Impacts and Susceptibility of Young Pine Stands to the Mountain Pine Beetle, *Dendroctonus ponderosae*, in British Columbia

Research Report

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Abstract

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytinae), is the most significant source of mortality of mature pine forests in western North America; however, in 2003–2004, high levels of mortality were observed in young pine stands in central British Columbia. This study investigates the impact of mountain pine beetle in these young pine stands. In 2005–2006, 24 plots were established throughout the outbreak area of British Columbia. Cumulative mortality reached 83% in some plots. Secondary bark beetles and other pests contributed to overall stand mortality and decline but to a far lesser degree than mountain pine beetle. Stem deterioration and falldown was very rapid and severe in young stands following attack. Over 70% of attacked trees in the Sub-Boreal Spruce ecosystem were severely deteriorated, or had fallen, less than 5 years after attack. The largest pines in young stands were attacked first, and brood production and emergence in these trees was more successful than in smaller, younger cohorts. Many attacked stands had received silvicultural treatments. Once the outbreak in adjacent mature stands had subsided, very little new attack occurred in young stands. Brood production was successful, albeit lower in young trees than in mature trees.

KEYWORDS: mountain pine beetle; secondary bark beetles; stand deterioration; young pine

Introduction

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytinae), is the single most destructive and significant source of mortality of mature pine forests in western North America (Shore et al. 2004; Taylor et al. 2006). Since 1995, the mountain pine beetle (MPB) has severely depleted lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) forests throughout the interior of British Columbia. In 2007, mapped mortality attributed to this beetle peaked in the south, central, and northern interior of the province, representing more than 10 million ha of pine attacked in 2006 (Westfall & Ebata 2008). By 2008, the beetle had affected almost 14 million ha of pine forests, an area 10 times larger than in any previously recorded outbreak (Safranyik et al. 2010). In 2009, a significant decline in the area affected by MPB was evident, owing to a much smaller 2008 flight, dwindling amounts of available and susceptible pine, and subsequently, a drastic decline in populations in 2010. The outbreak is currently

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limited to areas of susceptible mature lodgepole pine that remain in the south and south-eastern portions of the province (Buxton & Maclauchlan 2013) and the far northeast (Westfall & Ebata 2014). In total, more than 18.3 million ha of lodgepole pine have been affected (B.C. Ministry of Forests, Lands and Natural Resource Operations 2013).

Historically, MPB prefers larger diameter, mature pine with thicker phloem (Safranyik 1971; Shrimpton & Thomson 1985), and stands less than 60 years of age are seldom attacked (Amman et al. 1977; Shore & Safranyik 1992). Brood production in smaller, young trees is typically low because of thin phloem and excessive drying of the tree (Amman et al. 1977). However, with increased stand-tending activities, such as spacing, pruning and fertilization, lodgepole pine can attain a large size before 60 years of age, thus becoming a more acceptable host for the beetle.

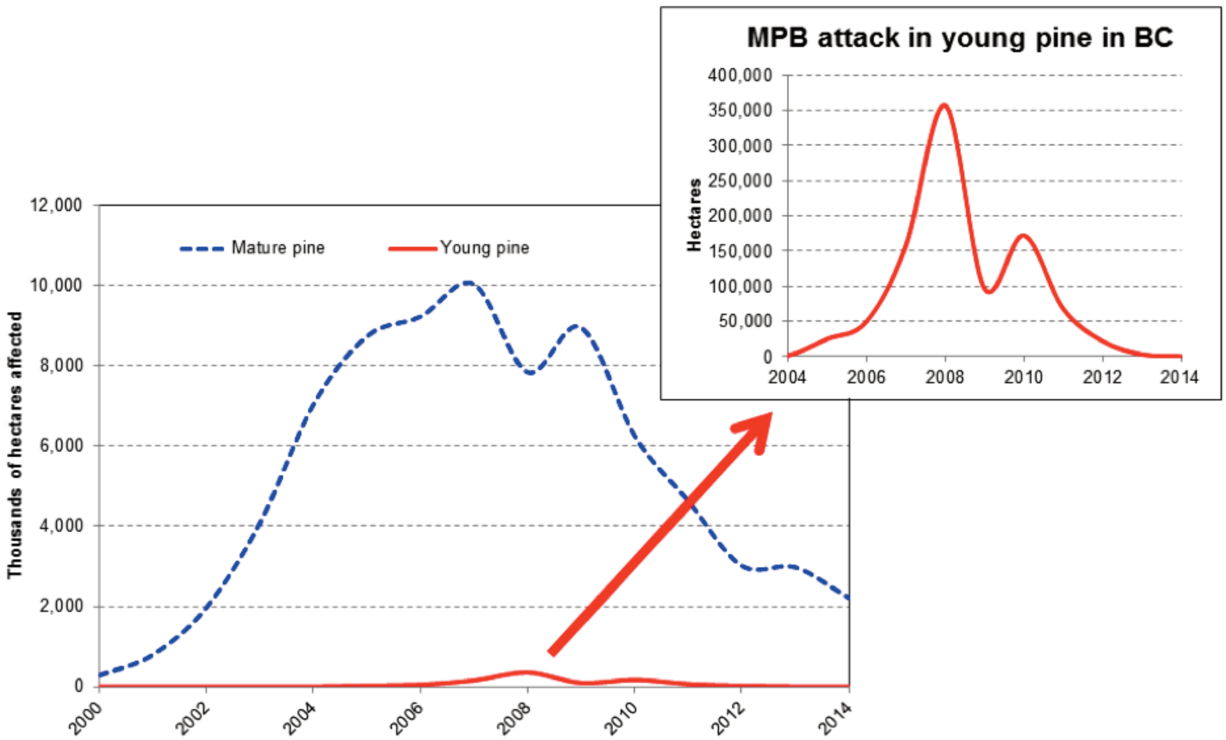

Figure 1. Hectares affected by mountain pine beetle in British Columbia from 2000 to 2014 in mature pine (blue dashed line) and immature pine stands (red line). Data obtained from Provincial Aerial Overview data (http://www2.gov.bc.ca/gov/content/environment/research-monitoring-reporting/monitoring/aerial-overview-surveys).

