Forests **2015**, *6*, 3483-3500; doi:10.3390/f6103483

OPEN ACCESS

forests

ISSN 1999-4907

www.mdpi.com/journal/forests

Article

Impact of a Mountain Pine Beetle Outbreak on Young Lodgepole Pine Stands in Central British Columbia

Amalesh Dhar [1,2,*], Nicole A. Balliet [1], Kyle D. Runzer [1] and Christopher D. B. Hawkins [1,3]

[1] Mixedwood Ecology and Management Program, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada; E-Mails: balliet@unbc.ca (N.A.B.); krunzer@unbc.ca (K.D.R.); chawkins@yukoncollege.yk.ca (C.D.B.H.)

[2] Earth & Environmental Sciences and Physical Geography, University of British Columbia, 1177 Research Road, Kelowna, BC V1V 1V7, Canada

[3] Yukon Research Centre, Yukon College, Whitehorse, YT Y1A 5K4, Canada

* Author to whom correspondence should be addressed; E-Mail: amalesh.dhar@ubc.ca; Tel.: +1-250-807-8168; Fax: +1-250-807-8001.

Academic Editors: Jan Stenlid, Jonas Oliva and Audrius Menkis

Received: 25 June 2015 / Accepted: 28 September 2015 / Published: 30 September 2015

Abstract: The current mountain pine beetle (MPB) (*Dendroctonous ponderosae* Hopkins) epidemic has severely affected pine forests of Western Canada and killed millions of hectares of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. latifolia Engelm.) forest. Generally, MPB attack larger and older (diameter > 20 cm or >60 years of age) trees, but the current epidemic extends this limit with attacks on even younger and smaller trees. The study's aim was to investigate the extent of MPB attack in young pine stands and its possible impact on stand dynamics. Although MPB attacks were observed in trees as small as 7.5 cm diameter at breast height (DBH) and as young as 13 years old, the degree of MPB attack (percent stems ha^{-1}) increased with increasing tree diameter and age class (13–20, 21–40, 41–60, and 61–80 years old) (6.4%, 49.4%, 62.6%, and 69.5% attack, respectively, by age class) which is greater than that reported from previous epidemics for stands of this age. The mean density of surviving residual structure varied widely among age classes and ecological subzones. Depending on age class, 65% to 77% of the attacked stands could contribute to mid-term timber supply. The surviving residual structure of young stands offers an opportunity to mitigate the effects of MPB-attack on future timber supply, increase age class diversity, and enhance ecological resilience in younger stands.

Keywords: ecological zone; lodgepole pine; mid-term timber supply; mountain pine beetle; residual trees; stocking

1. Introduction

Lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. latifolia Engelm.) and the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) have co-existed as a natural part of the ecosystem in western North American pine forests for millennia [1]. Endemic MPB populations periodically surge during a natural cycle and induce periods of considerable forest mortality as well as playing an important functional role in directing ecological processes and maintaining the biological diversity of forest ecosystems [2,3]. However, the current patterns of MPB outbreak appears to be more severe, and impacts have been documented across at least 18.5 million hectares of lodgepole pine forest killing approximately 723 million m^3 or 53% of the merchantable mature pine volume in British Columbia (BC) [4]. Active forest management by fire suppression increased the abundance of old pine in forests while climate change, such as mild winters from 1993 onwards, and drier summers resulted in a beetle population expanding exponentially and spreading across the BC landscape [3,5]. In central BC, there "is approximately 1.96 million ha of young lodgepole pine stands (<60 years) and more than 357,000 hectares of it had some level of attack during the current MPB outbreak [6].

Based on past MBP outbreaks, early predictions assumed that only mature stands older than 80 years would be significantly attacked by MPB, and stands 61 to 80 years old would have attack rates of about 50%, while stands 41 to 60 years old would be attacked occasionally and stands less than 40 years old would be very rarely attacked [7–9]. However, due to the tremendous amplification and expansion of the MPB population during the early 2000, young stands were attacked at increasingly greater rates [10–12]. According to MacLauchlan [10], in central BC 49.2% of young planted stands (stands aged ≤ 60 years old) contained some level of MPB-attack, as well as populations of secondary bark beetles. However detailed studies in young lodgepole pine stands are scarce. Therefore, this investigation provides a unique opportunity to understand the extent and impact of MPB in young lodgepole pine stands.

Timber supply analyses undertaken by both government and industry for various forest management units predicted a significant mid-term shortfall as a result of the current MPB epidemic [13] (mid-term = portion of the timber inventory that would be available for harvest within the middle of a normal management cycle *i.e.*, ~30–70 years in central BC [14]. It was estimated the allowable annual cut (AAC) would drop by approximately 12.6 million m^3 from the pre-MPB AAC [15]. At the provincial level, this shortfall in future harvests is likely to begin in approximately 2016 and last for up to 50 years [16]. Generally, post MPB epidemic estimated AAC is based on five assumptions: (1) oldest attacked stands are harvested first; (2) only mature stands are affected with attack rates of about 80 percent in age class 5 and older (>81 years old), and attack rates of about 50 percent in age class 4 (61–80 years of age); (3) no attack in age classes 1 to 3 (≤60 years old); (4) regeneration delay of 15 years in areas not logged; and (5) a shelf life of 10 years with five years for sawlogs [8]. The observed MPB-induced mortality in immature lodgepole pine stands invalidates two of the timber supply assumptions, numbers two and three, and is not reflected in current timber supply analysis for central BC [16]. Immature mortality caused by the MPB will result in an extension, and possibly a deepening, of the mid-term timber supply fall down period beyond that which has been predicted in any provincial timber supply analysis to date [16].

Further understanding of the role of MPB in immature/young stands (≤60 years) is critical to develop management strategies for these stands. In a previous investigation, Hawkins *et al.* [17] described the abundance of residual secondary stand structure (SSS) (seedlings, saplings, sub-canopy, and canopy trees that survived a beetle attack) in a wide range of age classes in central BC. Despite promising results, their report did not detail the role of MPB in young lodgepole pine stands nor young stand dynamics after MPB attack. Therefore, further investigation/analysis was carried out to fill this knowledge gap. The main objectives of this study were to describe (i) the extent of mountain pine beetle attack and (ii) post beetle stand dynamics in 13 to 80 years old lodgepole pine leading (dominated) stands in central BC.

2. Experimental Section

2.1. Stand Selection

The sampled area was located in the sub-boreal spruce (SBS) biogeoclimatic/ecological zone with three broad subzones dry, mesic, and moist of central British Columbia [18]. All investigated stands were lodgepole pine-dominated, unsalvaged stands. Before field reconnaissance, stands for possible sampling were identified on forest cover maps. Seventy percent (70%) of the sampled stands were selected randomly and the remaining thirty percent (30%) were targeted to ensure complete coverage of ecological zones and different age classes. Prior to temporary sample plot (TSP) establishment and sampling, reconnaissance was carried out to determine if stands met the following criteria: (a) lodgepole pine-leading (dominated); (b) within the SBS biogeoclimatic/ecological zone [18]; and (c) based on forest cover maps, age class 1 or AC1 (13–20 years), 2 or AC2 (21–40 years), 3 or AC3 (41–60 years) and 4 or AC4 (61–80 years) (Table 1). Large scale harvesting and silvicultural practices have created a legacy of managed age class 1 and 2 stands in central BC. These stands were established by clear cut logging and planting and generally no further management activities. Prior to the industrial logging era (1960) wildfires, followed by natural regeneration, was the primary disturbance agent and regeneration method for age class 3 and 4 stands. Age class 4 stands are transitional from young to mature stands and are thought to be more susceptible to MPB than younger stands [7]. They are included for comparison in our analysis as young stands.

