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Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada

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ABSTRACT

An outbreak of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB), currently affecting over 10.1 million hectares of lodgepole pine forests (*Pinus contorta* Dougl.) in British Columbia, Canada, is the largest in recorded history. We examined the dynamics of even-aged lodgepole pine forests in southern British Columbia, which were undergoing this MPB outbreak. Using dendroecology and forest measurements we reconstructed the stand processes of stand initiation, stand disturbances, tree mortality, and regeneration, and explained the current stand structure and the potential MPB impacts in selected stands. Our results indicate that stand-replacing fires initiated even-aged seral lodgepole pine stands in this region. In the absence of fire in the 20th century, multiple MPB disturbances, which each resulted in partial canopy removal, modified the simple one-layer structure of the fire-origin stands by the initiation of post-MPB disturbance regeneration layers, transforming the stands into complex, multi-aged stands. Despite high overstory mortality due to the current MPB outbreak, regeneration layers, which are likely to survive the current outbreak, will provide important ecological legacies and will contribute to mid-term timber supply.

1. Introduction

Ecological disturbances are the principal mechanisms that shape the composition and structure of most forest ecosystems (White, 1979), and understanding the characteristics of the disturbance regime are a starting point to understand its ecological effects (Oliver, 1981; Agee, 1993). As a natural agent of disturbance, the mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), is the most significant forest insect affecting lodgepole pine forests in western North America (Furniss and Carolin, 1977). MPB outbreaks play an important functional role in directing ecological processes and maintaining the biological diversity of forest ecosystems (Roe and Amman, 1970). While MPB normally kill the oldest and weakest trees scattered in a forest (Safranyik and Carroll, 2006), under epidemic conditions beetles mass-attack mature healthy trees, overcoming tree defenses, and in catastrophic outbreaks can kill trees over hundreds of thousands of hectares (Safranyik et al., 1974). All pine species in western North America are suitable hosts for MPB (Furniss and Carolin, 1977), however, lodgepole pine (*Pinus contorta* Dougl.) is one of the most susceptible and most widely distributed species in North America, and where the economic impacts are the heaviest.

Lodgepole pine forests typically consist of a single cohort of even-aged trees that germinate quickly following a stand-replacing crown fire (Logan and Powell, 2001). Lodgepole pine is described as a seral species, with low shade tolerance, possessing the ability to grow on almost any forest site (Pfister and Daubenmire, 1975). In the absence of fire or other disturbances, lodgepole pine stands are gradually succeeded by more shade tolerant species such as Douglas-fir (*Pseudotsuga menziesii* (Mirb). Franco), and spruce (*Picea* spp.) (Amman, 1977).

During the epidemic phase of the MPB, the largest lodgepole pines are killed (Safranyik et al., 1974), releasing the residual pine and accompanying shade tolerant species, which accelerate their growth in response to increased space and light. When the residual lodgepole pines are of adequate size and phloem thickness to support MPB broods, another infestation may develop (Amman, 1977). Recurrent MPB outbreaks have occurred in the northern Rocky Mountains of Wyoming and Idaho every 20–40 years (Cole and Amman, 1980), and every 28–53 years in central British Columbia (BC) (Alfaro et al., 2004; Taylor et al., 2006). Forest Insect and Disease Survey (FIDS) records and stand reconstructions indicate that there have been four to five significant MPB outbreaks in BC during the twentieth century (Alfaro et al., 2004; Taylor and Carroll, 2004; Taylor et al., 2006).

Historical ecology provides a long time sequence of measurements or observations so that meaningful information can be gained about changes in ecosystem structures, disturbance frequencies and other dynamic processes (Swetnam et al.,

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1999). Dendroecology, a tool in historical ecology, is useful to clarify the dynamic processes of forest disturbances, stand initiation, death and regeneration. Dendroecological techniques have been used to evaluate forest disturbances, such as those caused by MPB (Heath and Alfaro, 1990; Alfaro et al., 2004; Campbell et al., 2007), spruce bark beetle (Veblen et al., 1991; Berg et al., 2006) and spruce budworm outbreaks (Swetnam and Lynch, 1993; Antos and Parish, 2002; Zhang and Alfaro, 2002; Campbell et al., 2006). One dendrochronological method used to date past beetle outbreaks is based on detection of periods of accelerated growth in annual rings of trees that survive outbreaks, which take advantage of the additional growing space, often referred to as a *release period* (Roe and Amman, 1970; Heath and Alfaro, 1990; Veblen et al., 1991; Berg et al., 2006).

In British Columbia, lodgepole pine covers 14.9 million hectares of forest land, with mature pine contributing roughly 29% of the total volume in the provincial timber harvesting landbase (BC Ministry of Forests and Range, 2007). The current MPB outbreak in BC has infested over 10.1 million hectares of lodgepole pine forests as of 2007 (Westfall and Ebata, 2007) and has resulted in mortality of roughly 40% of the total merchantable pine volume (BC Ministry of Forests and Range, 2007). After its eventual collapse, forest managers will need to develop strategies to manage the large areas of forest left unsalvaged. For this they need information on stand dynamics processes associated with MPB outbreaks, such as host mortality, post-outbreak stand growth, recruitment rates and species composition following MPB outbreaks. Currently, this information is scant and our ability to estimate the long-term impacts of MPB outbreaks on BC forests is, therefore, limited.

Roe and Amman (1970) studied the dynamics of lodgepole pine stands in areas of western USA following outbreaks, and, more recently, Hawkes et al. (2004) studied stand composition following the 1980s outbreak in central BC. In this work we used dendroecology techniques and a case study approach, to characterize the disturbance history in lodgepole pine stands in the southern interior of BC. Specifically we address the following questions:

1. What is the composition of forests in the study area which are currently undergoing a MPB epidemic?
2. How have past fire and MPB disturbances interacted to shape the present day structure of these forests?