At the time of this study, approximately 2 million ha of 20–55-year-old lodgepole pine grew in British Columbia (Maclauchlan 2006). In 2003–2004, high levels of mortality were observed in young lodgepole pine stands within the core outbreak area (Maclauchlan et al. 2006; Westfall 2006). Aerial and ground surveys identified the primary cause of mortality as MPB, with secondary bark beetles such as *Ips pini* (Say) (Coleoptera: Scolytinae) also contributing to the observed mortality. The peak year of mortality in these young stands was 2008, when over 350 000 ha were mapped from the air (Figure 1) (Maclauchlan et al. 2009; Westfall & Ebata 2009).

The prevailing assumption was that MPB attacked young stands because of their proximity to surrounding populations in mature stands, and that the beetle would not have much reproductive success in these young trees. At the peak of the outbreak, tremendous aerial movement of beetles were evident from infested mature forests in the core outbreak area to peripheral zones (Maclauchlan 2006). Therefore, when beetle populations reached unprecedented levels, many young pine stands located adjacent to, and sometimes at great distance from, recently infested mature stands were attacked (Maclauchlan 2006). Historically, young or small diameter lodgepole pine becomes a "sink" for MPB during the declining phase of an outbreak. A beetle "sink" describes trees or stands that are not normally highly susceptible, due to age or size, and whose physiological characteristics are not suitable for beetle development, with relatively few brood successfully developing within attacked trees (Safranyik 1988). However, the most recent outbreak produced exponentially greater MPB populations over the landscape, and the phenomenon of young stands becoming "beetle population sinks" resulted in very high levels of tree mortality (Maclauchlan et al. 2009).

In 2005–2006, to more clearly understand the susceptibility and impact of MPB in young stands, we established 24 permanent sample plots throughout British Columbia's core outbreak area. The plots were assessed annually between 2005 and 2009, and again in 2013, to quantify the long-term impact of MPB, including stand mortality, stem deterioration and falldown, and residual stocking and ingress. These stands represent future harvests, wildlife habitat and forest structure, and are vital to the province's mid-term timber supply (B.C. Ministry of Forests and Range 2008).

Methods

Twenty-four 0.25 ha (50 m x 50 m) permanent sample plots with trees aged 20–55 years were established throughout the outbreak area (15 plots in 2005, 9 plots in 2006) to assess:

- attack patterns and tree mortality attributed to MPB;
- impact of secondary bark beetles and other forest health factors;
- significance of biogeoclimatic zone and previous silvicultural treatment;
- reproductive success (brood development and emergence);
- change in stand composition, structure, and stocking level after MPB attack; and
- tree deterioration and falldown.

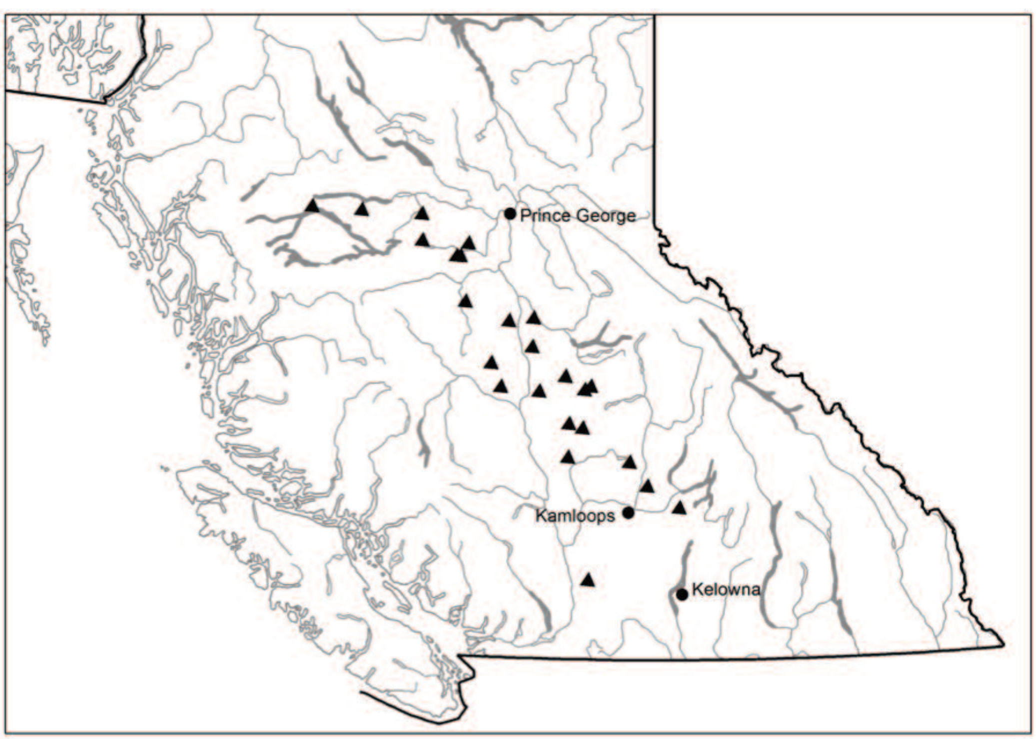

Figure 2. Location of 24 permanent sample plots established in 2005–2006.

Table 1. Location, district (designations at time of study), age, biogeoclimatic zone and subzone,[a] stems per hectare, and silvicultural treatment (before plot establishment) of 24 permanent sample plots (2005–2006).