In total, 309 lodgepole pine-dominated stands and 1527 TSP were sampled in age class 1 to 4 stands (Table 1). Approximately half of the samples were in age class 2 (21–40 years old) stands because this is the age class most crucial for forest management decisions regarding midterm timber supply.

Table 1. Number of stands sampled and temporary sample plots (TSP) established by age class and biogeoclimatic/ecological subzone.

Age Class (AC)	Age Range (Years)	Number of Stands	Stands by Biogeoclimatic Subzone			Number of TSP
			Moist	Mesic	Dry	
1	13–20	52	25	16	11	254
2	21–40	148	46	31	71	738
3	41–60	38	13	6	19	190
4	61–80	71	15	13	43	345
Overall		309	99	66	144	1527

2.2. Sampling Protocol

The entire survey was completed over the course of three years in the three different ecological subzones (dry, moist, and mesic). Initial stand assessment began in July 2005 in the dry (southwest), followed by the moist (southeast) in 2006, and finishing with the mesic (central) in 2007. Sampling commenced at least 50 m from stand boundaries, roads, trails or forest cover boundaries. At each sample locale, two different types of temporary sample plot (TSP) (5.64 m radius (100 m^2) for all residual mature trees (diameter at breast height; DBH ≥ 7.5 cm) and 3.99 m radius (50 m^2) for advanced regeneration (diameter at breast height (DBH) <7.5 cm and >4 m height) were established every 50 m along the transect line. When atypical plot locations were encountered, such as areas with excessive wind-throw or a water body, the plot was moved 25 or 50 m along the transect line. All TSPs had a minimum buffer zone of 50 m in all directions. Depending on the size and shape of the stand, 3–10 TSPs were established. For each TSP, site series (soil moisture and nutrient regime), site index (determined in the lab from a site tree core at DBH), and macro aspect (direction relative to noon sun) were recorded to identify and characterize the plot.

2.3. Surviving Residual Secondary Structure Data Collection

In this study, secondary stand structure was defined according to the 2008 BC Ministry of Forests and Range Forest Practices and Planning Regulation (FPPR) amendments [19]. However, to improve our assessment of residual secondary structure after MPB attack, live secondary structure was divided into two categories: (a) advanced regeneration (>4 m height but <7.5 cm DBH) and (b) residual mature trees (DBH > 7.5 cm). Any regeneration <4 m in height was not considered in this investigation to follow the FPPR amendments (for details, see Hawkins *et al.* [17]).

For each TSP, species, DBH, stage of MPB-attack, relative crown position (dominant, co-dominant, intermediate, and suppressed) were collected for residual mature trees (DBH ≥ 7.5 cm). The stage of MPB attack was classified according to current MPB attack status as: green attack (entrance holes visible, with or without boring dust, but crown still green), red attack (trees attacked the previous season, foliage red in color but still attached to branches), grey attack (trees killed by MPB two or more years ago, and no longer had any foliage) and no attack (no sign of the beetle). All attacked trees had evidence of MPB entrance holes and when bark was removed from grey trees there seldom was evidence of secondary beetle attack. Young green and red attacked trees were not examined for secondary bark beetles, though they may have been present. Therefore, secondary bark beetles may have a limited influence in the overall assessment. Based on the number of lodgepole pine trees attacked, each age class was divided into one of four lodgepole pine attack categories: A ≤25; B >25 to ≤50; C >50 to ≤75; and D >75% attack.

One tree core at DBH from the largest diameter, defect-free, dominant or co-dominant tree (site tree) was taken in each plot to verify stand age and calculate height over age site index [20] for mature trees and growth intercept site index for secondary structure (SI_{50} = site index is based on top height and a reference age of 50 years (breast height) in BC. Density and species composition of advanced regeneration (stems > 4 m in height with DBH < 7.5 cm) was also determined for each age class and ecological subzone.

2.4. Analysis

All reported MPB attack values are based solely on lodgepole pine. Simple linear regression was carried out to find the relationship between mean MPB attack (percent stems ha^{-1}) and mean pine DBH and overall stand density for each age class using SYSTAT version 12 ® (Systat Software, Inc., San Jose, CA, USA). The Kruskal Wallis [21] non-parametric test was conducted when attack categories (A, B, C and D, as the dependent variable) were compared against age classes (independent variables). A chi-squared test was applied to determine the relationship between DBH class and MPB attack. Further analysis was conducted to determine the effects of ecological subzones (dry, moist and mesic) and age class on density of secondary stand structure and MPB-attack percentages, where plots were averaged for each stand and stand average was used in the analysis. During analysis general linear model (GLM)-based analysis of variance (ANOVA) [21] was used instead of mixed-effect model [22] as the attack rates were similar among plots within a stand. Therefore, GLM-based ANOVA can easily cope with most of the variability after averaging the plots within the stands. In addition, pairwise comparisons were conducted using Tukey's multiple comparison test ($\alpha = 0.05$) to determine differences among age classes and ecological subzones [21]. In order to satisfy the ANOVA model assumptions variance, normality and homogeneity were checked before each analysis, and no transformations were required [21]. Analyses were conducted using the SYSTAT and programming language R (version 3.1.2) [23].

3. Results

3.1. MPB Attack

Simple linear regression of mean MPB-attack in lodgepole pine as a function of stand mean lodgepole pine DBH showed a significant relationship for all age classes. When regression analysis was carried out based on stand level mean MPB attack as a function of mean stand density only age classes 3 (41–60 years) and 4 (61–80 years) showed a significant relationship (Table 2). There was also a significant difference among age classes ($p < 0.001$; AC1 = 6.4%, AC2 = 49.4%, AC3 = 62.6%, AC4 = 69.5%) and ecological subzones ($p = 0.038$; moist = 50.6, Dry = 43.4, and mesic = 40.6%) based on the percentages of MPB-attack. Mean MPB-attack increased with increased age class and the greatest mean MPB attack was observed in age class 4 (69.5%), followed by age classes 3 (62.6%) and 2 (AC2: 21–40 year) (49.4%) (Figure 1). For ecological subzone, the moist subzone showed the greatest rates of attack and was followed by the dry and mesic subzones (Figure 1). Tukey's test for multiple comparisons ($\alpha = 0.05$) showed age class 1 (AC1: 13–20 years) was significantly ($p < 0.001$) different from the other age classes and AC2 was different from AC4 (Figure 1).