2. Methods

The study area is located in southern interior of BC, in the vicinity of Logan Lake (50°30′N, 120°48′W) which is characterized by a continental climate, with warm, dry summers, a long growing season, and cool winters. Annual average precipitation ranges from 275 to 320 mm, which mainly falls in mid-winter to early summer (Environment Canada, 2008). Stands were selected in the Interior Douglas-fir (IDF) biogeoclimatic (BEC) zone and the dry cool sub-zone (dk), which occupies low (350–850 m) to high (1100–1450 m) elevations of the southern interior (Meidinger and Pojar, 1991). The IDF landscape is occupied by mature Douglas-fir, however, where recent crown fires have occurred, mixed Douglas-fir and lodgepole pine are common. Lodgepole pine and trembling aspen (*Populus tremuloides*) are widely distributed successional species at higher elevations in this zone (Lloyd et al., 1990).

2.1. Field sampling

Pre-screening of suitable lodgepole pine stands was initiated using geographic information system (GIS) maps, which included information on forest cover types, age classes and BEC zones. Stands had to meet three criteria to be considered for sampling: (1) have lodgepole pine as a leading species, (2) were located in the IDFdk BEC zone, and (3) were at least 80 years old. Final stand selections were made based on ground reconnaissance in the Logan Lake area, and three stands were selected (Fig. 1).

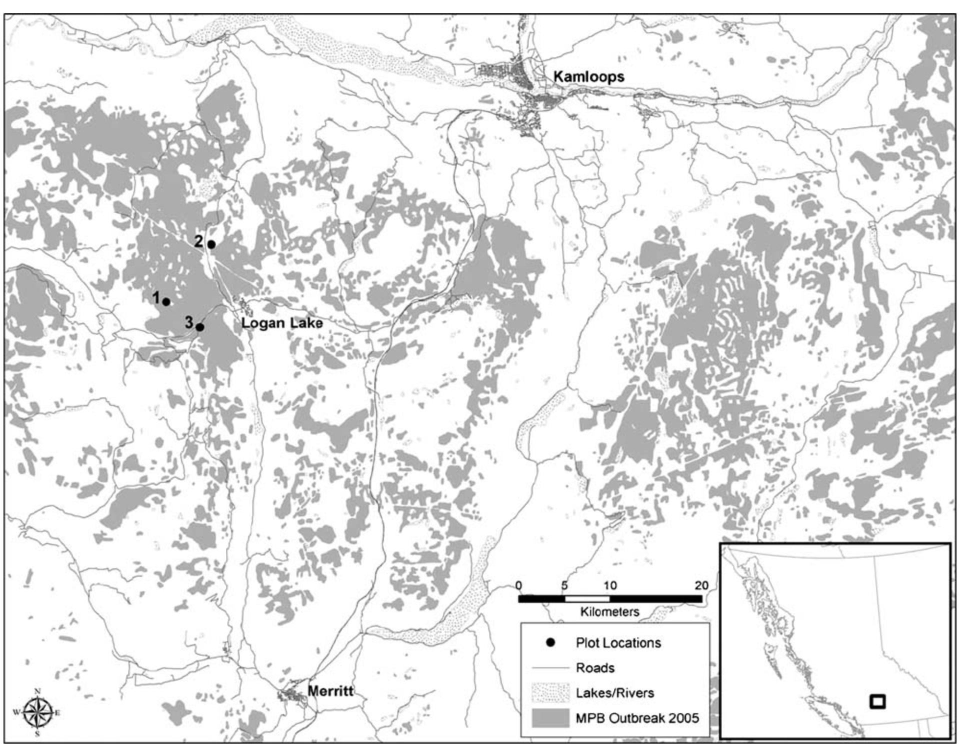

Fig. 1. Location of three stands west of Logan Lake, British Columbia, surveyed to study past fire and beetle disturbances in even-aged lodgepole pine forests.

Four fixed area sub-plots (5.64 m radius or 0.01 ha in area) were randomly sampled in each stand in a line roughly parallel to the stand edge. Sub-plots were established at least 50 m away from the stand edge, and were located 50 m away from one another. Considering all three stands, we measured 436 live and dead overstory trees (defined as trees ≥1.37 m tall). Trees were numbered, species recorded, and diameter-at-breast height (DBH, cm), and height (m) measured. In addition, pine were classified according to their current MPB attack status as: live (no sign of beetle), dead other causes (not from MPB), green attack (entrance holes visible, with or without boring dust, but crown still green), red attack (trees attacked previous season, foliage red in color but still attached to branches), and gray attack (trees killed by MPB 2 or more years ago, and which no longer have any foliage). In the understory we measured all live and dead advance regeneration trees (defined as ≥0.30 and <1.37 m tall), which were numbered, identified to species and measured for diameter-at-ground-height (cm), measured at the top of forest floor and above the root collar and height (m). A tally of all live seedlings (defined as trees that are <0.30 m tall) was taken by tree species.

For analyses purposes we combined sub-plot data for each stand and converted values of number of trees per plot to trees per hectare (trees/ha) and divided the overstory into two categories: canopy (≥1.37 m tall and ≥7 DBH) and the sub-canopy (≥1.37 m tall and <7 cm DBH).

For stand reconstructions we conducted increment core or disc sampling of the various canopy layers observed in the stands. Sample size varied according to the number of trees of each canopy level found in the plots. Increment core samples were collected from 186 live canopy and 30 sub-canopy trees by extracting two increment cores at breast height from a variety of DBH classes in each sub-plot. Trees were cored at breast height, a common procedure in forestry, though we do recognize that these samples underestimate true ages by about 5–10 years. To develop a correction factor, we destructively sampled 25 trees in the sub-canopy by collecting one disc at ground level and another from breast height in each sub-plot. This double sampling was conducted to get an estimate of how long it took for trees to reach breast height in this area. In addition, we sampled 12 trees at ground height in the advance regeneration layer.