Location[b]	District	Age (years)	Biogeoclimatic zone/subzone	Stems per hectare[c]	Treatment[d]
Binta Lake	Nadina	20–25	SBS dk	1460	Planting
Wistaria	Nadina	26–30	SBS dk	1140	Planting
Kluskus Lake	Vanderhoof	20–25	SBS mc	1084	Spacing
Kenney Dam	Vanderhoof	26–30	SBS dw	1280	Spacing
Tagai Lake	Prince George	20–25	SBS dw	1568	Spacing
Bobtail FSR	Prince George	31–40	SBS dw	1440	Spacing
Pelican FSR	Prince George	51–55	SBS mw	1420	Spacing
Nazko	Quesnel	20–25	SBPS dc	1208	Spacing
Dragon Lake	Quesnel	31–40	SBS dw	804	Spacing
Fish Lake	Quesnel	31–40	SBS dw	880	Spacing
Colpit Lake	Central Cariboo	20–25	IDF dk	1420	Planting
McLeese Lake	Central Cariboo	26–30	SBS dw	1244	Spacing
Strouse Lake	Central Cariboo	26–30	IDF dk	1204	Spacing
Spokin Lake	Central Cariboo	26–30	SBPS mk	1228	Spacing
Meldrum Creek	Central Cariboo	31–40	SBPS xc	1636	Natural regeneration
500 FSR	100 Mile House	20–25	SBS dw	1316	Spacing
Borthwick	100 Mile House	26–30	SBS dw	1160	Spacing
Chasm	100 Mile House	26–30	IDF dk	888	Natural regeneration
Little Fort	100 Mile House	41–50	IDF dk	1432	Natural regeneration
Exeter FSR	100 Mile House	51–55	IDF dk	876	Natural regeneration
Jamieson Creek	Thompson Rivers	26–30	MS dm	836	Spacing, pruning, fertilizing
Community Lakes	Thompson Rivers	31–40	IDF dk	1644	Spacing
Spius Creek	Cascades	26–30	MS mw	996	Planting, spacing, pruning, fertilizing
Blanc FSR	Okanagan Shuswap	20–25	MS dm	1164	Spacing, pruning[a]

a Biogeoclimatic zones are: IDF = Interior Douglas-fir; MS = Montane Spruce; SBPS = Sub-Boreal Pine–Spruce; SBS = Sub-Boreal Spruce. Biogeoclimatic subzone abbreviations are: dc = dry cold; dk = dry cool; dm = dry maritime; dw = dry warm; mc = moist cold; mk = moist cool; mw = moist warm; xc = very dry cold. **b** FSR = Forest Service Road. **c** Only trees ≥ 7.5 cm at diameter at breast height were tagged at the time of plot establishment. At Exeter FSR and Little Fort, trees ≥ 10 cm at diameter at breast height were tagged. **d** “Natural regeneration” signifies that the stand was naturally regenerated and had not undergone any silviculture treatment.

The plots were established throughout MPB-susceptible ecosystems (Figure 2; Table 1). The Vegetation Resource Inventory (B.C. Ministry of Forests and Range 2005) provided the necessary inventory database to determine stand history, age, and silvicultural treatment regimes. Before plot establishment, we confirmed that MPB was active in adjacent or proximal mature stands to ensure a possible source of future infestation for each young stand.

All plots contained between 200 and 450 trees. At plot establishment in 2005–2006, one increment core sample was taken at breast height to confirm the VRI data for stand age and 10 tree heights (cm) were measured per plot. Every tree over 7.5 cm diameter at breast height (dbh) was tagged with a unique number. For each plot tree, the following information was recorded annually between 2005 and 2009:

- species;
- live or dead;
- dbh (cm);
- presence of MPB attack (yes, no);
- year of MPB attack;
- attack success (mass, partial, unsuccessful); and
- other forest health factors.

In the spring of 2006 before beetle flight, we assessed beetle-affected plots to determine attack density, brood success, and overwinter mortality of MPB. Fifteen red-attacked trees in each plot were sampled by cutting a 15-cm square of bark from the north side of the bole to assess:

- number and length (cm) of parent galleries;
- number and status of life stage (larva, pupa, adult) present (live/dead); and
- percent occupation of sample by MPB larvae and galleries.

In late summer after beetle flight, we assessed a further five green-attacked trees located immediately adjacent to each plot for brood development and success.

In 2006, we measured the bark thickness at dbh of currently attacked trees. We also made ocular estimates of the following parameters to describe tree deterioration and breakdown:

- degree of bole checking (low, moderate, high);
- percent bark sloughing; and
- percent woodpecker activity.

In late March 2007, collections were made throughout the active outbreak area from adjacent young and mature stands, both of which had current MPB attack. The samples were compared (young vs. mature) for attack density (gallery starts), overwinter mortality, and population growth (*R*-value, or the ratio of successful beetle progeny to initial attack). We verified that emergence holes originated from pupal chambers and not from parent beetle galleries. The number of entry holes was used as the indicator of attack. Female beetles initiate attack, therefore the number of attack starts equates to the number of females in the population. The *R*-value was then calculated and used to interpret population trend as follows: 0–2.5 indicates a decreasing population; 2.6–4.0 indicates a static population; and greater than 4.1 indicates the population is increasing (Maclauchlan et al. 2005; Carroll et al. 2006).

From 2006 through 2009, we measured three types of tree deterioration in the permanent sample plots: (1) a visual estimation of bark removal by woodpeckers, (2) percent natural sloughing of the bark, and (3) degree of checking or cracking of the bole in MPB-killed trees. In 2013, we returned to the 24 permanent sample plots to conduct a final assessment. Tree deterioration, as well as the extent of tree falldown, was recorded for trees in each sample plot. We also recorded MPB and other secondary bark beetle attack that had occurred since 2009 and dbh was measured on all remaining live trees. A subsample of heights was taken from live trees. Any new forest health factors affecting tree health were noted. A qualitative description of stand ingress or understorey regeneration was made and a representative photograph was taken in each plot.

Data analyses

Average attack levels in plots were converted to percent trees attacked (number MPB-attacked pine ÷ total pine [live + dead] × 100) and a full analysis of variance (means separation, using Tukey's Studentized Range Test) was performed on the following using SYSTAT® 10.2 for Windows (SPSS Inc., Chicago, Ill.):

- percent MPB mortality, and tree deterioration parameters by biogeoclimatic zone;
- percent MPB mortality, and tree deterioration parameters by age category; and
- percent MPB emergence by dbh and attack level.