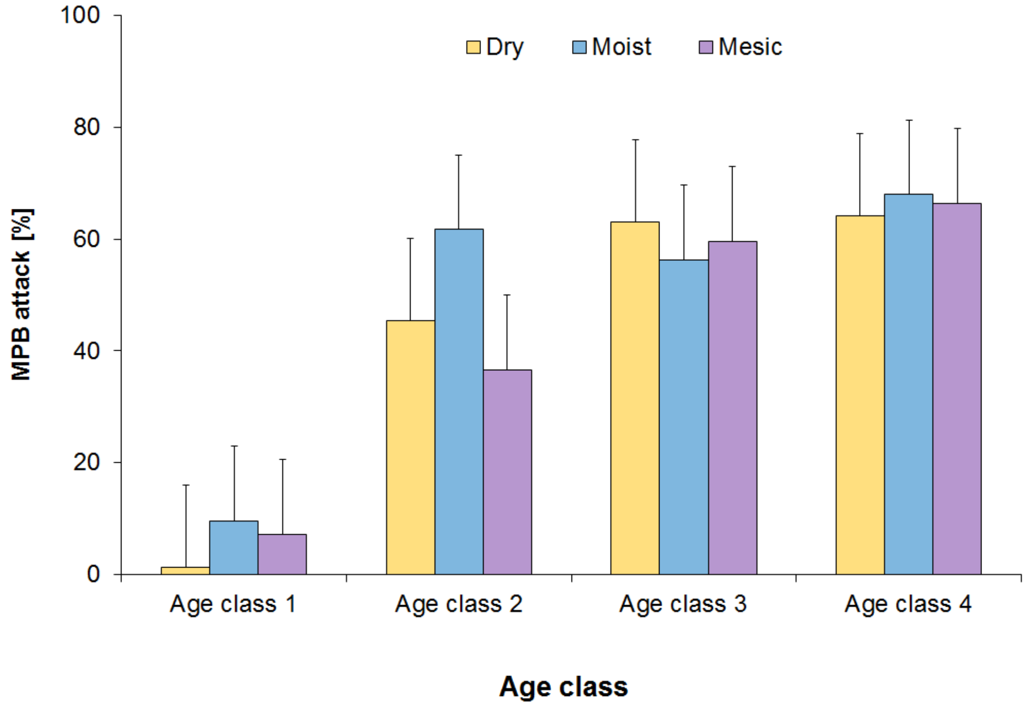


Figure 1. Mean MPB-attack (±SD) in lodgepole pine by age class and biogeoclimatic/ecological subzone.

Table 2. Linear regression of mean MPB-attack in lodgepole pine as a function of stand mean pine DBH (=X) and MPB attack as a function of stand mean stems ha^{-1} (=X) for each age class.

Age Class (Years)	Equation ($Y = a + bX$)	R^2	F	p	df
MPB attack as a function of stand mean pine DBH					
1 (13–20)	$-46.5985 + 4.4209 \times X$	0.1576	10.5387	**0.002**	1.50
2 (21–40)	$-46.5292 + 6.8968 \times X$	0.2133	40.8669	**<0.001**	1.146
3 (41–60)	$0.1895 + 4.4400 \times X$	0.3627	22.0534	**<0.001**	1.36
4 (61–80)	$11.2292 + 3.3448 \times X$	0.4426	56.5885	**<0.001**	1.69
MPB attack as a function of stand mean density (stems ha^{-1})					
1 (13–20)	$-1.2010 + 0.0050 \times X$	0.0000	0.6446	0.4258	1.50
2 (21–40)	$57.7120 - 0.0104 \times X$	0.0169	3.5194	0.0626	1.146
3 (41–60)	$79.2897 - 0.0132 \times X$	0.2392	12.6282	**0.0011**	1.36
4 (61–80)	$68.9088 - 0.0095 \times X$	0.0640	5.7830	**0.0189**	1.69

Significant ($\alpha = 0.05$) results are in bold. MPB: mountain pine beetle; DBH: breast height.

The Kruskal Wallis non-parametric test indicated that only MPB attack category "A" was significantly (H = 16.60, $df = 3$, $p < 0.001$) different among age classes, whereas the other categories

(B, C, D) were not different from each other. The percentage of stands in the lowest attack category "A" decreased with increasing age class while the opposite trend was observed for attack categories "C" and "D" (Table 3). When testing the differences in distribution of MPB-caused mortality percent across lodgepole pine DBH classes a significant ($p < 0.001$) relationship was observed. Overall beetle attacks increased with increased DBH class and attack rates exceeded 50% at a DBH of 13.0 cm, 11.0 cm, and 12.5 cm for age classes 2, 3 and 4, respectively (Figure 2). Attack rates were also examined for broader DBH classes: ≤15 cm, >15 to ≤20 cm, and >20 cm to determine MPB-attack preferences with respect to basal area (m^2 ha^{-1}) and density (stems ha^{-1}).The results indicated the only significant relationship was observed in the smallest DBH class (≤15 cm) as it lost greater basal area (38.7%) than density (stems ha^{-1}) (30.5%), whereas no detectable difference was observed for the two larger DBH classes (basal area and density for >15 to ≤20 cm = 67.9% and 67.9% and for >20 cm = 78.0% and 78.1%) (Figure 3).

Table 3. Mean percentage of lodgepole pine attacked by MPB and mean lodgepole pine DBH by age class and attack category.

Age Class (Years)	Attack Category	Total Number of Stands	Stands (%)	Mean MPB Pine Attack (%)	Mean Pine DBH (cm)
1 (13–20)	A (≤25%)	48	92	1.2	11.8
	B (25.1%–50%)	0	0	n/a	n/a
	C (50.1%–75%)	3	6	63.7	14.8
	D (>75.1%)	1	2	84.5	13.6
	Total	52	100	6.4	12.0
2 (21–40)	A (≤25%)	43	29	3.1	12.9
	B (25.1%–50%)	26	18	42.3	12.7
	C (50.1%–75%)	35	23	65.5	14.0
	D (>75.1%)	44	30	85.9	15.6
	Total	148	100	49.4	13.9
3 (41–60)	A (≤25%)	3	8	10.8	10.1
	B (25.1%–50%)	8	21	38.4	12.5
	C (50.1%–75%)	14	37	66.3	13.5
	D (>75.1%)	13	34	85.3	16.5
	Total	38	100	62.6	14.0
4 (61–80)	A (≤25%)	2	3	13.6	10.8
	B (25.1%–50%)	13	18	41.2	14.1
	C (50.1%–75%)	24	34	64.6	16.1
	D (>75.1%)	32	45	88.1	20.2
	Total	71	100	69.5	17.4

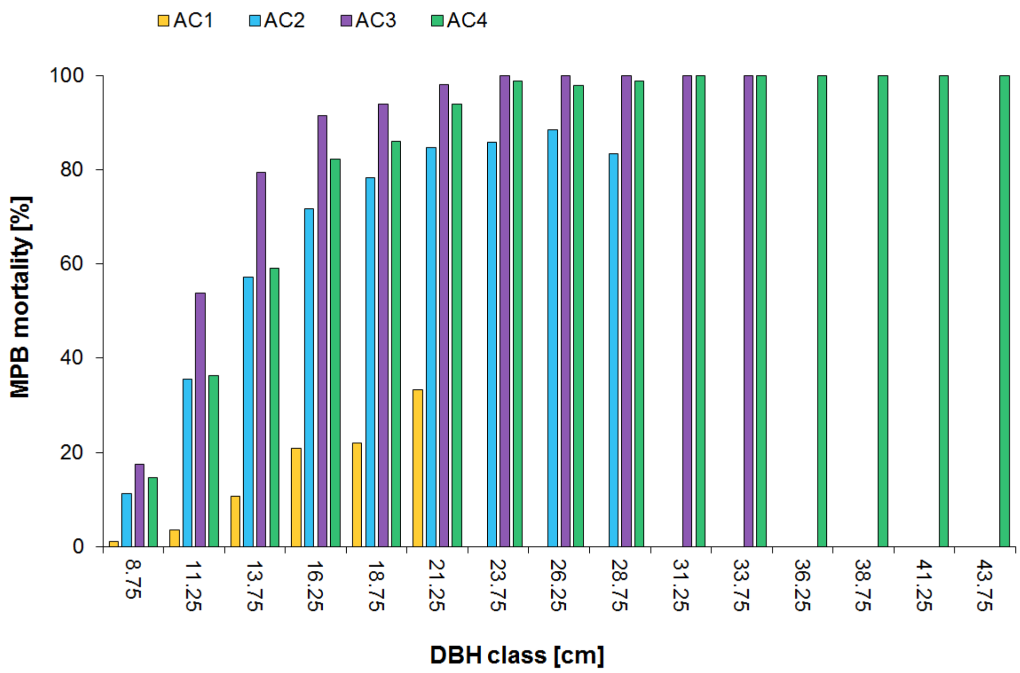


Figure 2. Mean percentage of lodgepole pine trees attacked for each age class ((AC) data from all biogeoclimatic/ecological zones pooled) by 2.5 cm diameter at breast height (DBH) class. (AC1 = age class 1; AC2 = age class 2; AC3 = age class 3; and AC4 = age class 4.)

