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Residual mature trees and secondary stand structure after mountain pine beetle attack in central British Columbia

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ABSTRACT

Lodgepole pine forests in British Columbia (BC) are experiencing the largest mountain pine beetle (MPB) epidemic in recorded history. Now that the peak of the epidemic has passed, information regarding the existing live secondary stand structure (height >4 m but DBH <7.5 cm), regeneration (⩽4 m in height) and residual mature trees (DBH >7.5 cm) in the MPB-attacked stands are needed to assess management options and future timber supply. In total, 459 MPB-attacked pine stands were sampled from eight different age classes (13–250 yr) in three different ecological subzones (dry, mesic, moist) of central BC. Mean MPB attack was greater than 40% when stand age was ⩾20 years. Secondary stand structure and residual mature tree layers offer significant opportunities for mitigating the effects of MPB attack on future commercial wood values and ecological processes. The mean density of secondary stand structure and regeneration varied widely within and among ecological subzones. Depending on stand age, 44–98% of stands still contained sufficient stems after MPB attack to be considered stocked. Species composition varied at the stand level, but most stands had sufficient amounts of BC's preferred commercial species. Due to MPB caused mortality, most of the stands were moving towards a mixed species and uneven aged condition. A SORTIE-ND model projection suggests that stands which had a minimum of 900 stems/ha of secondary structure >4 m in height can reach merchantable volumes within 30 years.

1. Introduction

Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) forests of British Columbia (BC) are experiencing the largest mountain pine beetle (MPB) (*Dendroctonous ponderosae* Hopkins) epidemic in recorded history. As of 2010, it was estimated that over 17.5 million hectares of lodgepole pine forests across BC were affected to varying degrees by MPB attack (BC Ministry of Forests and Range, 2011). It is projected that at least 59% of the of the total merchantable lodgepole pine volume (age >60 years) in BC will be killed in this epidemic (Walton, 2011). In addition, an estimated 50% of the immature lodgepole pine stands (age <60 years) may also be attacked (Westfall and Ebata, 2008). It is likely that the current epidemic will end only when most of the mature pine has been killed (BC Ministry of Forests and Range, 2006a) along with a portion of the immature pine (Runzer et al., 2008).

Generally, MPB attacks larger diameter (DBH >20 cm) (Amman et al., 1977) and older (ages >60 years) trees (Shore et al., 2006). However, the present MPB outbreak is more widespread and severe than past outbreaks. As a result, MPB also attacked younger stands (even <20 years old) if no mature trees were available to attack (Maclauchlan, 2006; Runzer et al., 2008). However, Shrimpton and Thomson (1985) mentioned that tree age had little predictive value for attack by MPB while Katovich and Lavigne (1986) suggested that phloem width was the best indicator of host susceptibility to MPB attack. Pine trees killed by the MPB emulate a thinning from above (Roe and Amman, 1970) and post attack stand dynamics will be driven by residual mature trees (⩾7.5 cm DBH), secondary stand structure (saplings <7.5 cm DBH and >4 m in height) and regeneration (⩽4 m in height). Almost 200 million m^3 of MPB-attacked timber may remain unsalvaged throughout BC (BC Ministry of Forests, 2004) due to low feasibility for salvage (accessibility, management objectives, lack of milling capacity, economic factors) and ecological concerns. However unsalvaged stands may have higher rates of surface fires due to the high deposition of fuel sources (Page and Jenkins, 2007).

The peak of the MPB epidemic has now passed the central BC interior (Walton et al., 2008) and efforts are required to determine the conditions of attacked stands. Therefore information regarding existing residual mature trees, secondary stand structure and

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regeneration are needed to project stand dynamics and future forest condition. In north central BC, Coates et al. (2006) reported that 20–30% of stands have enough secondary stand structure to contribute to a mid-term timber supply if left unsalvaged and an additional 40–45% of stands have sufficient understory to be considered stocked (stands have a minimum number of healthy stem, according to BC legislation 900 stem/ha if height is >4 m or 700 if height is >6 m for MPB-attacked stand) in a certain height group. Retaining such stands would reduce the rotation age by 10–30 years, compared to starting anew (Coates et al., 2006), help to mitigate the projected mid-term timber supply shortfall (Pousette and Hawkins, 2006; Pousette, 2010) and enhance ecological diversity. Coates et al. (2006) also suggested that only 20–25% of stands needed some form of intervention due to lack of secondary stand structure. Therefore, not all residual stands may need rehabilitation from a timber management or an ecological point of view. In this regard, a post MPB-attacked inventory in Central BC is needed to gain insight about residual mature trees, secondary stand structure and regeneration status. Such information will help to select those stands where immediate management intervention is required to meet timber supply obligations.

Forest dynamics is the change of forest composition and structure over time and understanding these is an important research question for MPB-attacked stands. The ability to accurately model complex forest dynamics and project future growth, yield and structure of stands is critical to sound forest management. Similarly understanding of regeneration patterns and stand dynamics including growth and mortality are vital factors when modeling stand development for management objectives (Coates et al., 2009).

The model SORTIE-ND (http://www.sortie-nd.org/) is an ecological modeling program that has been designed to predict stand dynamics based upon the growth of individual trees in multi-species, complex stands. This model is well suited to predict future growth for MPB-attacked stands in British Columbia (Coates et al., 2003). The model SORTIE-ND uses a combination of empirical and mechanistic sub-models to predict forest dynamics based on field experiments that measure fine-scale and short-term interactions among individual trees (Coates et al., 2010). This model can be adapted to a wide range of specific conditions and has the flexibility to incorporate new research findings model parameter files.