Because tree diameter was so variable among stands, trees were divided into categories and the proportional average diameter was calculated for each tree to compare attack status among plots. The categories were: killed by MPB; killed by secondary bark beetles or other forest health factors; and live. Proportional diameters were calculated by dividing each tree diameter by the average diameter of that category.

Differences in MPB attack density, production, and survival in mature and young lodgepole pine trees was compared using a two-sample *t*-test and Pearson Correlation.

Results

Table 2 illustrates the average percent cumulative lodgepole pine mortality caused by MPB, secondary bark beetles, and other forest health factors by biogeoclimatic zone. The mountain pine beetle caused the majority of lodgepole pine mortality. Secondary bark beetles such as *Ips pini*, *Hylurgops rugipennis* (Mannerheim), *Pityophthorus* sp. (Blackman), *Pityogenes* sp. (Chamberlin), and other forest health factors also attacked and killed trees. Western gall rust (*Endocronartium harknessii* [J.P. Moore] Y. Hiratsuka) and comandra blister rust (*Cronartium comandrae* Peck), as well as abiotic agents (such as heavy snow and wind), also contributed to tree mortality. By 2008, most MPB-caused mortality in young stands had declined substantially throughout the affected area. The mountain pine beetle was only active in the Montane Spruce biogeoclimatic zone between 2008 and 2013, primarily because these plots were located in the southern portion of the affected area, where MPB populations were later in both building and collapsing. Given the extent and amplitude of this outbreak, it does not appear that biogeoclimatic zone influenced MPB attack in young stands. No significant differences were evident among biogeoclimatic zones in percent mountain pine beetle or secondary bark beetle mortality (Table 2).

From the onset of this study, and as noted in others (Safranyik et al. 2004), secondary bark beetles were present in MPB-affected areas. With the decline of active MPB in the plots, secondary bark beetle populations increased and began contributing to tree mortality. By 2008, these secondary bark beetles were having a greater impact on trees than

Table 2. Average percent cumulative mountain pine beetle (MPB) and secondary bark beetle (SBB) mortality in 2008 and 2013, range in percent MPB mortality between 2008 and 2013, and total percent mortality in 2013 (includes MPB, SBB, and other forest health factors) is compared by biogeoclimatic zone.

		Average cumulative MPB mortality (% ± SE)		% range MPB mortality	Average cumulative SBB mortality (% ± SE)		Total % mortality
Biogeoclimatic zone[a]	No. plots	2008	2013	2008–2013	2008	2013	2013
IDF	6	55.3 ± 10.2	56.7 ± 10.4	11–78	9.6 ± 2.5	0.4 ± 0.2	60.9
MS	3	56.6 ± 20.7	63.8 ± 15.5	36–77	3.1 ± 1.7	1.2 ± 0.8	65.2
SBPS	3	22.4 ± 12.4	22.7 ± 12.5	1–61	11.2 ± 8.8	0.4 ± 0.4	29.9
SBS	12	48.4 ± 5.8	48.4 ± 6.8	1–83	7.6 ± 1.9	0.4 ± 0.2	51.5

[a] Biogeoclimatic zones are: IDF = Interior Douglas-fir; MS = Montane Spruce; SBPS = Sub-Boreal Pine Spruce; SBS = Sub-Boreal Spruce.

MPB, especially in smaller-diameter stems, with over 5% mortality attributed to secondary bark beetles at the time of the 2008 assessment. Secondary bark beetles acted as primary tree killers, as well as in conjunction with MPB. The highest levels of secondary insect attack were recorded in the Chasm (100 Mile House), Colpit Lake, and Meldrum Creek (Central Cariboo) plots with 16%, 17%, and 29% mortality, respectively. Trees at these three sites were, on average, smaller in diameter, likely because the stands were being naturally regenerated, and (or) because of site conditions.

At the time of the 2013 assessment, it was clear that secondary bark beetle attack had not persisted after the MPB outbreak had subsided. The highest percent mortality attributed to secondary bark beetles since 2008 was recorded in a Cascades District plot with slightly less than 3% mortality between 2009 and 2013.

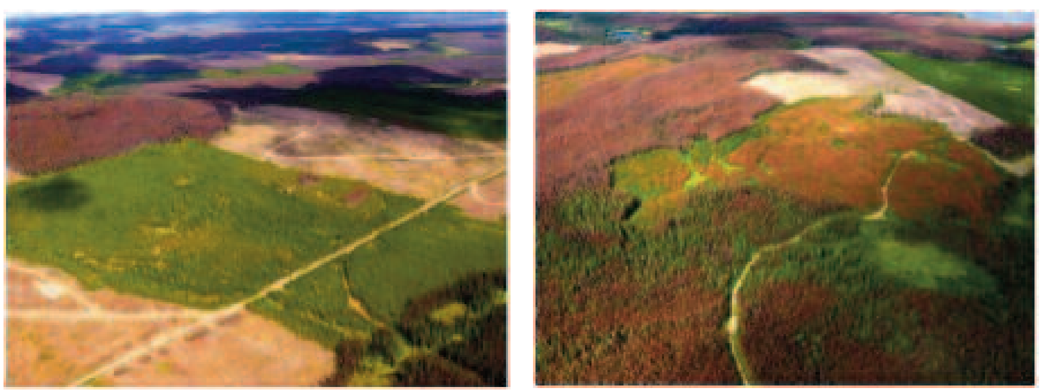

Figure 3. Young lodgepole pine stands surrounded by mature, mountain pine beetle-attacked lodgepole pine: the photograph on the left (taken near Quesnel, B.C., August 7, 2007) shows a stand too young to have MPB attack; the photograph on the right (taken near Kamloops, B.C., July 31, 2008) shows a young stand severely impacted by MPB.

This and a companion study (Maclauchlan & Brooks 2007) examined the relationship between biogeoclimatic zone, stand density, treatment (spacing, pruning, fertilizing), age, tree diameter at breast height, and location, with levels of attack by MPB. Neither biogeoclimatic zone nor stand density influenced levels of attack. Stand treatment effects were insignificant given the very high MPB numbers. Location or proximity to an active infestation, stand age, and tree diameter were key factors in MPB attack levels in these young stands (Figure 3).