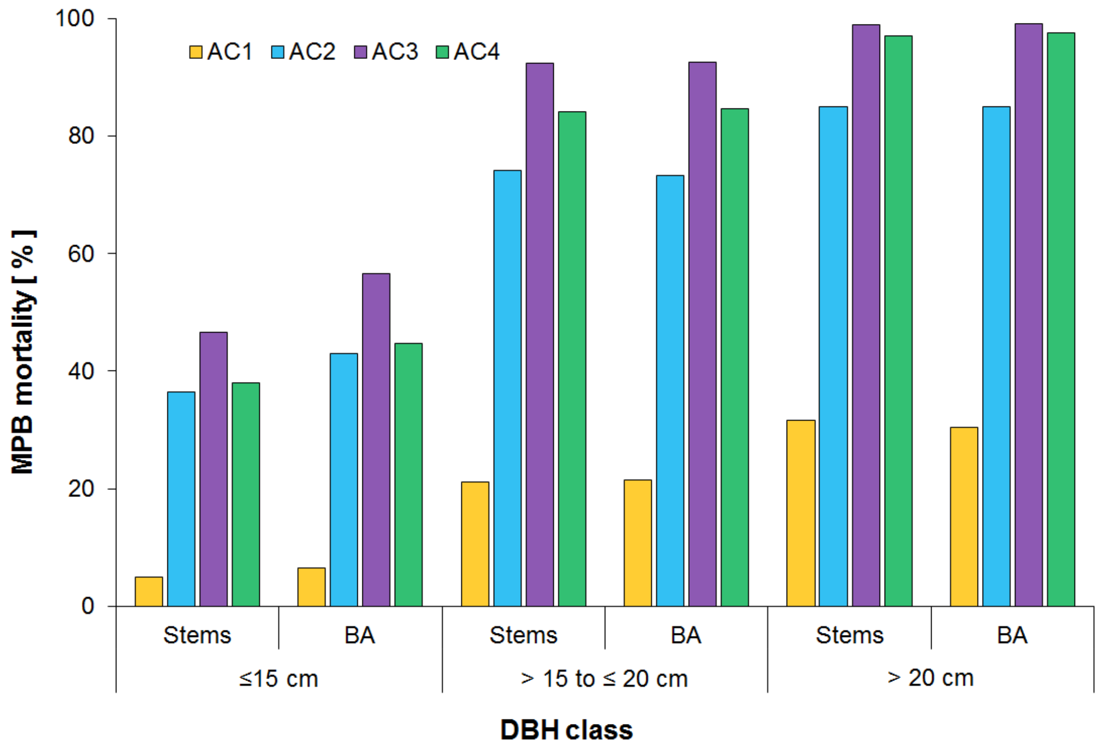


Figure 3. Percentage of lodgepole pine trees attacked by MPB using stems ha^{-1} or basal area (BA) as the metric for each age class (data from all biogeoclimatic/ecological sub-zones pooled) by three large DBH classes: ≤15 cm (3, 2.5 cm classes pooled), >15 cm to ≤20 cm (2, 2.5 cm classes pooled), and >20 cm (up to 10, 2.5 cm classes pooled). AC1 = age class 1; AC2 = age class 2; AC3 = age class 3; and AC4 = age class 4.

3.2. Surviving Residual Structure of Immature Stands

GLM (ANOVA) indicated that the density of residual mature trees (stem > 7.5 cm DBH) in post MPB attacked stands was significantly ($p < 0.001$) different among age classes but not ecological subzones ($p = 0.133$) (Table 4). The greatest number of residual trees was observed in age class 1 (13–20 years) followed by age classes 3 (41–60 years), and 2 (21–40 years) (Table 5). Tukey's test for multiple comparisons ($\alpha = 0.05$) revealed a significant difference among age classes except age class 2 and 4 were similar ($p = 0.941$) (Table 5).

Table 4. ANOVA results for the density of residual mature trees and advanced regeneration following MPB-attack based on age class and biogeoclimatic/ecological subzone.

Source	Mean Square	*df*	*F*	*p*
Residual mature trees (DBH ≥ 7.5 cm)				
Age class	6,627,569.67	3	22.815	**<0.001**
Biogeoclimatic/Ecological subzone	590,068.64	2	2.031	0.133
Error	290,491.55	303		
Advance regeneration (>4 m height and DBH < 7.5 cm)				
Age class	13,174,804.15	3	10.326	**<0.001**
Biogeoclimatic/Ecological subzone	5,184,251.71	2	4.063	**0.018**
Error	1,275,857.19	288		

Significant ($\alpha = 0.05$) results are in bold. ANOVA: analysis of variance.

Table 5. Mean density (stem ha^{-1}) of residual mature trees (RMT) and advanced regeneration (Adv. Reg.) by age class and biogeoclimatic subzone.

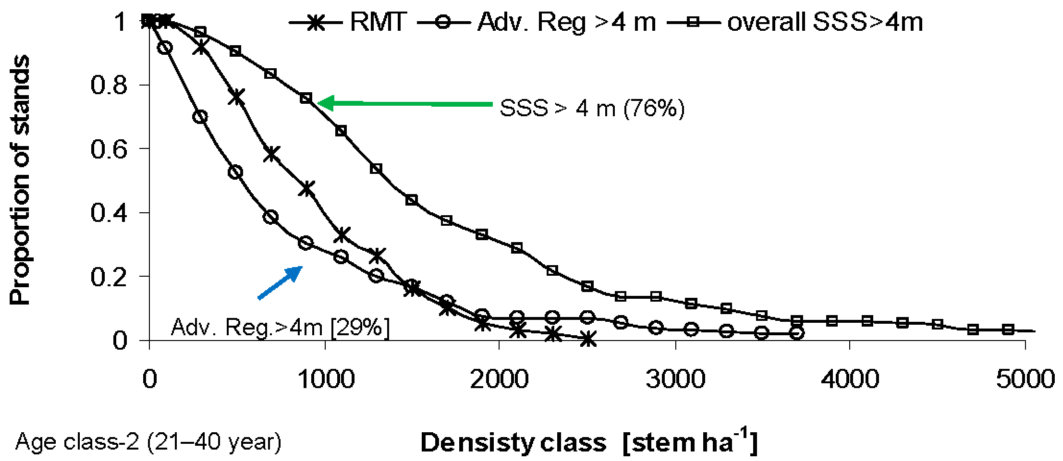
Age Class (Year)	RMT DBH ≥ 7.5 cm (stem ha^{-1})				Adv. Reg. Height >4 m DBH < 7.5 cm (stem ha^{-1})			
	Dry	**Moist**	**Mesic**	**Mean**	**Dry**	**Moist**	**Mesic**	**Mean**
1 (13–20)	1309	1403	1301	1338 c	789	592	850	744 b
2 (21–40)	847	733	989	856 a	714	1031	460	735 b
3 (41–60)	1097	1296	1098	1164 b	2000	1846	527	1458 c
4 (61–80)	969	821	626	805 a	688	773	203	555 a
Eco. Subzone (mean)	1056 *x*	1063 *x*	1004 *x*		1048 *y*	1061 *y*	510 *x*	

Different letters (for age class: a, b, c and for biogeoclimatic subzone: *x*, *y*): indicate a significant difference ($\alpha < 0.05$) in Tukey's test for multiple comparisons.