The main objectives of this study were (1) to determine the quality and quantity of residual mature trees and secondary stand structure in MPB-attacked stands, and (2) to predict the future growth and yield of some MPB-attacked stands based on secondary stand structure. The outcomes of the research will help to guide management activities in MPB-killed stands especially for growth and quality of secondary stand structure. Moreover, it also improves harvest scheduling in central BC by identifying which stands are most suitable for retaining or harvesting.

2. Materials and methods

2.1. Site selection

The sample area was located within the Prince George forest district from 53°22′ to 54°55′ N and 120°15′ to 125°04′ W with a total area of about 54,000 km^2 (Fig. 1). The area is in the sub-boreal spruce biogeoclimatic zone with three broad sub-zones dry, mesic and moist all with a cool thermal regime (Meidinger et al., 1991). Most of the sampled stands were lodgepole pine-dominated covering eight different age classes from 13 to 250 years (Table 1). Stands were attacked by MPB within the past 9 years and were 1–9 years post MPB disturbance. The origins of the sampled younger stands ($\leqslant$40 years) were harvest-based plantations whereas the older ones were of natural disturbance origin, primarily fire-based. Before reconnaissance, stands were identified on forest cover maps obtained from aerial photos and satellite images. Generally, 70% of the stands were selected randomly and the remaining 30% were targeted to ensure complete coverage of the study area, ecological zones and different age classes.

2.2. Data collection and sampling protocol

Data were collected from 459 stands across the district in 2005 (dry area) in 2006 (moist area) and in 2007 (mesic area) (Table 1). The initial sampling design was based on protocols and recommendations presented by BC Ministry of Forests (1998), and summarized in Rakochy (2005). Depending on stand area, 4–10 temporary sample plots (TSP) were established along a transect line at 50 m intervals in each stand. Transects commenced 50 m or at least two tree lengths off any given base line (road, timber type or age class change). All TSP plot centers were painted and GPS locations were recorded for future reference. Two different radii, (a) 5.64 m (100 m^2) plots for residual mature trees ($\geqslant$7.5 cm DBH) and (b) 3.99 m (50 m^2) plots for secondary stand structure (height >4 m but DBH <7.5 cm) and regeneration ($\leqslant$4 m in height) were established in each TSP. Inter-plot spacing was increased by increments of 25 m when unrepresentative areas were encountered (swamps, openings, or change in timber type). For each TSP, mean tree age, crown closure [using a densitometer (an instrument used for taking measurements of canopy cover) and hemispheric photos], stand age, site classification (slope, aspect, topographic location), and site index [SI_{50} = is defined as top height at a breast height reference age of 50 years (Nigh, 1999)] were measured. For the mature layer, all trees (DBH $\geqslant$7.5 cm) were numbered with tree marking paint and DBH, MPB attack status (current, older, strip attack, dead), Workers Compensation Board (WCB, now WorkSafe BC) danger tree code, tree health, and crown class were recorded at each TSP. For all secondary stand structure (DBH <7.5 cm) species, height, DBH, and vigor were recorded. Tree health was assessed based on four vigor codes: A = healthy and vigorous trees with no stem defects; B = healthy and vigorous trees with minor stem defects; C = unhealthy trees with major stem defects; and D = moribund trees (expected to die in the next 2–3 years).

2.3. Defined secondary stand structure

In 2008, the BC Ministry of Forests and Range initiated a Forest Planning and Practices Regulation (FPPR) amendment for secondary stand structure which indicated that MPB-killed stands with an "adequate stocking density" will not be harvested and only pine leading (pine-dominant) stands that have inadequate secondary structure will be harvested. According to FPPR amendments the term "adequate stocking density" is defined as a minimum number of certain sized suitable secondary structure trees per hectare that are necessary to produce a merchantable stand volume (150 m^3/ha) by the mid-term. The mid-term timber supply is a term that refers to that portion of the timber inventory that would be available for harvest within the middle of the normal management cycle. However mid-term timber supply for MPB-infested stands are associated with the end of the MPB-damaged pine salvage period. According to ABCFP (2011), the period of mid-term timber supply is normally 30–70 years in the BC interior. Based on growth and yield analysis by BC Ministry of Forests and Range (2008), the minimum stocking level for a MPB-attacked stand is 900 healthy stems/ha of trees >4 m in height or 700 stems/ha with height >6 m with at least 1.6 m separating each tree. During field investigation, the FPPR amendment was modified in two ways: (a) instead of a distance measurement we calculated the health of