The earliest attack in young lodgepole pine stands occurred in central British Columbia, near the epicentre of the outbreak (Westfall 2005) (Table 3). Overall attack levels in the more northern plots, including those in the Prince George, Quesnel, and Central Cariboo districts, declined dramatically in 2007 and 2008 from 2006 attack severities (now grey). Plots in the Vanderhoof-Nadina area saw only 1 year of significant attack in 2006, averaging 51% trees attacked. Plots located in the southern portion of the outbreak, from 100 Mile House south, also had the highest level of current attack in 2006 (Table 3). The only plots with substantial current attack in 2008 were located in the Cascades, Kamloops, and Okanagan-Shuswap forest districts. A few trees were attacked in 2008 in one plot in the southern portion of the100 Mile House Forest District (Table 3).

Table 3. Average percent MPB current year attack (green attack) in 2005 through 2008 in five geographic locations (forest district names reflect designations at the time of the study). The number of plots in each geographic location is shown.

Forest district	No. plots	Average percent green attack			
		2005	2006	2007	2008
Prince George–Quesnel	6	18.2	16.7	0.4	0
Central Cariboo	5	25.5	5.6	1.6	0
Vanderhoof–Nadina	4	0	51.1	0.4	0
100 Mile House	5	12.3	34.1	4.6	0.3
Kamloops/Cascades/ Okanagan–Shuswap	4	2.8	47.4	6.7	4.4

Older plots (41–55 years) had significantly more cumulative mass attack; on average, 77% of plot trees were killed (Table 4). The younger-aged plots were less affected. Nevertheless, between 43% and 53% of the trees 40 years and younger succumbed to MPB. At the time of the final 2013 re-assessment, MPB was not active in any of the plots (Table 4).

Table 4. Average percent MPB current year attack (green attack) grouped by age category in 24 permanent sample plots established in MPB-affected areas of the British Columbia interior.[a]

Age (years) at time of plot establish-ment	No. plots	Average percent green attack						
		Pre-2005	2005	2006	2007	2008	2013	Cumulative mortality (2005–2013)b
20–25	7	0	21.2	31.0	0.6	0	0	52.8 ± 6.7a
26–30	9	0.1	2.8	35.5	3.2	1.5	0	43.1 ± 7.6a
31–40	5	6.7	19.6	19.8	2.4	0.8	0	49.2 ± 4.4a
41–55	3	32.9	20.5	17.1	5.7	0.5	0	76.7 ± 1.2b

[a] This table only includes mass attacks and does not include partial or unsuccessful attacks by MPB.
[b] Means followed by the same letter are not significantly different (Tukey's $p > 0.05$).

Mountain pine beetle preferentially attacked larger-diameter trees, regardless of average tree size within each plot (Figure 4). Amman (1978) and Shore et al. (2006) noted a similar trend. Unsuccessfully attacked trees (i.e., trees attacked by the MPB) that did not result in mass attack or even a strip attack, and unattacked trees, were consistently smaller than the mass-attacked trees within each plot during the year of attack (Figure 4). Figure 4 clearly illustrates the delineation in size preference of MPB and *Ips*, with MPB selecting the largest cohort in each stand. Trees killed by *Ips* and other secondary bark beetles were fewer in number and often smaller in diameter than those killed by MPB.

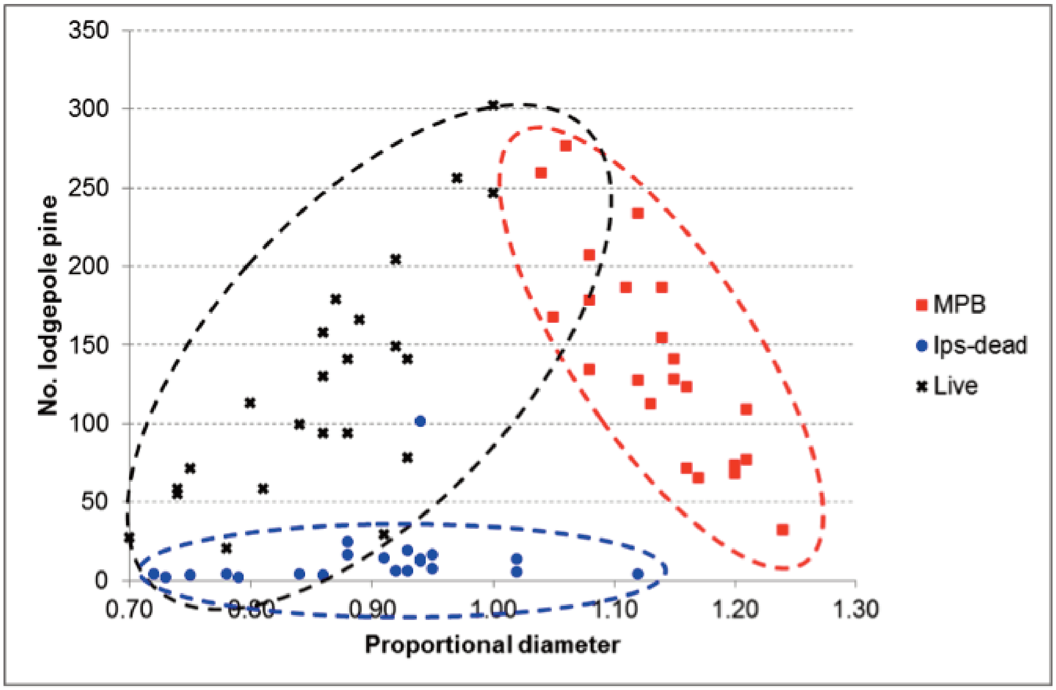

Figure 4. Scatterplot for proportional average diameter at breast height of MPB-attacked trees, live unattacked trees and Ips-attacked trees for 24 permanent sample plots. Using the MPB category as an example, the proportional average diameter was calculated for each category by dividing the diameter of MPB-attacked trees by the average diameter of all MPB-attacked trees.