To extend the tree chronologies into the past, beyond the period recorded by the living trees, we obtained a targeted sampling of coarse woody debris (CWD) and scarred trees in each stand. A total of 47 cross sections were collected from coarse woody debris (≥7 cm), and 21 samples were collected from scarred trees using a chainsaw. The limitation of assessing past stand disturbances using CWD is that much of the oldest downed debris has undergone some degree of decay and cannot be dated using the methods of dendrochronology, thus the number of datable samples decreases farther back in time.

2.2. Dendroecological analyses

All wood samples were processed using standard dendrochronology methods (Stokes and Smiley, 1968). Samples were scanned and measured using WinDendro^{TM} (v.2002a Regent Instruments Inc., 2003), with a measurement precision of 0.01 mm. All the measured ring-width series were plotted and the patterns of wide and narrow rings were cross-dated among trees to identify possible errors in measurement due to false or locally absent rings. The program COFECHA (Holmes, 1983) was used to detect errors and verify cross-dating. Dated tree-ring series from each stand were used to cross-date and determine year of death of dead trees and CWD. Scarred samples were compiled by stand, and scar origin was determined as fire or MPB strip attack, based on scar characteristics (Mitchell et al., 1983; Stuart et al., 1983). Scars that could not be identified as either fire or MPB origin were classified as 'Other'. Dated tree-ring series were standardized with the program ARSTAN (Cook and Holmes, 1986) to produce a mean ring-width chronology. A horizontal line through the mean was used to standardize the measurement series as it retains low frequency variability and facilitates the detection of deviations from the average growth rate, especially the sustained growth releases associated with canopy disturbances (Veblen et al., 1991). Chronologies were developed for lodgepole pine in each stand, and for Douglas-fir in Stand 1. Other species were not present in the other two stands.

The tree-ring program JOLTS (Holmes, 1999, unpublished, University of Arizona) was used to detect growth releases in individual trees, by computing a ratio of the forward and backward 10-year running means of ring-widths for each year. If this ratio exceeded 1.25 (i.e., a 25% increase in radial growth) for a given year, we counted a release for that year. Running means have been found to produce results that agree well with documented canopy disturbances (Rubino and McCarthy, 2004), and the 10-year window has been found to sufficiently smooth ring-width variability due to short-term climatic variation (Berg et al., 2006). The ratio of 1.25 has been used in previous studies to document growth releases and effectively identifies periods of canopy thinning due to MPB outbreak (Alfaro et al., 2004; Taylor et al., 2006; Campbell et al., 2007).

3. Results

3.1. Current stand structure

The lodgepole pine forests sampled in the Logan Lake area consisted of closed canopy mature stands of leading lodgepole pine with scattered Douglas-fir veterans. At the time of the field surveys (fall 2006) the canopy was sustaining the heaviest mortality by the MPB. The average stocking of the canopy was 2283 trees/ha (live and dead), where the lodgepole pine component (98%) included only 29% live trees (Table 1), mainly in the smaller DBH classes (5–10 cm) (Fig. 2). The average stocking in the sub-canopy was 1508 trees/ha (live and dead), where the lodgepole pine component (78%) included 25% live trees (Table 1). Mortality in this layer was largely attributed to suppression, though there was some (<5%) mortality attributable to the MPB (Fig. 2).

In the understory, advance regeneration was sparse, averaging 275 trees/ha (live and dead) (Table 2). There was no lodgepole pine present in this layer, which consisted instead of more shade tolerant species such as Douglas-fir and spruce. Seedling recruitment was extremely low, with an average stocking of 250 trees/ha (live) and also favored shade tolerant species, though some lodgepole pine seedlings did occur (Table 2).

3.2. Fire and MPB history based on scarred samples

Scarred samples, 91% of which were snags or CWD, indicate that both wildfire and MPB have been important disturbance agents in the sampled stands. Analysis of the fire scars on a stand basis indicated several fires, starting in 1706 (Fig. 3a). However, the fire year 1869 was common to all three stands indicating that this was a widespread fire (Figs. 3a–5a). In Stand 3, all the samples recorded the 1906 fire also suggesting that this was a stand replacement fire in this stand (Fig. 5a), and possibly in Stand 2 (see below). MPB strip attack scars occurred from 1840s to the mid-1970s (Figs. 3a–5a).

3.3. Origin of the canopy

Comparing fire scar dates with establishment dates provides evidence of fire severity. When fire scar dates are recorded by

Table 1
Overstory composition in three lodgepole pine stands near Logan Lake, BC, used to study the impacts of past beetle and fire disturbances. The canopy is defined as ≥1.37 m tall and ≥7 DBH, and the sub-canopy as ≥1.37 m tall and <7 cm DBH.

Stand no.	Trees/ha (live and dead)	Mean DBH (cm) (S.E.)	Mean height (m) (S.E.)	Percent species[a]	Trees/ha Pl (live and dead)	Percent live Pl	Percent dead Pl
Canopy							
1	2550	12.02 (0.12)	13.1 (0.07)	96 Pl; 4 Fd	2475	26	74
2	2550	12.25 (0.08)	14.20 (0.05)	99 Pl; 1 Fd	2525	27	73
3	1750	12.97 (0.12)	14.22 (0.07)	100 Pl	1750	35	65
Mean	2283	12.41	13.84	98 Pl; 2 Fd	2258	29	71
Sub-canopy							
1	1225	4.54 (0.04)	6.39 (0.08)	88 Pl; 8 Fd; 2 At; 2 Sx	1075	14	86
2	1575	4.10 (0.04)	6.54 (0.08)	90 Pl; 10 Fd	1425	23	77
3	950	5.26 (0.03)	7.28 (0.06)	100 Pl	950	37	63
Mean	1508	4.55	6.54	93 Pl; 6 Fd; 0.6 Sx;0.4 At	1175	25	75

[a] Species abbreviation: At: Trembling aspen; Fd: Douglas-fir; Pl: Lodgepole pine; Sx: Interior spruce.