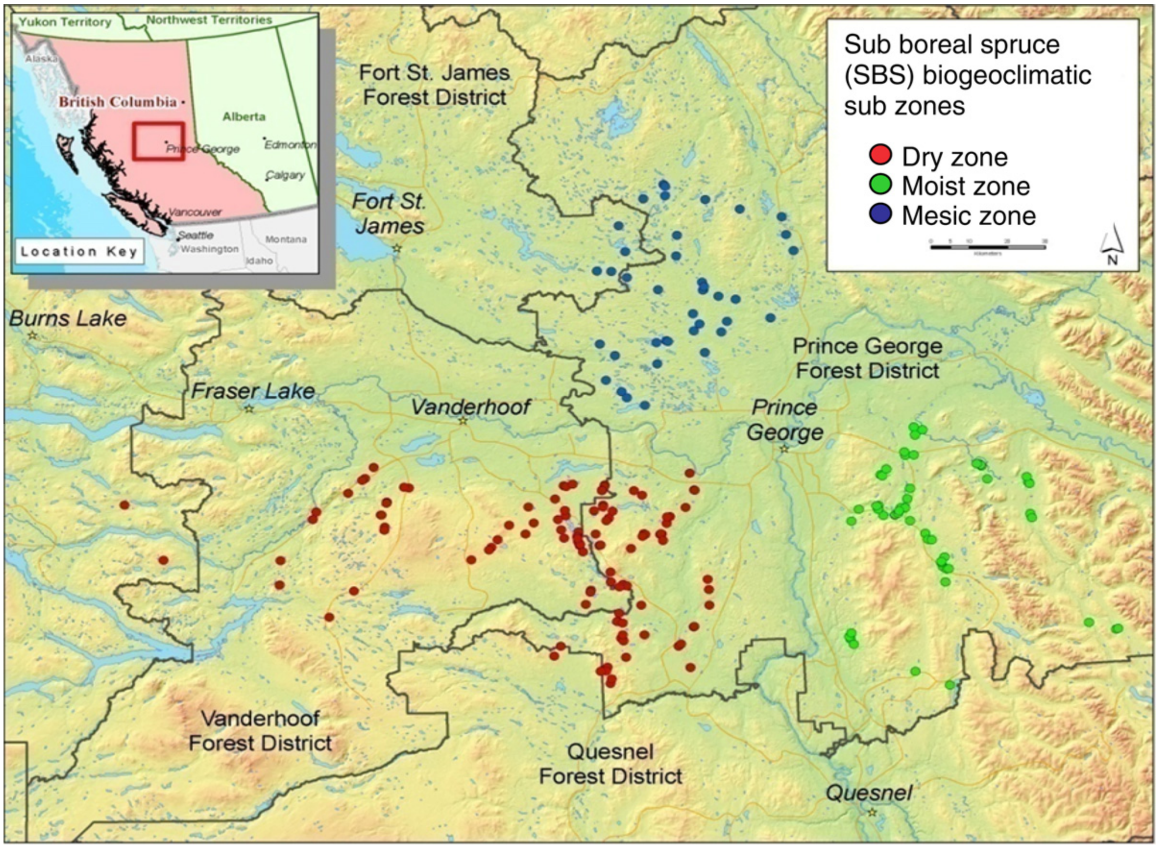

Fig. 1. Study location of the central BC interior by dry, mesic and moist sampling areas.

Table 1
Mean MPB attack (percentage of mature stems) for all species and only pine by age class and number of sampled stands based on ecological subzone and age class.

Age class	Age [year]	Mean MPB attack [%]		Sampled ecological zone			Sampled stands	Total temporary sample plots
		All species	Pine	Dry	Moist	Mesic		
1	13–20	6	7	12	16	27	55	270
2	21–40	40	47	64	44	41	149	739
3	41–60	46	54	17	16	5	38	191
4	61–80	43	55	38	27	6	71	345
5	81–100	48	64	12	6	7	25	125
6	101–120	46	62	10	9	3	22	106
7	121–140	36	65	31	7	7	45	223
8	141–250	37	70	21	21	12	54	180

each secondary stand structure tree using the health measurement protocol and (b) included an upper limit of diameter (<7.5 cm DBH) for secondary stand structure which was not mentioned in the original amendment. Generally, inter-tree distance was ⩾1 m. It was assumed this approach would provide more in depth information about secondary stand structure after MPB attack. Therefore, secondary stand structure stems >4 m and >6 m in height with DBH <7.5 cm were measured for each age class (1–8) in different ecological zones (Table 1). Furthermore, density of regeneration ⩽4 m in height was also measured for each age class and ecological zone. Pivot tables were developed by stand, plot and species to identify the distribution of stems and species across stands and the landscape.

2.4. SORTIE-ND modeling and analysis

There is not enough information to model regeneration capabilities across a variety of ecosystems after MPB attack (Dhar and Hawkins, 2011). Therefore, the proportion of stands which fall within the FPPR amendments for secondary structure categories (>900 stems/ha with height >4 m) was determined for each age class and several SORTIE-ND (version 6.09) (Coates et al., 2003) runs were carried out. The parameter file used was a generic one which was developed for the sub boreal spruce (SBS) biogeoclimatic zone in central BC by Coates et al. (2006). Our investigation was carried out in the same biogeoclimatic zone, therefore stand data from our study were pooled and a stocking list (species, DBH, number) was used as the SORTIE-ND tree list for the model run. The only simulation in the run was the killing in the tree layer by the MPB. The main goal of this projection was to only see if there would be 150 m^3/ha timber available for mid-term harvest. As MPB attack was recent, there are no local growth data to compare or validate the model projections.

Tree lists representative of data from: (1) a stand with an average level of remaining live secondary stand structure for the age class and (2) a stand which met minimum stocking (>900 stems/

Table 2
ANOVA results for density of secondary stand structure and regeneration following MPB attack by age class and ecological zones.

Source	Mean square	df	F	P
Residual mature tree				
Age class	2118,698.54	7	8.778	**<0.001**
Ecological zone	122,593.51	2	0.508	0.602
Error	241,374.42	449		
FPPR amendments of secondary stand structure [>900 stems/ha with >4 m in height]				
Age class	21,895,432.99	7	8.93	**<0.001**
Ecological zone	7329,234.75	2	2.99	0.051
Error	2451,427.19	453		
Regeneration [stems ⩽4 m in height]				
Age class	17,616,406.99	7	2.95	**0.005**
Ecological zone	84,527,318.38	2	14.15	**<0.001**
Error	5972,108.018	453		

Significant (α = 0.05) results are in bold.

ha, >4 m in height) for secondary structure were used. The growth of secondary stand structure (>4 m in height, but <7.5 cm DBH) was projected for 100 years. The calculated data and model projections were assessed to see if minimum mid-term timber supply were achieved.

All statistical analysis was carried out using (SYSTAT® version 12.0) and an analysis of variance (ANOVA) was conducted to determine the effects of biogeoclimatic subzone (dry, moist and mesic) and different age classes on density of residual mature trees, secondary stand structure and regeneration.