Considering the density of advanced regeneration (stem >4 m in height and <7.5 cm DBH) age classes ($p < 0.001$) and ecological subzones ($p = 0.018$) were significantly different following MPB-attack (Table 4). The density of advanced regeneration, however, varied considerably across age class and ecological subzone. The greatest number (1485 stems ha^{-1}) of advanced regeneration was found in age class 3, whereas age class 4 had the least (555 stems ha^{-1}) (Table 5). Dry and moist ecological subzones of age class 3 (41–60 years) and the moist subzone of age class 2 (21–40 years) had >1000 stems ha^{-1}. Tukey's test for multiple comparisons showed age class 3 and 4 were significantly different from the other age classes while the mesic subzone was significantly different from dry and moist subzones (Table 5).

The study also suggests that species composition of secondary stand structure (stem > 4 m height) generally varied from stand to stand. After MPB-attack of lodgepole pine, secondary stand structure in age classes 1 to 3 was dominated by broadleaf species with minor components of conifer species. The most common species for these age classes were aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), black cottonwood (*Populus trichocarpa* Torr. & A. Gray), lodgepole pine, hybrid spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry), and sub-alpine fir (*Abies lasiocarpa* (Hook.) Nutt). Conifer species lodgepole pine, hybrid spruce, and sub-alpine fir dominated age class 4 secondary stand structure.

Depending on the age class, 65%–77% of the stands were satisfactorily stocked (2008 FPPR amendments) with ≥900 stems ha^{-1} (stem height > 4 m) of secondary structure (Figure 4). However when we consider residual mature trees (DBH > 7.5 cm), the results reveal that all stands within the sampling area met minimum stocking levels for MPB attacked stands (minimum residual tree stocking 600 stems ha^{-1} based on BC Ministry of Forests and Range [24] protocols). If we consider only advanced regeneration (stem >4 m height but <7.5 cm DBH) 22%–46% of stands had ≥1000 stems ha^{-1}.



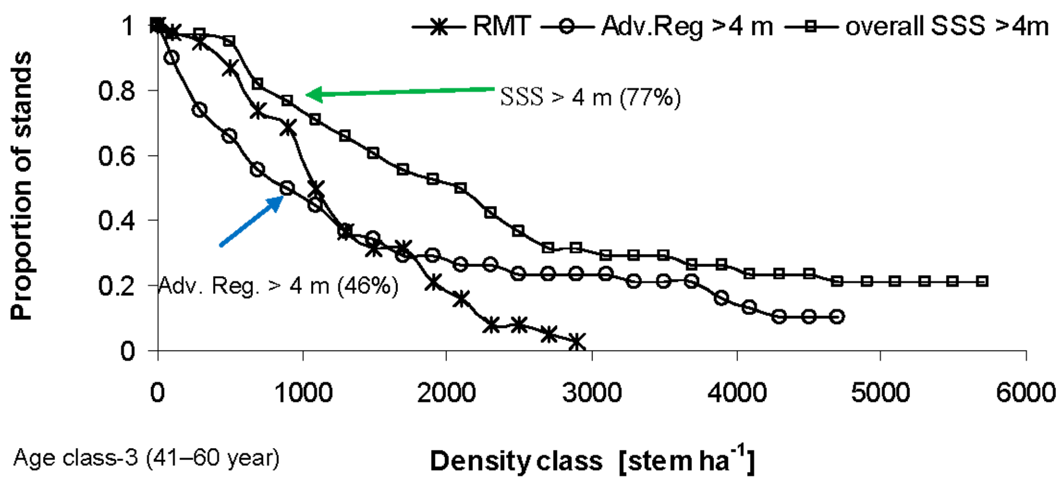


Figure 4. *Cont.*

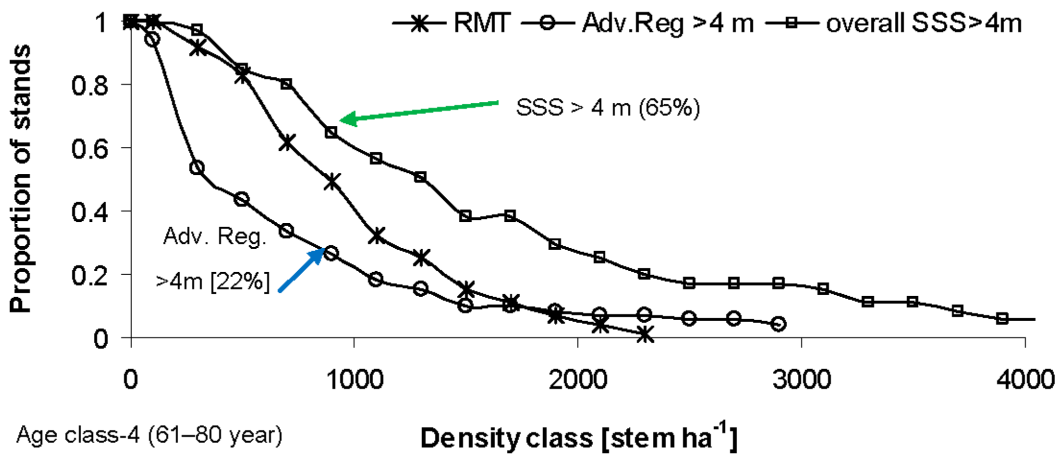


Figure 4. Proportion of age class 2, 3, and 4 stands meeting BC's (British Columbia) legislated residual secondary stand structure (overall SSS > 4 m height) (residual mature trees ≥ 7.5 cm DBH + advanced regeneration >4 m in height and <7.5 cm DBH), only residual mature trees (≥7.5 cm DBH) and advanced regeneration (>4 m in height and <7.5 cm DBH). (RMT = Residual mature tree, Adv. Reg. = Advanced regeneration, SSS = Residual secondary stand structure).

4. Discussion

4.1. MPB Attack

This study indicated the MPB-attack rate in immature or young pine leading stands was a function of tree size, age, and to a lesser extent, stand density. MPB attack percentage increased in young lodgepole pine leading stands with increasing mean stand DBH and age. According to Safranyik and Carroll [1], mountain pine beetle attacks and brood production are directly related to tree age and DBH. Larger trees have thicker bark and phloem, offering more protection for the insects and larvae from natural enemies, extreme temperatures, and sapwood drying. Resistance to MPB-attack is also a function of carbon allocation to resin duct production rather than radial growth [25,26]

The average level of MPB-attack for age class 1 stands was very low (6.4%); as a result, these stands will only be brought into the discussion when pertinent. For the other age classes, the percentages of lodgepole pine attack were much higher than the previously reported [7,27,28]. According to studies from previous MPB outbreaks, younger stands are less susceptible to MPB attack and have lower brood production due to a thinner phloem and higher growing densities. Other than for age class 3, our regression analysis supports this observation (Table 2). However pre-MPB stand density may not a good predictor of MPB-attack because the mean densities of age class 3 were approximately 40% greater than that of age class 1 and almost double that of age class 4 (Table 5). This suggests less density-dependent mortality in this age class as MPB-induced mortality was similar between age classes 3 and 4.