Initially, we observed a distinct pattern of annual attack in several of the older permanent sample plots—that is, plots that had significant attack one year did not support a MPB population in the next; however, the subsequent year saw another increase in current attack. These alternate attack years support the theory that beetles fly into, but do not emerge from and (or) build up a population from within young stands; that the trees act as "beetle sinks" rather than "beetle sources" where more beetles emerge than attack (Safranyik & Carroll 2006).

In 2007, we looked at the successful emergence of beetles from trees in 16 plots that had been successfully attacked by MPB in 2006. Nine of these plots had at least 50% emergence from mass-attacked trees, ranging from 50 to 91%. We did not quantify emergence; rather, we made a qualitative assessment of whether the trees had produced brood. Many factors influence MPB fitness, including attack and larval density (Safranyik & Jahren 1970; Cole 1973; Safranyik & Linton 1985). Raffa and Berryman (1983) determined that reproductive success of MPB decreased at attack densities greater than 80 galleries per square metre. Extremely high attack densities were observed in many of our plots. The average number of galleries per square metre did not vary significantly between trees with successful emergence (> 50%) and those with less emergence (< 50%), with an overall average of 232 versus 239 of galleries per square metre, respectively. However, the average dbh for trees in the plots that had more than 50% emergence was larger than the average for plots with less than 50% emergence. In 2006, we also measured the bark and phloem thickness of mass-attacked trees from 17 plots and found, on average, that it fell between 3.1 ± 0.1 mm and 6.3 ± 0.4 mm, within the range needed for successful MPB development (Safranyik & Carroll 2006). These findings support the literature that MPB prefers larger trees for brood development (Safranyik & Carroll 2006).

Collections made from adjacent young and mature stands in late March 2007 were compared for attack density (gallery starts) and population growth (*R*) (Table 5). Mountain pine beetle attack density (number of gallery starts) was not significantly different on the mature and young pine sampled (Table 5). However, attack density on both mature and young pine was well over the optimal density of 80 of galleries per square metre (Raffa & Berryman 1983), at 105 and 102 of galleries per square metre, respectively, suggesting lower survival rates and more cannibalism among brood (Safranyik & Carroll 2006; Vega & Hofstetter [editors] 2015).

The most significant observation was the difference in live larvae per square metre and the *R*-value of mature versus young pine. The average number of live larvae per square metre was almost threefold higher in mature, mass-attacked pine (Table 5) with an *R*-value of over 10, indicating very high population growth. *R*-values greater than 4 indicate expanding populations. The *R*-value for the MPB attacking young pine was slightly less than 4, so it did not significantly contribute to the growth of the population. Very few live overwintering larvae were found in young trees. Thus, the contribution to the overall MPB population from overwintering brood in younger stands is small.

Table 5. Mountain pine beetle attack density, production, and survival in mature and young lodgepole pine trees in southern British Columbia.

Parameter	Average ± SE[a]	
	Mature pine (N = 333 trees)	Young pine (N = 35 trees)
Gallery starts per m^2	104.6 ± 2.5a	102.4 ± 7.0a
Live larvae per m^2	669.6 ± 29.4a	231.7 ± 35.4b
Dead larvae per m^2	429.1 ± 23.6a	213.3 ± 58.8b
% larval mortality	41.6 ± 1.2a	45.1 ± 4.8a
R-value [b]	10.7 ± 1.1a	3.9 ± 1.1b

[a] Means followed by the same letter are not significantly different (t-test $p > 0.05$).
[b] The "N" for R-value is number of sites: N (mature pine) = 33; and N (young pine) = 4.

Recent studies have examined the decline in wood quality in recently MPB-killed mature lodgepole pine (Lewis & Hartley 2005, 2006; Lewis et al. 2006; Lewis & Thompson 2008); however, little has been done on the rate and severity of stem deterioration in young lodgepole pine killed by MPB. Biogeoclimatic zone and stand age affected the rate and severity of stem deterioration (Figure 5). Beetle-killed trees degraded more rapidly in wetter ecosystems than in the drier sites (Figure 5). In particular, plots in the Interior Douglas-fir, Montane Spruce, and Sub-Boreal Pine–Spruce subzones had a significantly ($df = 3, F = 85.4, p < 0.0001$) lower percentage of trees (16.7 ± 0.7, 21.8 ± 1.0, and 24.8 ± 0.9, respectively) affected by bark sloughing than those in several Sub-Boreal Spruce subzones (31.7 ± 0.6). The Sub-Boreal Spruce zone saw the highest percent of trees with severe deterioration or falldown, at over 70% (Figure 5). Lewis and Hartley (2005) also found decay losses higher in wetter ecosystems. The oldest cohort of pine exhibited the highest levels of stem deterioration and falldown, at over 70% (Figure 5). Younger trees had fewer severe deterioration or decay symptoms (Figure 5). This could partly be attributed to the attack of younger, smaller trees later in the outbreak cycle, so that stem deterioration was not as advanced.

The largest trees were the most degraded, presumably because they had been dead for the longest time. Trees in the severe-down category had significantly ($df = 2$, $F = 108.7$, $p = 0$) larger dbh (14.8 ± 0.1) (Tukey's Test, $p < 0.05$) than other tree deterioration categories.