3. Results

3.1. Mountain pine beetle attack

When all species were considered, mean MPB attack (based on number of stems) increased noticeably from age class 1 (13–20 yr) to 2 (21–40 yr) but rate of attack was variable from age class 2–7 (Table 1). When only lodgepole pine were considered, the percentage of MPB attack also increased markedly from age class 1–2 and exceeded 50% for age class 3 (41–60 yr) and older (>61 yr) (Table 1). The greatest mean MPB attack (70%) for lodgepole pine was observed in the oldest age class (141–250 yr).

3.2. Density by ecological subzone and age class

ANOVA results showed that density of residual mature trees (DBH ⩾7.5 cm) and secondary stand structure (stems >4 m in height) varied significantly among age classes (P < 0.001) while ecological zones were not significantly different from each other for mature trees (P = 0.602) but were almost significant for secondary stand structure (P = 0.051) (Table 2). On average, all age classes exhibited an acceptable minimum level of stocking [based on BC Ministry of Forests and Range (2006b) minimum stocking 600 stems/ha] of residual mature trees except age class 6 (592 stems/ha) (Table 3). Secondary stand structure, however, varied considerably across age classes and ecological zones and only age class 3 (41–60 yr) stands had an adequate amount of secondary stand structure. Considering ecological units, younger age classes (2 and 4) on dry and mesic sites had a sufficient number of stems according to the FPPR amendments (Table 3, Fig. 2). However, the overall density of regeneration (stems ⩽4 m in height) was quite high (range from 1631 to 3086 stems/ha) and differed significantly (P < 0.001) among the ecological units and age classes (Tables 2 and 3, Fig. 2). Looking at overall stem density with height >4 m, all age classes except 6 (101–120 yr) had at least 1000 stems/ha.

3.3. Species distribution

The species distribution of the residual mature tree layer and secondary stand structure varied from stand to stand and at the landscape level. For age classes 1–4, lodgepole pine comprised the majority of the residual mature stems and larger secondary stand structure, whereas hybrid spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) made up the majority of the regeneration layer (Table 4). In older age classes (5–8), lodgepole pine has been replaced by hybrid spruce and subalpine fir in the residual mature tree layer; whereas a mixture of species, including lodgepole pine, hybrid spruce and subalpine fir, dominated the larger secondary stand structure. The dominant species in the regeneration layer (⩽4 m height) changed with age class and varied by site. There were more shade-tolerant species (subalpine fir) prevalent in the older age classes (Table 4). Although pine was present in all age classes, with the exception of the regeneration layer, pine is the most abundant species for age classes 1 and 2.

Table 3
Overall mean density ± SD (stems/ha) of all residual trees and secondary structure by age class and height category.

Height category	Age class [year]							
	1 [13–20]	2 [21–40]	3 [41–60]	4 [61–80]	5 [81–100]	6 [101–120]	7 [121–140]	8 [141–250]
Residual mature tree [DBH ⩾7.5 cm]	1261 ± 389	841 ± 205	1136 ± 245	857 ± 151	704 ± 112	592 ± 80	684 ± 97	687 ± 83
Secondary stand structure (DBH <7.5 cm) by height category								
Secondary structure height >6 m height	238 ± 379	409 ± 659	1056 ± 1488	345 ± 540	164 ± 299	94 ± 138	98 ± 228	88 ± 158
Secondary structure height >4 m height	708 ± 773	692 ± 852	1550 ± 2035	558 ± 747	311 ± 421	244 ± 252	290 ± 481	369 ± 494
Regeneration ⩽4 m height	1754 ± 1935	1726 ± 2827	2359 ± 3920	1631 ± 2186	1707 ± 1345	2147 ± 1675	2570 ± 2393	3086 ± 2651
Overall stems [mature + secondary] >4 m	1969 ± 965	1533 ± 1162	2686 ± 2523	1415 ± 1121	1015 ± 731	836 ± 403	974 ± 744	1056 ± 741

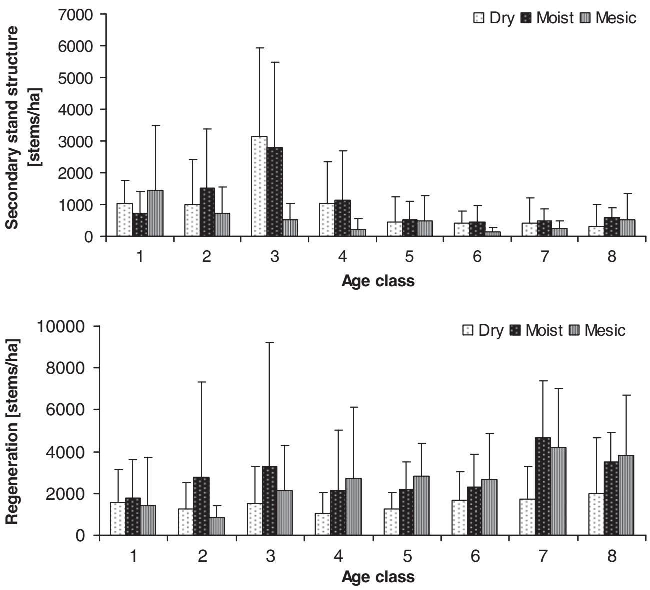

Fig. 2. Secondary stand structure (stems >4 m height but DBH <7.5 cm) and regeneration (stems ⩽4 m height) density by ecological zones.

The proportion of stands by density class for each age class were determined based on secondary stand structure (Ministry of Forests and Range, 2008) and stand level stocking. Among the seven age classes, only three are presented as they cover the greatest (age class 6), middle (age class 2) and the least (age class 5) range of observed responses (Fig. 3). Generally, the younger age classes (1–4) exhibited a lower proportion of stands with secondary stand structure compared to the older age classes (5–8).