From historical observations it was reported that more than 50% of lodgepole pine trees with a DBH > 25 cm and a small proportion of trees with a DBH between 10.5–25 cm were attacked by MPB whereas no attack was observed for younger and smaller trees (DBH < 10 cm) [7,9,27]. However depending on age class and DBH our study suggests that MPB killed >95% of lodgepole pine trees with a DBH > 23 cm in age class 3 and 4 and 85% with a DBH >22.5 cm in age class 2 (Figure 2). The difference in observations is likely due to the immensity of the current MPB outbreak in central BC compared to previous outbreaks. A similar observation was reported by the BC Ministry of Forests in its 2008 aerial overview survey where around 95% of trees > 22.5 cm DBH were killed by the MPB [6]. Based on trees with a DBH ≤15 cm, 35% to 45% of the stems and 45% to 58% of the basal area was killed for age classes 2 to 4 and such mortality levels have previously only been reported for trees with DBH larger than 25 cm [1,7,29]. According to Amman *et al.* [7] MPB-caused lodgepole pine mortality is 1% for trees with a DBH ≤ 10 cm, 20% for a DBH ≤ 20 cm, and 55% for a DBH ≤ 30 cm, whereas Safranyik and Carroll [1] and Björklund *et al.* [29] observed 10% mortality for trees with a DBH ≤ 10 cm, 40% for trees with a DBH ≤ 20 cm and 70% for trees with a DBH ≤ 30 cm in central BC. Progar *et al.* [30] observed mortality rates in the Rocky Mountain states of <40% for trees with a DBH below 23 cm and >80% for trees larger than 33 cm. The data from our study demonstrates that small lodgepole pine were attacked by MPB at much greater rates (exceeding 50% at DBH's of 13.0 cm, 11.0 cm and 12.5 cm for age classes 2, 3 and 4 respectively) than previously reported. This indicates that although MPB preferentially attacked the larger lodgepole pine they likely indiscriminately select hosts when their population densities are extreme [11] and no other host choices exist.

4.2. Post Beetle Stand Dynamics of Immature Stands

Extensive attacks in young stands demonstrate the need for inventory data collected at layers below the canopy level. Highly variable attacks at stand levels also demonstrate the need to collect inventory data on a stand-by-stand basis. For age class 1 stands, except in a few instances, there are no management concerns about their growth and future productivity, unless there is another MPB outbreak within the next 20 years (Figure 1).

Considering residual mature trees (stem ≥ 7.5 cm DBH), most of the MPB-attacked stands met minimum stocking levels of 600 stems ha^{-1} for all age classes and ecological subzones which is comparable to Hawkins *et al.* [17] study. According to the BC Ministry of Forests and Range to contribute to mid-term timber supply, [30] the minimum stocking level for residual mature trees in MPB-attacked stands is 600 stems ha^{-1}. Like other studies, density of advanced regeneration (stem > 4 m height but <7.5 cm DBH) was found to be variable across age classes and ecological subzones [17,31–33].

Depending on stand age, 65%–77% of stands can be considered stocked with advanced regeneration and live residual trees (secondary stand structure) after MPB attack. A stocked stand is expected to provide at least 150 m^3 ha^{-1} of timber at harvest [19]. Based on a study by Coates *et al.* [31], around 25% to 57% of stands had enough secondary structure after MPB-attack in the Cariboo-Chilcotin region of BC to be considered stocked. This study also suggested that about 23%–35% stands within these age classes (age classes 2 to 4) required further attention to achieve the mid-term timber supply goal. This is comparable to a study by Coates *et al.* [31] in central BC where they suggested a single blanket management approach may not be possible for MPB affected stands. Severely impacted stands will have to be surveyed on a stand-by-stand basis. Only those stands which do not meet the mid-term timber supply minimum volume will need rehabilitation for timber management. Moreover, these attacked stands have also started to release within three to five years after MPB attack [20] and grow at rates proportional to trees that have never been suppressed [34,35]. Therefore, retention of stands with suitable secondary structure can shorten rotation age greatly [31] compared to starting a new plantation after logging. Additionally, by retaining stands with suitable secondary stand structure, structural and species diversity will be promoted [20,35–37] and future stand dynamics and age class distribution will be controlled [38]. Moreover, the forest landscape will convert to heterogeneous structures where mosaics of even-aged and uneven-aged patches intermingle in space and time [39,40]. This heterogeneous natural system is more resilient than homogeneous systems, as a significant portion of the biological legacies of that particular ecosystem remain intact [41–43] and this allows it to "remember" genetically, compositionally, and structurally pre-disturbance conditions of the stand to build a new complex ecosystem [43,44] which could be more adaptable to a changing climate [41,45]. Therefore, stands that have arisen after MPB-attack may have enhanced resilience to both biotic and abiotic stressors, as well as could significantly reduce susceptibility to future MPB infestation [43,46].

When managing MPB-attacked stands it is important to set priorities with respect to which stands should be visited first. This can be done by considering two important stand characteristics: geographic location and stand age. Geographic location is important because some regions are more affected by MPB than others [47]. For example, in this study, the moist subzone was more severely impacted by MPB than the other subzones. Stand age is also important because the level of MPB attack and tree diameter generally increase with stand age [7] as was demonstrated in the present study. Older stands generally have larger diameter pine trees and are more susceptible to MPB attack than younger stands.

5. Conclusions

About 5% of trees less than 10 cm in DBH were attacked and attack rates greater than 80% were observed in trees with a DBH ≥ 20 cm. Beetle attack rates significantly relate to stand densities of older age classes (2 and 3) while the moist subzone is more severely attacked than the other subzones. Clearly there will be some immature stands that are best logged for biomass and planted today to achieve future timber supply. However it appears a majority of the stands may be best left alone after MPB-attack, allowing them to make contributions to the mid-term timber supply albeit, in some cases, at reduced yields, as well as maintain long-term ecological benefits and services for human well-being [17,36,48,49]. Additionally, the occurrence of a MPB outbreaks can result in more structurally and compositionally diverse stands [36,43,48–51] which should significantly contribute to forest resilience against predicted climate change-related disturbances (*i.e.*, future MPB attack). In addition, minimizing management intervention in these stands would allow the money allocated to stand establishment activities to be utilized for other needed management activities to increase quality or volume. Moreover, these stands are not only important for ecological restoration, they also provide a unique opportunity to reshape our knowledge regarding regeneration and stand dynamics under complex conditions following a MPB outbreak [41,39].

Acknowledgments

This work was funded by the Canadian Forest Service Mountain Pine Beetle Initiative Projects 8.23 and 8.59 and the BC Forest Investment Account, FSP Projects M065002, M075024, Y061021, Y071058, and Y090118. Bruce Rogers, Cindy Baker, and Deanna Danskin assisted with data collection and project management. We are grateful to five anonymous reviewers for their constructive feedback on the manuscript.

Author Contributions

Nicole A. Balliet, Kyle D. Runzer and Christopher D.B. Hawkins designed the experiments and compiled data; Amalesh Dhar contributed to data analysis; Amalesh Dhar and Christopher D.B. Hawkins wrote the paper.