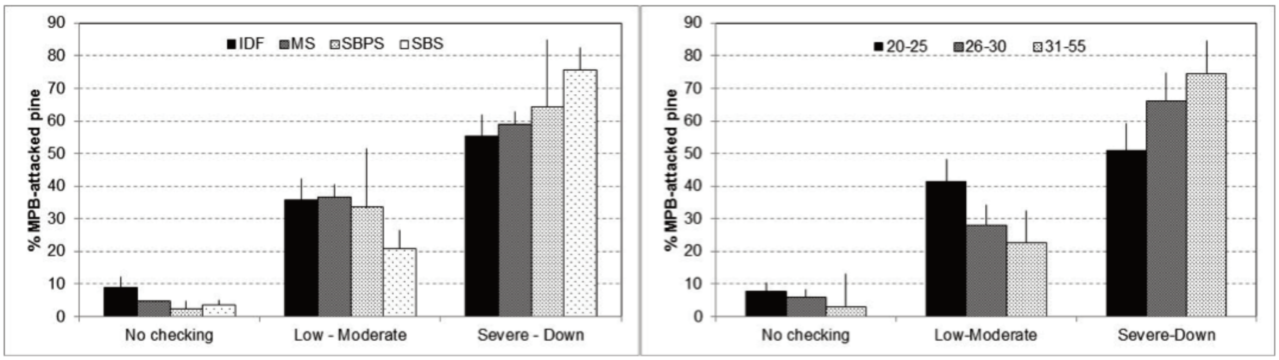

Figure 5. Influence of biogeoclimatic zone (left graph) and age (right graph) on the deterioration of MPB-killed trees between 2008 and 2013. The mean percent lodgepole pine (± S.E.) in four biogeoclimatic zones, and three age categories, are grouped by severity of stem deterioration: no checking; low to moderate checking; and, severe checking or down. Biogeoclimatic zone abbreviations: IDF = Interior Douglas-fir; MS = Montane Spruce; SBPS = Sub-Boreal Pine–Spruce; SBS = Sub-Boreal Spruce.

Many MPB-killed trees had very large checks down the bole, visible from the scaling activity of woodpeckers and general bark sloughing. In half the permanent sample plots assessed in 2007, over 45% of the dead plot trees had woodpecker activity. Overall, the deterioration of young trees attacked by MPB was rapid and likely hastened by very aggressive and thorough woodpecker activity on infested trees.

Since plot establishment, only two plots had no MPB attack or mortality. Of the remaining 22 plots, 21 would have been considered not sufficiently restocked (i.e., according to B.C. Ministry of Forests, Lands and Natural Resource Operations [2014] stocking standards) to meet mid-term expectations without intervention. "Not sufficiently restocked" (NSR) means inadequate stocking, and in this study we used 700 stems per hectare as a basis for satisfactory restocking. To be considered "satisfactorily restocked" (SR), the regeneration (trees) must contain a minimum number of well-established, healthy trees that are free from noncrop-competition and sufficient to produce a merchantable timber stand at rotation (Public Works and Government Services Canada, 2015). By the 2013 assessment, 13 stands were considered NSR, 7 were considered SR, 2 had been replanted, and 2 were fully or partially destroyed by fire and road building. This assignment was based solely on the level of mortality in plots caused by MPB and other mortality factors. If other pest incidence and damage were considered (trees affected – not dead, but unacceptable), then four additional stands would be considered NSR.

In 2007–2008, we counted and assessed plot understorey trees for forest health issues. We did not perform standardized surveys; however, we made a visual estimate of inter-tree spacing (regular or clumped distribution). In general, sufficient well-spaced understorey trees were available to re-establish a stand but often ingress was sporadic and clumped throughout the stand, which could result in areas of insufficient stocking. In many plots, extensive feeding by hares occurred on lodgepole pine regeneration (< 1 m in height), and occasionally, comandra blister rust and lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) were present when residual infected mature trees were nearby. Nigh et al. (2008) had similar results from another study in lodgepole pine in the Montane Spruce ecosystem in British Columbia.

Discussion

The recent mountain pine beetle outbreak in British Columbia encompassed the beetle's entire historic range, as well as areas and host parameters outside its norm (Taylor et al. 2006; Safranyik et al. 2010). Climate, weather, and the inherent characteristics of trees, stands, and landscapes are critical determinants of the success, distribution, and abundance of MPB (Cudmore et al. 2010; Safranyik et al. 2010). As these parameters change in light of climate change and forest management, so must we continually assess the reaction of MPB to these changes. Our study highlights one such parameter of MPB ecology, that of attack in young stands.

The most recent outbreak has killed a cumulative total of 723 million m^3 of pine in British Columbia, and approximately 752 million m^3 (or 56%) of the pine volume in the province is predicted to be killed by 2017 (Walton 2013). During the peak and early decline years of the MPB outbreak in the mature pine component, MPB attacked and killed thousands of hectares of pine under the age of 60 years. By our final assessment in 2013, 17 of the 24 plots would be considered NSR owing to the level of MPB mortality and damage from other pests. The peak year of mortality in these young stands was 2008 (resulting from 2007 attack), when more than 350 000 ha were mapped from the air (Figures 1, 3) (Maclauchlan et al. 2009; Westfall & Ebata 2009).

An associated study on the impact of MPB in young stands (Maclauchlan 2006; Maclauchlan & Brooks 2007), conducted detailed aerial assessments on over 3600 young pine stands in 2005 and 2006 in the interior of British Columbia. The proportion of stands sustaining MPB attack increased from 49% in 2005 (Maclauchlan 2006) to 74% in 2006 (Maclauchlan & Brooks 2007). This landscape-level study puts into perspective the detailed information we have elucidated from these study plots and the level of remediation that may be warranted.

Managed second-growth lodgepole pine may be more susceptible to MPB than naturally regenerated stands. Most harvested stands are now planted and may have had significant silvicultural investment through spacing, pruning, or fertilizing to increase value and growth, thereby decreasing the number of years to harvest. As a result, the current parameters of susceptibility may change with increasingly intensive management regimes. Changing climate conditions may also affect MPB brood survival or the trees' defense response to pitch out attacking beetles. Thus, susceptibility systems should be re-evaluated to accommodate future stand management, and changing climatic and outbreak parameters.