In age class 2, 64% of the total stands had >900 stems/ha of stems with height >4 m and 43% of the stands had >700 stems/ha of stems with height >6 m (Fig. 3). Lodgepole pine-dominated both the residual mature layer and secondary stand structure in age class 2. In age class 5, 32% of the stands had >700 stems/ha stems with height >6 m and 45% of the stands had >900 stems/ha stems with height >4 m (Fig. 3). The majority of stands of age class 5 were dominated by lodgepole pine and hybrid spruce. Age class 6 stands were comparatively poorly stocked. Only 23% of the stands had >700 stems/ha stems with height >6 m and 42% of stands had >900 stems/ha stems with height >4 m (Fig. 3). When combined, secondary stand structure (>4 m height) plus the residual mature tree layer (DBH ⩾7.5 cm), more than 75% of stands were stocked with preferred or acceptable commercial species (Fig. 3).

3.4. Health condition of secondary stand structure

We only considered viable secondary stand structure ['Viable' stocking is defined as the sum of all healthy secondary stand structure and all stems >4 m in height but <7.5 cm DBH] Based on vigor codes A and B, viable secondary structure decreased markedly from age class 1–2 and then held between 59% and 66% for age classes 3–8 (Table 5). Considering healthy species, lodgepole pine was the dominant species (⩾50% of stems) in the younger age classes (age classes 1–4), whereas in older age classes (5–8) there was

Table 4
Density of residual mature trees (RMT), secondary stand structure (SSS) and regeneration (Reg.) by species, age class and height category (healthy trees only).

Age class [year]	Height category	Species composition [stems/ha]									
		Lp	Hs	Sf	Df	Bs	Wh	Wrc	Ta	Pb	Bc	Total
1 [13–20]	RMT	1118	54	17	5	2	–	–	59	3	3	1261
	SSS > 6 m	130	10	2	–	1	–	–	87	6	2	238
	SSS > 4 m	413	56	15	1	3	–	–	170	24	26	708
	Reg ⩽ 4 m	357	643	118	26	1	31	–	281	275	22	1754
2 [21–40]	RMT	636	76	32	9	6	1	–	65	12	4	841
	SSS > 6 m	274	22	5	4	2	–	–	78	14	10	409
	SSS > 4 m	359	116	29	9	13	–	–	124	26	16	692
	Reg ⩽ 4 m	185	786	320	23	50	25	28	170	110	29	1726
3 [41–60]	RMT	770	139	13	48	75	3	–	51	34	3	1136
	SSS > 6 m	778	77	3	83	32	5	–	21	57	–	1056
	SSS > 4 m	919	241	31	155	78	7	–	31	88	–	1550
	Reg ⩽ 4 m	123	1192	567	122	269	27	7	32	20	–	2359
4 [61–80]	RMT	463	168	25	29	140	1	–	20	7	4	857
	SSS > 6 m	188	60	8	4	81	–	–	–	2	2	345
	SSS > 4 m	240	123	30	13	145	1	–	–	4	2	558
	Reg ⩽ 4 m	246	297	425	69	478	93	–	8	12	3	1631
5 [81–100]	RMT	276	232	53	14	110	–	–	18	1	–	704
	SSS > 6 m	69	58	6	2	27	–	–	2	–	–	164
	SSS > 4 m	81	143	39	2	43	–	–	3	–	–	311
	Reg ⩽ 4 m	378	635	428	2	243	–	–	16	2	3	1707
6 [101–120]	RMT	190	207	68	32	57	–	–	29	9	–	592
	SSS > 6 m	69	13	3	5	4	–	–	–	–	–	94
	SSS > 4 m	113	38	63	13	15	–	–	2	–	–	244
	Reg ⩽ 4 m	473	281	938	45	345	–	–	44	21	–	2147
7 [121–140]	RMT	101	294	129	95	31	–	–	10	23	–	684
	SSS > 6 m	16	39	15	24	1	–	–	3	–	–	98
	SSS > 4 m	25	104	102	52	4	–	–	3	–	–	290
	Reg ⩽ 4 m	172	396	1611	143	229	–	–	19	–	–	2570
8 [141–250]	RMT	47	225	202	36	110	38	6	9	14	–	687
	SSS > 6 m	6	15	22	1	28	2	1	9	4	–	88
	SSS > 4 m	17	48	198	5	75	6	3	12	5	–	369
	Reg ⩽ 4 m	109	418	1920	34	401	80	48	60	15	1	3086

Where Bc = Black cottonwood, Ta = Trembling aspen, Sf = Subalpine fir, Pb = Paper birch, Df = Douglas-fir, Lp = Lodgepole pine, Bs = Black spruce, Wh = western hemlock, Wrc = western red cedar and Hs = Hybrid spruce.