Conflicts of Interest

The authors declare no conflict of interest.

References

1. Safranyik, L.; Carroll, A.L. The biology and epidemiology of the mountain pine beetle in Lodgepole pine forests. In *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine*; Safranyik, L., Wilson, B., Eds.; Natural Resources Canada: Victoria, BC, Canada, 2006; pp. 3–66.
2. Roe, A.L.; Amman, G.D. *The Mountain Pine Beetle in Lodgepole Pine Forests*; Research Paper INT-71; USDA Forest Service Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1970. Available online: http://www.usu.edu/beetle/documents2/197Roe_Amman_MPBin_LPP_Forests.pdf (accessed on 18 May 2015).
3. Taylor, S.; Carroll, A. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective. In *Mountain Pine Beetle Symposium: Challenges and Solutions*; Information Report BC-X-399; Shore, T., Brooks, J., Stone, J., Eds.; Canadian Forest Service: Victoria, BC, Canada, 2004; pp. 44–51.
4. Walton, A. *Provincial-Level Projection of the Current Mountain Pine Beetle Outbreak: Update of the Infestation Projection Based on the Provincial Aerial Overview Surveys of Forest Health Conducted from 1999 through 2012 and the BCMPB Model (Year 10)*; BC Ministry of Forests, Lands and Natural Resource Operations: Victoria, BC, Canada, 2013. Available online: http://www.for.gov.bc.ca/ftp/hre/external/!publish/web/bcmpb/year10/BCMPB.v10.BeetleProjection.Update.pdf (accessed on 15 May 2015).
5. Alfaro, R.; Axelson, J.; Hawkes, B. Mountain pine beetle increases the complexity of fire-origin lodgepole pine stands in British Columbia, Canada. *J. Ecosyst. Manag.* **2008**, *9*, 1–5.
6. Westfall, J.; Ebata, T. *Summary of Forest Health Conditions in British Columbia*; Pest Management Report Number 15; BC Forest Service: Victoria, BC, Canada, 2008. Available online: http://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial_Overview/2008/Aerial%20Overview%202008.pdf (accessed on 8 May 2015).
7. Amman, G.D.; McGregor, M.D.; Cahill, D.B.; Klein, W.H. *Guidelines for Reducing Losses of Lodgepole Pine to the Mountain Pine Beetle in the Rocky Mountains*; UT. Technical Report INT-36; USDA Forest Service; Intermountain Forest and Range Experiment Station: Ogden, UT, USA, 1977; p. 28.

8. Eng, M.; Fall, A.; Hughes, J.; Shore, T.; Riel, B.; Hall, P.; Walton, A. *Provincial Level Projection of the Current Mountain Pine Beetle Outbreak: An Overview of the Model (BCMPB v2) and Results of Year 2 of the Project*; BC Forest Service: Victoria, BC, Canada, 2005. Available online: http://www.llbc.leg.bc.ca/public/pubdocs/bcdocs/376681/bcmpb_mainreport_2004.pdf (accessed on 12 May 2015).
9. BC Ministry of Forests and Range. *Timber Supply and the Mountain Pine Beetle Infestation in British Columbia: 2007 Update*; Forest Analysis and Inventory Branch; BC Ministry of Forest and Range: Victoria, BC, Canada, 2007; p. 32.
10. MacLauchlan, L. *Status of Mountain Pine Beetle Attack in Young Lodgepole Pine Stands in Central British Columbia*; Report for the Chief Forester of British Columbia; BC Ministry of Forests and Range: Victoria, BC, Canada, 2006. Available online: http://www.for.gov.bc.ca/rsi/ForestHealth/PDF/Young%20Pine%20Report_CF_final.pdf (accessed on 14 May 2012).
11. Runzer, K.; Hawkins, C.D.B. *Success Rate of MPB (Mountain Pine Beetle) Attack in Young Stands*. *Executive Summary*; FIA FSP Project M065002; BC Ministry of Forests and Range: Victoria, BC, Canada, 2006. Available online: http://www.for.gov.bc.ca/hfd/library/FIA/HTML/FIA2008MR194.htm (accessed on 7 May 2015).
12. MacLauchlan, L.E.; Brooks, J. *Determining Susceptibility of Young Pine Stands to the Mountain Pine Beetle, Dendroctonus Ponderosae, and Manipulating Future Stands to Mitigate Losses*; Final Technical Report; FIA FSP Project Y072003; BC Ministry of Forests and Range: Victoria, BC, Canada, 2007. Available online: http://www.for.gov.bc.ca/hfd/library/FIA/HTML/FIA2008MR194.htm (accessed on 15 April 2015).
13. Nussbaum, A. Forecasting the effects of species choices on long-term harvest levels: Sub-component of the provincial mountain pine beetle analysis project. In Proceedings of the Northern Silviculture Committee 2006 Winter Workshop, Victoria, BC, Canada, 2006. Available online: http://www.for.gov.bc.ca/hts/tsa/tsr3/rationale.pdf (accessed on 15 April 2015).
14. Association of British Columbia Forest Professionals (ABCFP). *Mid-Term Timber Supply Advocacy Report*; Association of British Columbia Forest Professionals: Vancouver, BC, Canada, 2011.
15. Bogdanski, B.; Sun, L.; Peter, B.; Stennes, B. *Markets for Forest Products Following a Large Disturbance: Opportunities and Challenges from the Mountain Pine Beetle Outbreak in Western Canada*; Report BC-X-429; Natural Resource Canada, Canada Forest Services: Victoria, BC, Canada, 2011. Available online: http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/32226.pdf (accessed on 18 April 2015).
16. Pousette, J.; Hawkins, C. An assessment of critical assumptions supporting the timber supply modelling for mountains-pine-beetle-induced allowable annual cut uplift in the Prince George Timber Supply Area. *BC J. Ecosyst. Manag.* **2006**, *7*, 93–104.
17. Hawkins, C.D.B.; Dhar, A.; Balliet, N.; Runzer, K.D. Residual mature trees and secondary stand structure after mountain pine beetle attack in central British Columbia, *For. Ecol. Manag.* **2012**, *277*, 107–115.
18. Meidinger, D.; Pojar, J.; Harper, W.L. Sub-boreal spruce zone. In *Ecosystems of British Columbia*; Meidinger, D., Pojar, J., Eds.; BC Ministry of Forests: Victoria, BC, Canada, 1991; pp. 195–207.