Table 2
Composition of advance regeneration and seedlings in three stands sampled near Logan Lake, BC, used to study the impacts of past beetle and fire disturbances.

Stand no.	Trees/ha	Mean DGH[a] (cm) (S.E.)	Mean height (m) (S.E.)	Percent species[b]
Advance regeneration				
1	650	1.65 (0.02)	0.83 (0.01)	88 Fd; 12 Sx
2	125	1.32 (0.14)	0.73 (0.05)	60 Fd; 40 Sx
3	50	0.55 (0.05)	0.76 (0.05)	100 At
Mean	275	1.17	0.77	49Fd; 33 At; 18 Sx
Seedlings				
1	275	–	–	82 Fd; 18 Sx
2	450	–	–	72 Pl; 28 Fd
3	25	–	–	100 Fd
Mean	250	–	–	70 Fd; 24 Pl; 6 Sx

[a] dgh: diameter-at-ground-height, measured above root collar.
[b] Species abbrev: At: Trembling aspen; Fd: Douglas-fir; Pl: Lodgepole pine; Sx: Interior spruce.

many samples, and this is followed by a rapid pulse of establishment, we conclude that the fire was stand replacing. On the contrary, when fire scars are infrequent for a given date and establishment occurs over a prolonged period we conclude that fires were less intense.

Wildfire was responsible for the establishment of the lodgepole pine canopy in each stand. In Stand 1, establishment occurred rapidly between the early 1870s to mid 1880s, following the 1869 fire (i.e., between 1 and 11 years after the fire) (Table 3 and Fig. 3b). Live Douglas-fir veterans, which occurred sporadically throughout this stand originated from 1786 to 1826, and were legacies that survived this fire (Table 3). In Stands 2 and 3 the canopy established primarily from the 1910 to 1920s, 4 and 14 years after the 1906 fire (Table 3 and Figs. 4b and 5b). Although in Stand 2 we did not find any scars to support fire origin, the canopy showed an abrupt pulse of establishment starting in 1910, indicating that the 1906 stand replacement fire also occurred in this stand.

3.4. Origin of the sub-canopy

MPB outbreak was responsible for establishment of the lodgepole pine sub-canopy, which occurred over multiple decades. In all three stands there was a prolonged pulse of regeneration in the 1930s and 1940s (Table 4 and Figs. 3b–5b), which we believe is a response to canopy thinning following documented MPB outbreaks in this area starting in the late 1920s (Koot and Hodge, 1992; Wood and Unger, 1996).

The overall median age of the sub-canopy at ground height was 68 years and ranged from 55 to 82 years (i.e., establishment

Table 3
Age of the canopy in three lodgepole pine stands sampled near Logan Lake, BC, used to study the impacts of past beetle and fire disturbances.

Stand no.	Species	No. of dated trees	Median age (corrected)[a] (years)	Range (min–max)	Median date of origin	Range (min–max)
1	Lodgepole pine	30	124	73–35	1882	1871–1934
1	Douglas-fir	7	80	61–201	1926	1786–1946
2	Lodgepole pine	37	88	66–101	1919	1884–1941
3	Lodgepole pine	46	84	61–102	1924	1903–1946
Median[c]			84	66–101	1919	1884–1941

[a] Canopy tree age corrected to compensate for coring height.
[c] Median based on lodgepole pine only.