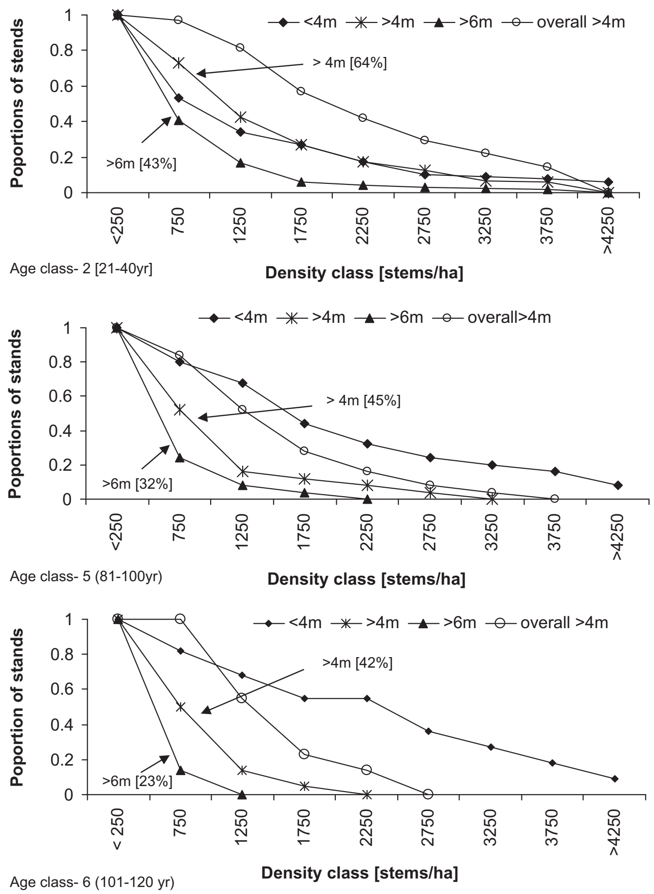

Fig. 3. Proportion of age class 2, 5 and 6 stands with density of stems ⩽4 m in height, >4 m in height, >6 m in height and overall >4 m (stems >4 m height + all residual mature trees).

a greater mixture of species but the more shade-tolerant spruce and subalpine fir were the healthiest (Table 5).

3.5. SORTIE-ND model run results

A SORTIE-ND model projection showed that stands representing the average MPB attack in age classes 1–4 can produce sufficient volume [$\geqslant$150 m^3/ha based on BC Ministry of Forests and Range (2008)] within 30 years to meet the merchantability requirement (Table 6). This indicated, irrespective of MPB attack, all stands in age classes 1–4 can produce an economically viable timber supply within 30 years. Projected yields based on average MPB-attacked stands are below the volume threshold for age classes 5–8 (Table 6). In stocked stands, lodgepole pine will comprise the major share of merchantable timber over the next 60 years in the age class 5 (Fig. 4a) whereas in age class 7 (121–140 yr) subalpine fir will provide the majority of merchantable timber over the next 60 years (Fig. 4b). In age class 2 (21–40 yr) before MPB attack almost all the yield comes from lodgepole pine (Fig. 5a), but the spruce contribution to volume in age class 2 stands with average MPB attack are more complex because lodgepole pine is replaced by spruce and subalpine fir (Fig. 5b).

4. Discussion

MPB attack percentages were greater than previously reported for age class 1–3 stands (Table 1). The present mortality rates in older age class pine stands were greater than those observed in previous MPB outbreaks (Safranyik et al., 1974; Amman et al., 1977; Shore et al., 2000) but similar to recent observations in Colorado (Klutsch et al., 2009). The consequence of tree mortality caused by MPB accelerates the mixed species nature and uneven age structure for both older and younger age class stands (Dhar and Hawkins, 2011; Oliver and Larson, 1996, p. 161). In the case of younger age classes, this shift occurred due to a thinning of pine from above (Roe and Amman, 1970) and the potential release (Romme et al., 1986; Heath and Alfaro, 1990) of the diversity of secondary stand structure species.

4.1. Stand structure

Although the forests of central BC appear to have been devastated by the mountain pine beetle, residual mature and secondary stand structure layers revealed that this was not the case. Abundant residual green tree structure remains within MPB-attacked stands and on average, stands of all age classes are stocked with currently acceptable commercial species. Similar observations were made in other MPB studies in southeastern (Coates, 2008), southcentral (Vyse et al., 2009) and Cariboo-Chilcotin (Coates et al., 2009) regions of BC. In each of these studies, it was determined that the residual mature tree and secondary stand structure layers may offer significant opportunities for mitigating the effects of the MPB on future timber values and ecological processes (Vyse et al., 2009). However, Coates (2008), Coates et al. (2009) and Vyse et al. (2009) reported considerable variation in the amount of secondary stand structure among stands and we also observed a similar high variation among stands. This suggests that blanket or 'one size fits all' treatments will not be possible for MPB affected areas and stands will have to be surveyed and managed on a stand by stand basis.

Our study revealed that species composition and density varied among the stands in general but not by dry, mesic or moist ecological unit (Table 2). However, when looking at the regeneration (stem ⩽4 m in height) layer, the results showed that species composition

Table 5
Health status of residual secondary stand structure by age class following MPB attacked.

Age class	Unhealthy vigor code C & D [%]	Healthy vigor code A & B [%]	Viable (healthy) secondary stand structure >4 m height based on vigor codes A & B Species composition [%]
1 [13–20]	8.31	91.69	Lp = 78, Ta = 12, Hs = 6, Sf = 2, Pb = 1, Bc = 1
2 [21–40]	27.1	72.89	Lp = 66, Ta = 12, Hs = 12, Sf = 4, Pb = 3, Df = 1, Bs = 1, Bc = 1
3 [41–60]	35.9	64.09	Lp = 63, Hs = 14, Df = 7, Bs = 6, Pb = 5, Ta = 3, Sf = 2
4 [61–80]	33.7	66.28	Lp = 50, Hs = 20, Bs = 20, Sf = 4, Df = 3, Ta = 1, Pb = 1, Bc = 1
5 [81–100]	36.9	63.03	Hs = 37, Lp = 35, Bs = 15, Sf = 9, Df = 2, Ta = 2
6 [101–120]	40.7	59.34	Lp = 36, Hs = 29, Sf = 16, Bs = 9, Df = 5, Ta = 4, Pb = 1
7 [121–140]	33.6	66.41	Hs = 41, Sf = 24, Df = 15, Lp = 13, Bs = 4, Pb = 2, Ta = 1
8 [141–250]	33.7	66.22	Sf = 38, Hs = 26, Bs = 17, Lp = 6, Df = 4, Wh = 4, Ta = 2, Pb = 2, Wrc = 1

Where Bc = Black cottonwood, Ta = Trembling aspen, Sf = Subalpine fir, Pb = Paper birch, Df = Douglas-fir, Lp = Lodgepole pine, Bs = Black spruce, Wh = western hemlock, Wrc = western red cedar and Hs = Hybrid spruce.