19. BC Ministry of Forest Range. *Explanation of the Forest Planning and Practices Regulation Amendments to Protect Secondary Structure*; B.C. Forest Service: Victoria, BC, Cananda, 2008. Available online: http://www.for.gov.bc.ca/hfp/silviculture/secondary_structure/secondary_structure_reg.pdf (accessed on 14 April 2015).
20. Hawkins, C.D.B.; Dhar, A.; Balliet, N. Radial growth of residual overstory trees and understory saplings after mountain pine beetle attack in central British Columbia. *For. Ecol. Manag.* **2013**, *310*, 348–356.
21. McDonald, J.H. *Handbook of Biological Statistics*, 3rd ed.; Sparky House Publishing: Baltimore, MD, USA, 2014; p. 291.
22. Bates, D.; Maechler, M.; Bolker, B.M.; Walker, S. Fitting linear mixed-effects models using lme4; Journal of Statistical Software. Available online: http://arxiv.org/abs/1406.5823 (accessed on 16 September 2015).
23. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2012. Available online: http://www.R-project.org/ (accessed on 15 March 2014).
24. BC Ministry of Forests and Range. *FFT Walk through Ground Reconnaissance Survey Procedures for Stands Impacted by MPB*; BC Forest Service: Victoria, BC, Canada, 2006. Available online: http://www.for.gov.bc.ca/ftp/hfp/external/!publish/FIA%20Documents/Standards/FFT_Survey/MPB_Survey_Standard_PGTSA.pdf (accessed on 18 April 2015).
25. Kane, J.M.; Kolb, T.E. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. *Oecologia* **2010**, *164*, 601–609.
26. Ferrenberg, S.; Kane, J.M.; Mitton, J.B. Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. *Oecologia* **2014**, *174*, 1283–1292.
27. Shore, T.L.; Safranyik, L.; Lemieux, J.P. Susceptibility of lodgepole pine stands to the mountain pine beetle: Testing of a rating system. *Can. J. For. Res.* **2000**, *30*, 44–49.
28. Klutsch, J.G.; Negrón, J.F.; Castello, S.L.; Rhoades, C.C.; West, D.R.; Popp, J.; Caisse, R. Stand characteristics and downed woody debris accumulations associated with a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in Colorado. *For. Ecol. Manag.* **2009**, *258*, 641–649.
29. Björklund, N.; Lindgren, B.S.; Shore, T.L.; Cudmore, T. Can predicted mountain pine beetle net production be used to improve stand prioritization for management? *For. Ecol. Manag.* **2009**, *257*, 233–237.
30. Progar, R.A.; Blackford, D.C.; Cluck, D.R.; Costello, S.; Dunning, L.B.; Eager, T.; Jorgensen, C.L.; Munson, A.S.; Steed, B.; Rinella, M.J. Population densities and tree diameter effects associated with verbenone treatments to reduce mountain pine beetle caused mortality of lodgepole pine. *J. Econ. Entomol.* **2013**, *106*, 221–228.

31. Coates, K.D.; Glover, T.; Henderson, B. *Abundance of Secondary Structure in Lodgepole Pine Stands Affected by the Mountain Pine Beetle in the Cariboo-Chilcotin*; Mountain Pine Beetle Working Paper 2009–20; Canadian Forest Service, Pacific Forestry Centre: Victoria, BC, Canada, 2009. Available online: http://cfs.nrcan.gc.ca/pubwarehouse/pdfs/31195.pdf (accessed on 12 May 2015).
32. Vyse, A.; Ferguson, C.; Haggard, D.J.; Roach, J.; Zimonick, B. Regeneration beneath lodgepole pine dominated stands attacked or threatened by the mountain pine beetle in the south central Interior, British Columbia. *For. Ecol. Manag.* **2009**, *258*, S36–S43.
33. Axelson, J.N.; Alfaro, R.I.; Hawkes, B.C. Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia. *For. Chron.* **2010**, *86*, 87–99.
34. Veblen, T.T.; Hadley, K.S.; Reid, M.; Rebertus, A.J. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* **1991**, *72*, 213–231.
35. Murphy, T.E.L.; Adams, D.L.; Ferguson, D.E. Response of advance lodgepole pine regeneration to overstory removal in eastern Idaho. *For. Ecol. Manag.* **1999**, *120*, 234–244.
36. Amoroso, M.M.; Coates, K.D.; Astrup, R. Stand recovery and self-organization following large-scale mountain pine beetle induced canopy mortality in northern forests. *For. Ecol. Manag.* **2013**, *310*, 300–311.
37. Dhar, A.; Coates, K.D.; Rogers, B.; Hardy, K. Impact of mountain pine beetle on mid-term timber supply in sub boreal spruce zone of British Columbia. In Proceedings of the 16th International Boreal Forest Research Association (IBFRA) Conference, Edmonton, AB, Canada, 7–10 October 2013; p. 28.
38. Astrup, R.; Coates, K.D.; Hall, E. Recruitment limitations in forests: Lessons from an unprecedented mountain pine beetle epidemic. *For. Ecol. Manag.* **2008**, *256*, 1743–1750.
39. Dhar, A.; Hawkins, C.D.B. Regeneration and growth following mountain pine beetle attack: A synthesis of knowledge. *J. Ecosyst. Manag.* **2011**, *12*, 1–16.
40. Agee, J.K. *Fire ecology of Pacific Northwest Forests*; Island Press: Washington, DC, USA, 1993; p. 505.
41. Lindenmayer, D.B.; Burton, P.J.; Franklin, F.J. *Salvage Logging and its Ecological Consequences*; Island Press: Washington, DC, USA, 2008; p. 246.
42. Fedrowitz, K.; Koricheva, J.; Baker, S.C.; Lindenmayer, D.B.; Palik, B.; Rosenvald, R.; Beese, W.; Franklin, J.F.; Kouki, J.; Macdonald, E.; *et al*. REVIEW: Can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl. Ecol*. **2014**, *51*, 1669–1679.
43. Dhar, A.; Parrott, L. Salvage logging after mountain pine beetle outbreaks reduces the social-ecological resilience of forest landscapes. In Proceedings of the Mountain Pine Beetle Information Exchange Forum, Edmonton, AB, Canada, 22–23 April 2015; p. 17.
44. Drever, R.C.; Peterson, G.; Messier, C.; Bergeron, Y.; Flannigan, M. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res*. **2006**, *36*, 2285–2299.
45. Park, A.; Puettmann, K.; Wilson, E.; Messier, C.; Kames, S.; Dhar, A. Can boreal and temperate forest management be adapted to the uncertainties of 21st century climate change? *Crit. Rev. Plant Sci.* **2014**, *33*, 251–285.

46. Faccoli, M.; Bernardinelli, I. Composition and elevation of spruce forests affect susceptibility to bark beetle attacks: Implications for forest management. *Forests* **2014**, *5*, 88–102.
47. Nelson, T.A.; Boots, B.; Wulder, M.A.; Carroll, A.L. Environmental characteristics of mountain pine beetle infestation hot spots. *J. Ecosyst. Manag.* **2008**, *8*, 91–108.
48. Dhar, A.; Parrott, L.; Heckbert, S. Consequences of mountain pine beetle outbreaks on forest ecosystem services in western Canada. In Proceedings of the Mountain Pine Beetle Information Exchange Forum, Edmonton, AB, Canada, 22–23 April 2015; p. 17.
49. Dhar, A.; Parrott, L.; Heckbert, S. Mapping the impact of mountain pine beetle outbreaks on forest ecosystem services in British Columbia, Canada. In Proceedings of the IUFRO Landscape Ecology Conference Sustaining Ecosystem Services in Forest Landscapes Concepts, Research, and Applications, Tartu, Estonia, 23–30 August 2015. Available online: http://iufrole2015.to.ee/download/m55d4ea9be5748#iufrole_2015_abstracts_pdf (accessed on 02 September 2015).
50. Pec, G.J.; Karst, J.; Sywenky, A.N.; Cigan, P.W.; Erbilgin, N.; Simard, S.W.; Cahill, J.F., Jr. Rapid increases in forest understory diversity and productivity following a mountain pine beetle (*Dendroctonus ponderosae*) outbreak in pine forests. *PLoS ONE* **2015**, *10*, e0124691.
51. Stone, W.E.; Wolfe, M.L. Response of understorey vegetation to variable tree mortality following a mountain pine beetle epidemic in lodgepole pine stands in northern Utah. *Vegetatio* **1996**, *122*, 1–12.