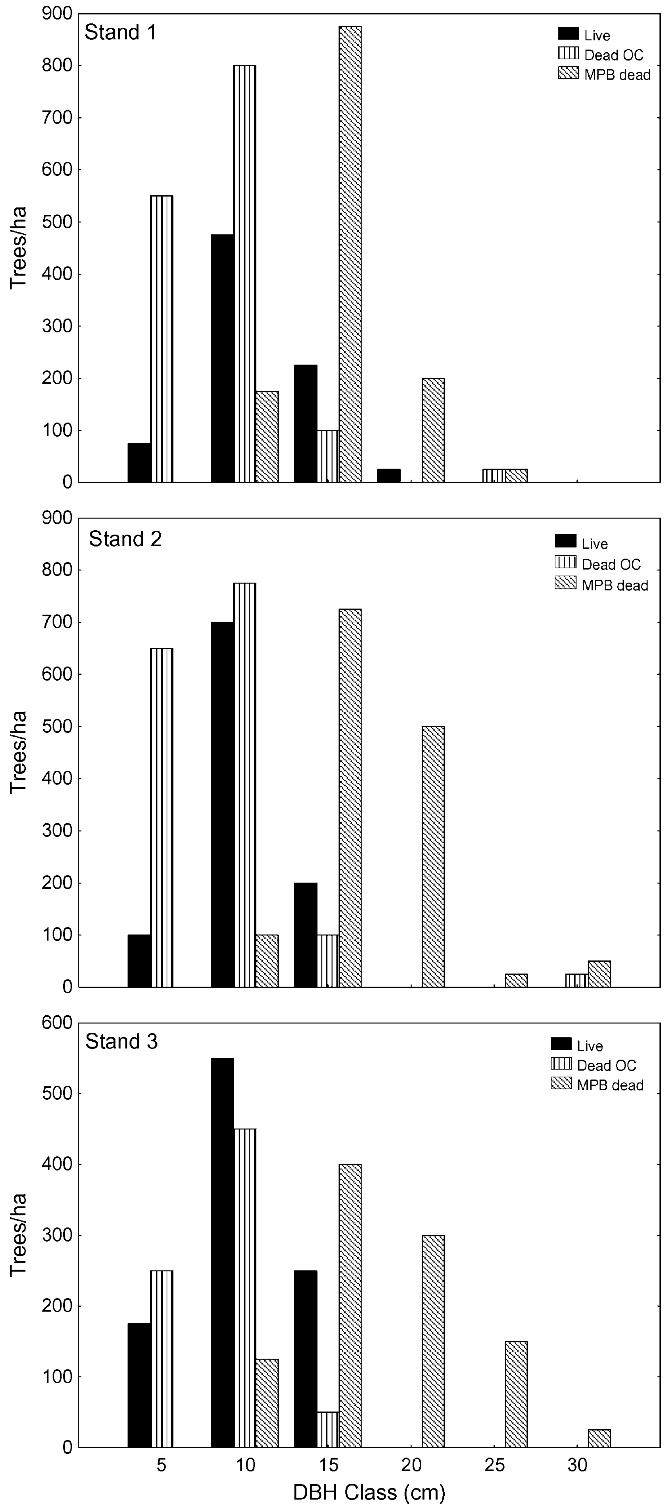

Fig. 2. Distribution of lodgepole pine by DBH class tabulated by tree mortality status for the overstory of three stands near Logan Lake, BC. Trees were identified as live, dead other causes (OC), which included mortality due to causes other than mountain pine beetle (MPB), and MPB dead which included green, red and gray attacked trees.

occurred over a period of 27 years). The median age at breast height was 57 years and ranged from 51 to 78 years (Table 4). Using median ages, the number of years it took trees in this locality to grow from ground height to breast height was 11 years.

3.5. Tree-ring evidence of past MPB disturbances

Extended periods of accelerated growth in tree-rings, indicative of widespread canopy disturbance events, occurred in canopy trees in all three stands. We attributed these growth releases to canopy thinning caused by documented past MPB outbreaks. The exception to this was in Stand 1, where Douglas-fir veterans, which pre-dated the establishment of the lodgepole pine canopy, underwent growth release during the 1840s and 1870s. We attributed the 1870s growth release to thinning caused by the 1869 fire, which these trees survived (Fig. 3a and c_2). We suggest that the 1840s release could have been due to stand thinning by fire or beetle (Fig. 3c_2).

There is a delay in growth response of trees to beetle thinning, and as not all trees are killed in 1 year during an outbreak, growth releases are not precisely simultaneous (Eisenhart and Veblen, 2000). For dating these releases we assumed a lag of 3 years between initiation of an outbreak and initiation of a release response (based on Heath and Alfaro, 1990). In Stands 1 and 2, two release periods were detected, during the 1930s and the 1970s (Table 5 and Figs. 3$c_{1,2}$ and 4c), indicating that outbreaks started in the late 1920s and the early 1970s coinciding with documented outbreaks in this area (Koot and Hodge, 1992; Wood and Unger, 1996). An additional minor release occurred in Stand 1during the 1960s (Fig. 3c_1). In Stand 3 a single release was recorded in the 1970s (Fig. 5c), though this stand had sub-canopy establishment in the 1930s and 1940s in a pattern indicative of MPB outbreak (Table 4 and Fig. 5b).

On average, the percentage of trees that sustained a growth release was 30%, releases lasted 13 years, with 36 years passing between consecutive releases (Table 5). Since we attribute growth releases to abrupt thinning of the canopy by MPB, we hypothesize the 36 years is the interval between MPB outbreaks in this region.

3.6. Origin of the coarse woody debris

Dating lodgepole pine and Douglas-fir coarse woody debris, which comprised 91% and 9% of samples, respectively, allowed us to identify distinct periods of tree mortality. Tree mortality occurred in pulses which coincided with releases in the tree-ring record, and periods of known MPB outbreaks for this area (Koot and Hodge, 1992; Wood and Unger, 1996). Multiple pulses of mortality in Stand 1 occurred in the1920s, 1940s, 1960s and 1990s (Fig. 3d), which all followed periods of growth release (Fig. 3$c_{1,2}$). In Stand 2 the largest amount of mortality occurred from the1980s to 1990s (Fig. 4d), coincident with a period of growth release starting in the late 1970s (Fig. 4c). In Stand 3 mortality began in the 1960s and peaked in the 1970s (Fig. 5d) following a significant growth release period that started in the 1970s (Fig. 5c). The limitation of this analysis is that the oldest CWD is not datable using tree ring-width dating techniques and therefore we were unable to assess the long-term mortality in the selected stands.

3.7. Origin of the advance regeneration

The establishment of advance regeneration, currently shade tolerant species, also followed MPB infestations. In Stands 1 and 2 advance regeneration originated over a period of 20 years, between the 1960s and 1970s (Figs. 3e and 4e) and coincides with periods of overstory release during the 1970s (Figs. 3c and 4c). In Stand 3 advance regeneration establishment was delayed until the early 2000s (Fig. 5e). This is a long gap between the 1970s growth release of the overstory in response to the MPB outbreak, which ended in the 1980s (Fig. 5e), suggesting that either light conditions or seedbed, or a combination of both factors, were inadequate to