Table 6
SORTIE-ND model projections by age class and stand type [projecting development of secondary stand structure independent of residual trees 30 years into the future].

Age class [year]	Stand	Stand type	Current/now (0 yr) stems/ha [>4 m]	30 years from now		
				Stems/ha [> 4 m]	Basal area [m²/ha]	Volume [m³/ha]
1 [13–20]	582/S	Stocked	920	1270	32	235
	265	Ave. attack (6%)	1600	894	29	239
2 [21–40]	22	Stocked	920	844	31	236
	466	Ave. attack (40%)	1280	1219	32	239
3 [41–60]	470	Stocked	920	860	32	255
	105	Ave. attack (46%)	440	479	25	208
4 [61–80]	9	Stocked	920	890	29	243
	352	Ave. attack (43%)	320	366	20	159
5 [81–100]	934	Stocked	920	878	30	253
	125	Ave. attack (48%)	80	150	8	68
6 [101–120]	703	Stocked	840	806	26	217
	334	Ave. attack (46%)	233	318	10	63
7 [121–140]	56	Stocked	918	923	24	149
	287	Ave. attack (36%)	0	95	2	11
8 [141–250]	407	Stocked	1200	1184	28	167
	144	Ave. attack (37%)	160	229	13	112

Stocked = stands that had a minimum of 900 stems/ha of secondary structure >4 m in height at year 0 (now). Average attack = stands with an average level of MPB attack for that age class.

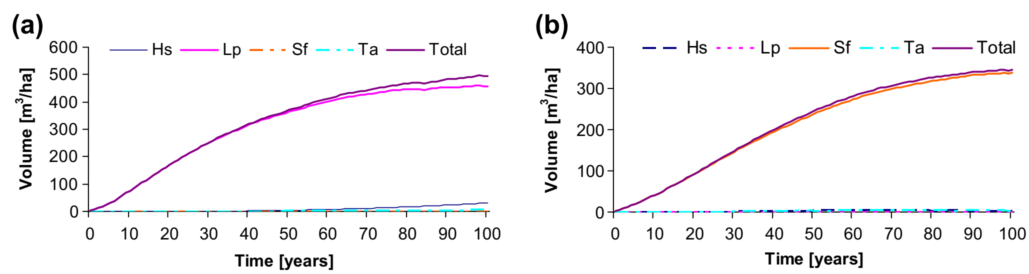

Fig. 4. Stem volume (m³/ha) of stocked stands projected by SORTIE-ND for 100 years (a) age class 5 (81–100 yr) and (b) age class 7 (101–120 yr) stands. [Hs = hybrid spruce, Lp = lodgepole pine, Sf = subalpine fir, Ta = trembling aspen. Stocked = stands that had a minimum of 900 stem ha^{-1} with height >4 m but <7.5 cm DBH].

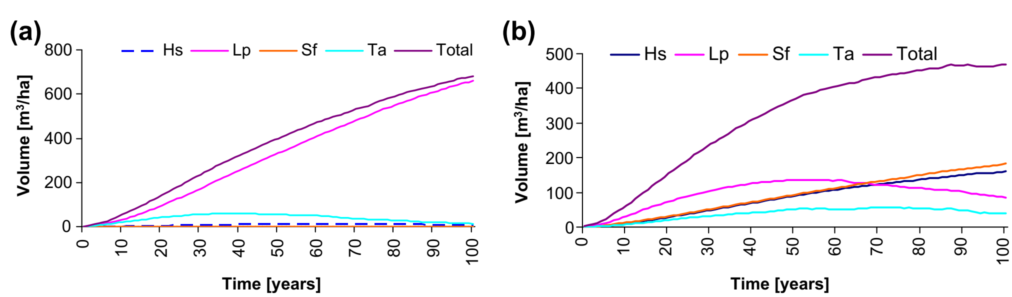

Fig. 5. Stem volume (m³/ha) of age class 2 (21–40 yr) stands projected by SORTIE-ND for 100 years (a) for stocked stands and (b) for average MPB attacked stands. [Hs = hybrid spruce, Lp = lodgepole pine, Sf = subalpine fir, Ta = trembling aspen, Stocked = stands that had a minimum of 900 stem ha^{-1} with height >4 m but <7.5 cm DBH].

and density varied significantly by ecological unit (Table 2). This was supported by Coates et al. (2009) and Vyse et al. (2009) studies in lodgepole pine dominated stands in the sub-boreal spruce and montane spruce biogeoclimatic zones in BC. In another study, Heath and Alfaro (1990) reported that MPB attack affected species composition more in the overstorey compared to the understorey. After MPB attack, lodgepole pine tended to be most abundant in the younger age classes (1–4), whereas hybrid spruce and subalpine fir tended to dominate the older age classes (5–8) (Table 4). Hybrid spruce, subalpine fir and black spruce were the most abundant species in the regeneration layer throughout all of the age classes because they are more shade-tolerant than the other species (Burns and Honkala, 1990) (Table 4). A high proportion of subalpine fir regeneration in the post-MPB recruitment layer was also observed by other studies in central British Columbia (Astrup et al., 2008; Nigh et al., 2008; Vyse et al., 2009).

