations (Klutsch et al., 2009; Simard et al., 2012). Conversely, mortality decreased with elevation in a meta-analysis including plots across the mountain pine beetle native range (Björklund and Lindgren, 2009). This elevational pattern could be explained by a negative correlation between beetle survival and cold winter temperatures (Logan and Powell, 2001; Carroll et al., 2003; Hicke et al., 2006; Björklund and Lindgren, 2009). We did not find any significant differences in beetle-induced mortality with elevation in our study (Table 1), despite decreasing differences in BAI between beetle-killed and surviving trees over the elevation range.

One possible explanation for this phenomenon is that the higher elevation trees were older than those at low elevations (Table 1; Fig. A.2). Competition may have been lower in older stands, resulting in decreased competition for resources and more similarity in stress levels among trees within a stand. Additionally, growth at higher elevations was more correlated with late summer temperatures than precipitation

(Table A.1), so high CWD and late summer temperatures may have impacted trees less at higher elevations. Physiological responses to stress may also vary with age (Knapp and Soule, 2011), so the older median age of the higher elevation sites may further explain the different climatic responses at those sites relative to low-elevation sites.

4.3. Growth-climate relationships and comparisons between beetle-killed and surviving trees

Growth of both beetle-killed and surviving trees was influenced by the same climate variables and showed mostly similar correlation strengths. Consistent with results from lodgepole pine in interior British Columbia, low-elevation tree growth was correlated with precipitation, while mid- and high-elevation growth was most strongly correlated with late summer temperatures (Lo et al., 2010). While beetle-killed trees did have somewhat stronger correlations with climate, the pattern was not consistent. Interactions between mortality and climate variables were insignificant in all growth models, and mortality category (i.e., beetle-killed vs. surviving) only had a significant impact on growth at low elevations. This suggests that both surviving and beetle-killed trees generally respond similarly, but may differ when conditions are stressful to growth as is the case at lower, more water-limited, sites. The model of growth difference magnitude (Table 3) supports this theory, as both late summer temperatures and CWD were significant in influencing the low-elevation BAI differences. However, overall, our correlation and model results do not provide substantial evidence that beetle-killed trees are more sensitive to stressful climatic conditions and thus more vulnerable to beetle outbreaks.

Increased allocation towards defenses over growth theoretically should result in increased resistance to stressful climate conditions due to enhanced stored carbon resources. As such, we expected to find interactions between mortality categories (i.e., beetle-killed vs. surviving)

and climate variables in the mortality risk and BAI-climate models. Our results were contrary to this expectation, with both beetle-killed and surviving trees showing similar responses to stressful climate events, according to the models. While unexpected, these results may be in line with Bentz et al. (2015), in which no significant differences in phloem chemistry were found between attacked and non-attacked lodgepole pine in the Greater Yellowstone Ecosystem. In this case, beetles had no apparent selective preference for trees that were less chemically resistant to mountain pine beetles, but rather focused on the larger trees in the study stands (Bentz et al., 2015). In short, while trade-offs between growth and defense may exist, they may not significantly influence mortality risk during severe pine beetle outbreaks.

4.4. Caveats

Trees have varying growth patterns depending on their age (Shrimpton and Thomson, 1985), thus it is possible that tree age may have had some influence on our results. However, no strong patterns emerged for differences in age and age-growth relationships between beetle-killed and surviving trees (Table 1; Fig. A.2). While beetle-killed trees were older, the trees had no identifiable trend in growth over the study period and were mature, with a median age of $\bar{x} = 124$ ($\bar{x}_{BK} = 125$; $\bar{x}_S = 122$). In short, age may have resulted in a greater size of those trees which died, but those trees also had higher growth rates. Further research controlling for age would be useful in disentangling the two variables. Interestingly, there was no substantial relationship between age and growth rate for this study, and our BAI model results suggest that age did not have a strong influence on growth rate.

Additionally, while faster-growing trees may have greater constitutive defenses (Hood and Sala, 2015; Pinnell, 2016), slower-growing trees may have greater induced defenses (de la Mata et al., 2017). The trade-off between constitutive and induced defenses (Moreira et al., 2014) is such that the allocation of resources towards defenses may have differed between beetle-killed and surviving trees in a way that we did not measure in this study. This phenomenon could explain why we found growth differences, despite few clear differences in host tree climate-growth relationships, as those conditions would not activate induced defenses.

4.5. Management implications

Our results indicate that severe mountain pine beetle outbreaks in lodgepole pine forests may lead to a dominance of slower-growing individuals by way of higher mortality rates among faster-growing individuals. Further work should be done to determine the heritability of growth rate, and whether or not slower growth rate is in fact being selected for during these outbreaks. It should also be noted that the preference of beetles for fast-growing trees, either due to increased size or reduced defenses, runs counter to the aim of many breeding programs which seek high growth. A more moderated program in which increased growth diversity is sought would be beneficial for the resilience of forests to future outbreaks.

4.6. Conclusions

In conclusion, we found differences in growth between beetle-killed and surviving trees, with significant differences seen at low elevations. Models demonstrated that higher growth rates and age increased the probability of mortality during the outbreak, and also that CWD and previous-year August maximum temperatures were related to the magnitude of growth differences between beetle-killed and surviving trees. Overall, while there was limited evidence that beetle-killed trees were more susceptible to successful bark beetle attack due to increased climatic stress, the impact was potentially diminished by differences in growth environment between the trees. It is likely that many of the beetle-killed trees grew more quickly simply due to earlier recruitment,

better slope position, or lower resource competition. The extreme pressure of the outbreak may also have partially masked or reversed any natural differences in mountain pine beetle resistance within stands, particularly at more water-limited low elevations where the largest growth differences were observed. Our results do not rule out that some individuals are more or less susceptible to bark beetle attack, but they do not provide strong evidence in that direction. Further work should compare responses to past beetle outbreaks, investigate growth differences following a lower severity beetle outbreak, and investigate genetic differences between beetle-killed and surviving trees.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.05.048>.

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