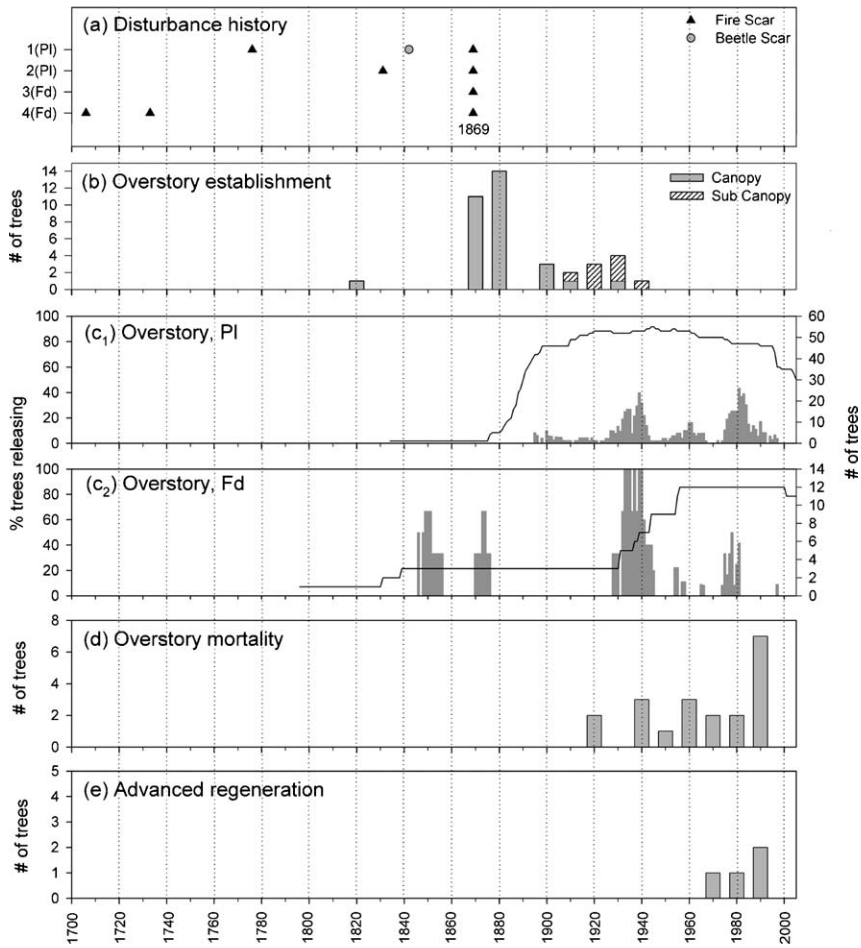

Fig. 3. Disturbance history reconstruction of Stand 1: (a) fire and beetle disturbance history from dated discs; (b) approximate establishment date of the overstory (age at DBH); (c_1) percent of lodgepole pine; (c_2) Douglas-fir showing growth releases in a given year (left-axis), and sample depth (right-axis); (d) date of death of coarse woody debris (CWD); (e) date of establishment of understory advance regeneration.

Table 4
Age of sub-canopy in three lodgepole pine stands sampled near Logan Lake, BC, used to study the impacts of past beetle and fire disturbances.

Stand no.	Species	No. of dated trees	Median age at DGH[a] (years)	Median age at DBH (years)	Difference (years)[b]	Median date of origin[c]	Range (min–max)
1	Lodgepole pine	10	82	78	4	1922	1912–1926
2	Lodgepole pine	12	55	51	4	1949	1924–1972
3	Lodgepole pine	11	68	57	11	1936	1926–1944
Median			68	57	4	1936	1924–1944

[a] dgh: tree diameter at ground level (cm).
[b] Difference: dgh – dbh, number of years taken for trees to grow from ground level to dbh height (1.37 m).
[c] Samples collected at ground height.

Table 5
Growth releases attributed to mountain pine beetle identified in tree-ring chronologies from trees in the overstory in three stands near Logan Lake, BC percent of stand releasing is an average of the entire release period.

Stand no.	Species	Release dates	Average percent of stand releasing	Duration of release (years)	Interval between consecutive releases[a]
1	Lodgepole pine	1930–1943	22.7	13	
		1975–1990	20.4	15	32
	Douglas-fir	1932–1944	75.4	12	
		1974–1981	27.1	7	30
2	Lodgepole pine	1927–1941	20.1	13	
		1972–1986	21.8	14	45
3	Lodgepole pine	1974–1994	23.4	20	–
Mean			30	13	36

[a] The interval is calculated from the end of one release to the start of the next release.