Even though there was considerable variation among stands, there were sufficient numbers of healthy residual mature trees (⩾7.5 cm DBH) present throughout the sampling area to meet minimum stocking levels (600 stems/ha) in MPB-attacked stands. According to the BC Ministry of Forests and Range (2006b), mean minimum stocking levels for residual mature stands in MPB-attacked stands is 600 stems/ha. Also, generally there was a huge number of vigorous regeneration (⩽4 m in height) in all age classes; suggesting a high potential for future stand growth and productivity (Klutsch et al., 2009). Similar results were also reported by Coates (2008) and Vyse et al. (2009) in MPB-killed stands. Secondary stand structure (>4 m but <7.5 cm DBH), however, was found to be quite variable, and only age class 3 stands, on average, were found to have sufficient stocking of healthy stems to meet the FPPR amendments for secondary structure. According to Coates et al. (2009), approximately 70% of their sampled stands exceeded 1000 stems/ha of seedlings (10–130 cm height) and saplings (0–<7.5 cm DBH) in the Cariboo-Chilcotin region of BC. On the other hand, Vyse et al. (2009) reported that half of all of their plots had in excess of 600 stems/ha of advanced regeneration (>1.3 m height and <7.5 cm DBH). The differences were due to how secondary stand structure is defined between the studies and none of these studies followed the FPPR amendment. Moreover inter-tree spacing of these stems was uncertain. Although these stands were sufficiently stocked, inter-tree spacing is likely clumpier in naturally regenerated stands than one would find in an artificially regenerated stand (Griesbauer and Green, 2006) and a result maybe more voids (open areas).

Age class 1 had little MPB attack and 98% of the stands were stocked. On the other hand, younger age classes 2–4 (53%, 74% and 61%) and older age classes 5–8 (44%, 95%, 91% and 91%) have sufficient secondary stand structure to meet the FPPR amendment criteria even though all these stands had more than 40% MPB attack. Age class 5 (81–100 years old) stands may not have the same high stocking levels compared to other older age classes because of gap dynamics, tree mortality, and the initial recruitment of more shade-tolerant species (Oliver and Larson, 1996). Older age classes are further along the understory re-initiation pathway (Oliver and Larson, 1996), and have more regeneration available to contribute to secondary stand structure. It has been suggested that retention of stands with suitable secondary stand structure can shorten rotation ages significantly compared to establishing a new plantation (Coates et al., 2006, 2009).

Based on 'viable stocking' for secondary stand structure (stems >4 m height but DBH <7.5 cm), greater stocking was observed in younger age classes (1–4) than in older age classes (5–8) (Table 2). This likely occurs due to tree mortality which generally increases with stand age (Chen et al., 2008). The increase in viable stems between age classes 2 and 3 is probably due to the fact that age class 3 stands are of fire disturbance origin whereas age class 2 stands were logged and planted with density control. Although our results indicate that most of the MPB-attacked stands were adequately stocked, the major difference between pre and post MPB-attacked stands will be the substantial move from pine-dominated even-aged stands to mixed species uneven-aged stands in all age classes (Oliver and Larson, 1996, p. 161; FPB, 2007). Based on the FPB (2007) report, MPB-attacked pine stands create unique multi-aged and size stand structures. The shift from even-aged pine dominated stands to uneven-aged mixed species' stands will also result in a variety of forest vegetative condition including mitigation of future MPB impacts (Dhar and Hawkins, 2011). Variation in stand structure, stand development and species composition will potentially lead to different or new major commercial species and ecological values (Oliver and Larson, 1996, p. 169).

4.2. SORTIE-ND projections

SORTIE-ND runs on select, representative stands for each age class indicated that stands which are currently stocked with a minimum of 900 stems/ha of secondary stand structure (>4 m height but $\leqslant$7.5 cm DBH) reach minimum merchantable volumes (150 m^3/ha) in all age classes within 30 years. A similar result was reported by Coates (2008) when the stands were stocked according to the FPPR amendment 2008: five MPB-killed stands will fully recover to their pre-attack basal areas within 30 years without any intervention. These stands initially had levels of MPB attack ranging from 51% to 79% which is within the attack range observed in this study. Similar observations of residual vegetative radial growth were reported following MPB outbreaks in Wyoming (Romme et al., 1986) and the central BC interior (Heath and Alfaro, 1990). Romme et al. (1986) indicated release rates decreased when moving from understory trees to sub-canopy trees to residual trees. In stands with an average level of MPB attack and based on their secondary stand structure, it was determined that only age classes 1 through 4 will have stands with sufficient volume in 30 years time to be considered economically viable (Table 6). The other age classes have insufficient initial secondary stand structure to become commercially viable within 30 years. It is mentionable that the growth of the residual mature tree layer has not been accounted for in the SORTIE-ND yield projections. Therefore given the stocking of the residual tree layer, a minimum harvest level could be maintained over the next 30 years, if required.

5. Conclusion

Our data suggests that MPB-attacked stands will regenerate without assistance – under certain circumstances. Although stocking was highly variable, stands that are currently stocked can reach merchantable volumes within 30 years regardless of the level of MPB attack. Species composition is also highly variable and almost 75% of all stands are stocked with preferred or acceptable commercial species. The spatial distribution of secondary stand structure tends to be clumpier than that found in an artificially regenerated stand; providing opportunities for thinning, spacing or fill planting activities, if warranted. Almost 69% of secondary stand structure and 30% of residual mature trees were healthy and vigorous at the time of assessment although they likely will be susceptible to health problems as the stand develops.

There is a high degree of variability among stands and no accurate predictors (model) of secondary stand structure have been found to date. This suggests that management of MPB-attacked stands must be done at the stand level. As a result, we need new or better inventory data as traditional forest inventories do not account for vegetation below the canopy tree layer. Regardless of age class or ecological unit or level of MPB attack, forest managers will need to determine if a stand is stocked to assess its future economic and ecological viability.

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