Most young stands in our study sustained MPB attack for 3–4 years; however, typically one peak year of extreme attack occurred. As an example, the Central Cariboo stands in our study saw, on average, over 25% green attack in 2005, with a rapid decline in the following years. In four of the northern plots located in the Vanderhoof-Nadina area, attack levels went from no attack in 2005 to an average of 51.1% in 2006, with a rapid decline to less than 1% by 2007. This pattern clearly shows that beetles flew in from adjacent, attacked mature pine stands upon depletion of the mature host resource. In the more southerly portions of the province (from 100 Mile House south), the pattern of attack was similar, but low-level attack persisted for longer in these sites. Nine plots were located in southern British Columbia within some of the highest climatic hazard zones of the province (Shore & Safranyik 1992). These sites offer the most favourable conditions for MPB including: warm summers that allow the most cold-hardy larval stages to enter the winter season (Logan & Bentz 1999); mild winters that promote survival (Safranyik & Linton 1998) and drought stress to the host during the growing season, which has a negative impact on host resistance (Safranyik & Carroll 2006). Therefore, MPB may persist and sustain population levels in younger cohorts beyond the period of beetle immigration from mature stands. Although some of the highest single-year attack rates in young pine were seen in the harsher climatic zones of the Sub-Boreal Pine–Spruce and Sub-Boreal Spruce zones (with in-stand mortality reaching up to 83%), the highest average cumulative mortality occurred in the milder Interior Douglas-fir and Montane Spruce zones. By 2013, average mortality had reached almost 57% and 64% in the Interior Douglas-fir and Montane Spruce, respectively, compared to only 23% cumulative mortality in the Sub-Boreal Pine–Spruce, and 52% mortality in the Sub-Boreal Spruce.

Host selection by MPB in young pine stands mirrored that in mature stands, with the oldest cohort, 41–55 years of age, and largest trees within each plot being attacked first. We found that secondary bark beetles had a distinct preference for smaller trees in all stands, compared to MPB, which selected the larger trees, thus creating a clear separation among host resources.

Although the diameters of some individual trees in mature stands were not significantly different from those in younger stands, other characteristics such as bark thickness, canopy closure, temperature, and moisture within mature stands play a role in attractiveness and susceptibility to the MPB (Safranyik & Carroll 2006). In the core outbreak area of the Central Cariboo and north, it was only after the mature hosts were depleted that MPB moved into younger stands (Maclauchlan et al. 2009), whereas in the more southerly study plots, attack occurred in young stands despite the availability of mature hosts.

Larger-diameter trees usually have thicker bark and phloem where MPB brood develops. Thick bark and phloem afford protection against the elements; consequently, the likelihood of successful brood production is increased. Safranyik and Carroll (2006) determined that MPB requires a minimum bark thickness (about 1.5 mm) beneath which the insects construct their galleries. Our results show that in most young stands attacked by MPB, bark thickness should not have been a limiting factor in beetle development; however, very high larval gallery density, coupled with rapidly drying phloem due to larval activity, did not optimize survival of developing brood. We observed that the bark and phloem were less thick on unsuccessfully attacked trees, so when beetles attempted to excavate egg galleries under thin bark, they often broke through to the outside (personal observations; Safranyik & Carroll 2006) especially on trees with exceptionally high attack density. Winter temperatures are colder under thin bark and could contribute to overwintering mortality (Amman et al. 1990).

The presence of woodpeckers feeding on MPB and other beetle larvae in the fall and spring was an important regulatory factor influencing the success of beetle emergence in the study (personal observations). During outbreaks, predators and parasites do not control bark beetle populations (Amman 1984; Bellows et al. 1998), but they do have a negative effect on reproductive success.

In less than 10 years following attack by MPB, over 70% of attacked trees in the Sub-Boreal Spruce zone and older age categories either had fallen, or displayed very severe deterioration and checking. Snags are very important for wildlife foraging and nesting and are an integral component of a healthy forest. Nevertheless, excessive tree mortality and falldown as witnessed in this recent MPB outbreak can have negative repercussions for wildlife, forest health, wildfire risk, and economics. Our study revealed that the longevity of standing dead young pine is short, often less than 5 years, and is influenced by size, age, and ecosystem. The breakdown of MPB-killed young pine was rapid and necessitates remedial action in these affected stands. The young pine in our study began falling 3 years after death, which is similar to results seen in mature, thinned, MPB-killed lodgepole pine stands in Oregon (Mitchell & Preisler 1998). Thinned stands in the Mitchell and Preisler (1998) study saw 50% of dead trees down within 8 years, and the smaller-diameter trees fell at a faster rate than larger-diameter trees. Thus, our observation of rapid decline in young stands can be expected to hold across the province where young pine has been killed.

The impact of MPB on young stands depended partly on species composition, tree size and spacing, geographic location, and relation to the general outbreak. Past spacing programs have promoted diameter growth; consequently, these stands were at a higher risk of attack and suffered higher levels of mortality. Plans should consider the future MPB risk when prescribing management activities such as spacing and other silviculture treatments that will increase growth and susceptibility of pine. Calculation of a susceptibility index for lodgepole pine forests requires detailed data regarding the inherent characteristics of stands and landscapes that affect the likelihood of attack by, and damage due to, MPB populations (Shore & Safranyik 1992). The results of our study suggest that certain parameters of susceptibility should be re-evaluated in light of this most recent outbreak, as well as future outbreaks. Intensive silviculture, such as spacing, fertilizing, and planting of genetically superior trees, could increase the susceptibility of the province's next generation of lodgepole pine to MPB attack at a younger (earlier) stage. Substantial areas of mature lodgepole pine in the southern portions of the province could still act as a "wick" for the next MPB outbreak. Given the ever-increasing effects of climate change, the cross-over of MPB from mature to young hosts may be even more rapid in future outbreaks.

In conclusion, our study offers the following critical messages.

- The high levels of MPB attack in young stands were primarily attributed to the proximity to severely infested mature pine.
- Young stands do not produce many beetles, but far fewer MPB were required to kill young trees compared to mature trees.
- Silviculture treatments, particularly spacing, enhanced diameter growth of trees, and therefore lead to higher levels of MPB attack in these treated stands.
- The attack of young stands by MPB may be considered an unusual event, but the effects of this past, and possible future events, have far-reaching implications for British Columbia's timber supply.

Future research should focus on understanding MPB biology and population dynamics under changing environmental and host conditions. This information is critical for assessing the threat to our forest resource and for developing effective management strategies.

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