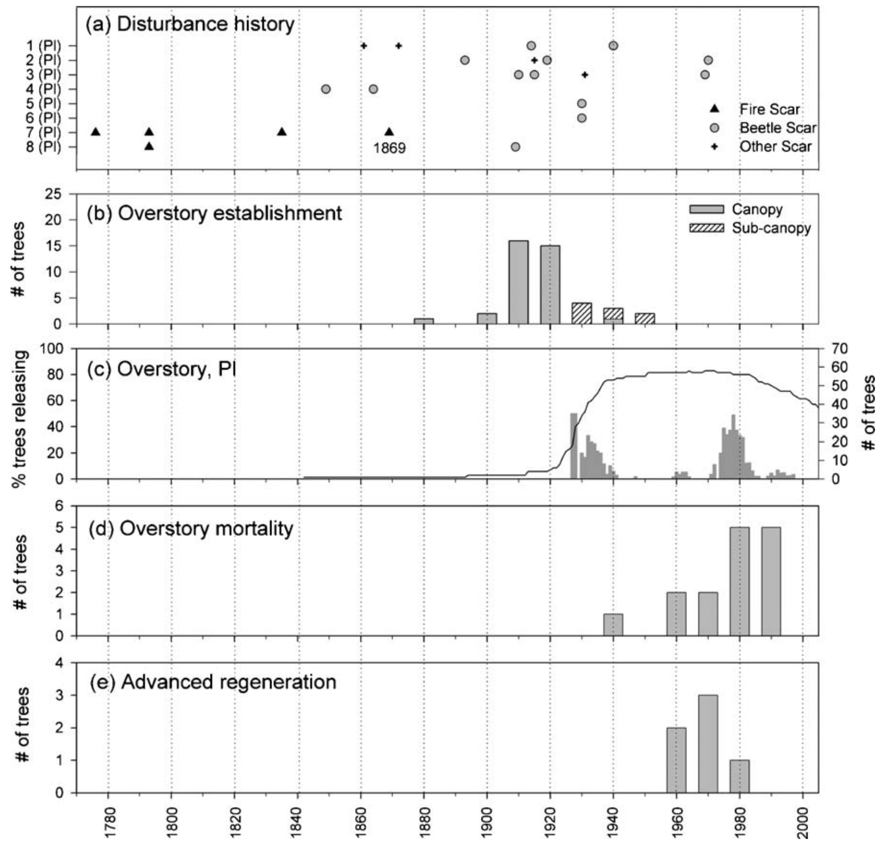

Fig. 4. Reconstruction of disturbance history for Stand 2: (a) beetle disturbance history from dated discs; crosses indicate disturbance by other causes, possibly mechanical damage; (b) approximate establishment date of the overstory; (c) percent of lodgepole pine showing growth releases in a given year (left-axis), and sample depth (right-axis); (d) date of death of coarse woody debris (CWD); (e) date of establishment of understory advance regeneration.

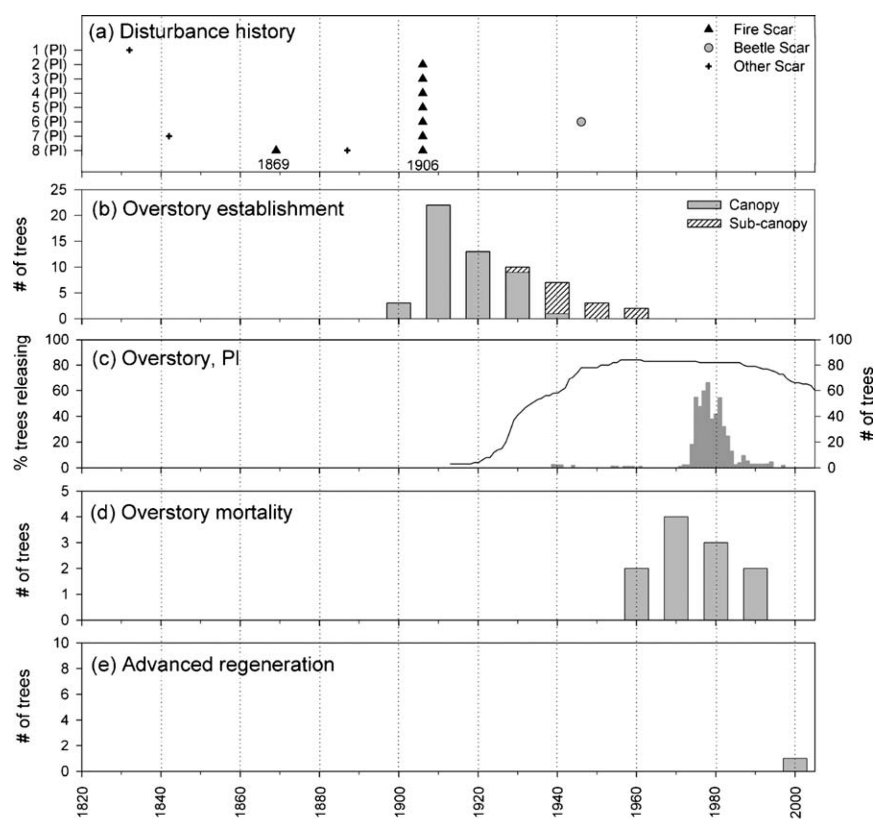

Fig. 5. Reconstruction of disturbance history for Stand 3: (a) fire and beetle disturbance history from dated discs; crosses indicate disturbance by other causes, possibly mechanical damage; (b) approximate establishment date of the overstory; (c) percent of lodgepole pine showing growth releases in a given year (left-axis), and sample depth (right-axis); (d) date of death of coarse woody debris (CWD); (e) date of establishment of understory advance regeneration.

promote seedling establishment in this stand after canopy thinning by MPB.

4. Discussion and conclusion

Using a dendroecological case-study approach we determined the role of MPB in creating complexity in the otherwise simple structures created by stand-replacing fires in lodgepole pine, in the Logan Lake area of southern British Columbia. We also characterized the ecological processes of overstory establishment, timing and magnitude of growth releases, tree mortality and regeneration.

4.1. Disturbance history

The presence of multiple stories and age cohorts in the sample stands, which were thought to be even-aged, reflected the disturbance history of these stands. Fire scar dates (Figs. 3a–5a), in conjunction with establishment dates, indicated that the present canopy, which is undergoing the majority of the MPB outbreak, resulted from stand replacement fire. In each stand a single, locally important fire was recorded by large proportion of the samples. These fires were followed by pulses of recruitment which occurred relatively quickly over a few decades, and make up the current canopy (Table 3 and Figs. 3b–5b).

After 1906, none of our samples recorded fire scars, indicating a fire-free interval of 100 years. This length of time is over two times greater than the historical maximum fire-free interval reported by Iverson et al. (2002). This may be, in part, due to fire control and increases in human activities, such as clearing for cattle grazing and harvesting (Taylor and Carroll, 2004). In the absence of fire, the main disturbance agent in the Logan Lake area has shifted to MPB. Previous studies (Romme et al., 1986; Heath and Alfaro, 1990; Alfaro et al., 2004; Hawkes et al., 2004; Campbell et al., 2007) indicate that MPB outbreaks have resulted in significant levels of lodgepole pine tree mortality resulting in crown openings, growth releases in the residual stands, and prolonged episodes of regeneration.

Based on the time period between consecutive growth releases, we estimated that the interval between MPB outbreaks, averaged 36 years (Table 5). This beetle return frequency is similar to that described for the Chilcotin Plateau of central British Columbia (~200 km north of Logan Lake), where releases in response to MPB were detected during the 1930s and 1970s with an average duration of 14 years, and an interval between consecutive releases of 42 years (Alfaro et al., 2004).

4.2. Forest structure following disturbance

The severity of disturbances determines which species will dominate the forest following the disturbance (Oliver, 1981). In a fire-dominated disturbance regime, lodgepole pine regenerates quickly after a stand-replacing fire (Lotan, 1976). However, ecosystem response following MPB outbreak seems to be slower than to fire, with seedlings establishing over several decades following a MPB outbreak (Waring and Pitman, 1985). This was the case in our sample stands, where the lodgepole pine canopy established quickly post-fire, and subsequent MPB-induced cohorts (sub-canopy and advance regeneration) established slowly over multiple decades (Tables 3 and 4). Despite slow establishment, the current sub-canopy is likely to survive the current MPB outbreak and will form reasonably well stocked new stands (Table 1), which is supported by the findings of Nigh et al. (2008).

In northern BC Astrup et al. (2008) found that overall low recruitment following MPB infestation was likely due to the lack of disturbance of the moss dominated forest floor. We suggest that this is also occurring in our locality, where we noted that the stands measured had an undisturbed layer of duff, and a continuous grass cover (unpublished observation by the authors). Forest regeneration after MPB disturbances, even under intense MPB outbreaks such as the current outbreak, is a slow process. This is illustrated by the poor seedling recruitment in response to the current outbreak (Table 2), which is the most intense MPB outbreak on record. The low levels of recruitment of seedlings and advance regeneration, especially for pine is likely due to the lack of a suitable seedbed, and additionally that the closed canopy created by the still dense stocking of dead (many dead trees still have needles present) and live overstory trees provide abundant shade.

With respect to species composition following disturbance, we hypothesize that low or moderate intensity MPB disturbances, as measured by the amount of overstory canopy removed by MPB, do not result in significant increases in light reaching the forest floor. This will favor the regeneration of shade tolerant species such as Douglas-fir and spruce. On the other hand, intense MPB disturbance, such as the current outbreak, which removes the majority of the overstory, will favor regeneration of shade intolerant species such as lodgepole pine and aspen. This hypothesis is supported by the difference in species composition in the sub-canopy and understory cohorts in our plots (Tables 1 and 2). At the time of our surveys not enough time has elapsed to determine if the future species composition in the seedling cohort would shift to shade intolerant species after this intense outbreak has run its course. Further work is needed to test this hypothesis.

MPB disturbance processes, repeating in approximately the same way in each stand, led us to the development of a conceptual model, which describes the progression of even-aged stands to more complex, multi-aged stands, as a result of repeated MPB outbreaks (Fig. 6). Our model shows that, in the absence of fire, MPB becomes the main disturbance agent directing forest dynamics and structure in the Logan Lake area of the southern interior of BC. Fire suppression interrupts the historic cycle of lodgepole pine renewal through stand-replacing fires, leading to the creation of multi-aged layers and cohorts initiated through various levels of MPB disturbance over time.

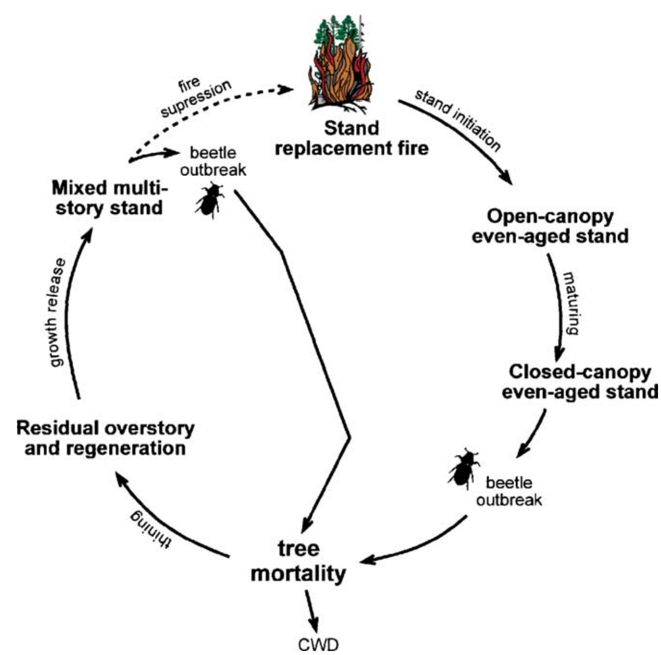

Fig. 6. Conceptual model of the stand dynamics cycle over the last 138 years in lodgepole pine stands in the IDFdk1 in the Logan Lake area of southern BC. Dotted line represents the interruption of the fire cycle due to human intervention.

4.3. Conclusion

Our study clarified the relationship between fire and MPB disturbance and allowed us to describe the role of MPB as a modifier of the simple stand structures, which form after stand-replacing fire. Regeneration cohorts that arise in response to canopy thinning by MPB will form the next crop after the present canopy is destroyed by the current outbreak.

In summary we found that in the Logan Lake area:

- In the absence of wildfire for much of the 20th century in our study area, the MPB has played a significant role in directing stand dynamics in lodgepole pine stands.
- Stand-replacing fires initiated even-aged seral lodgepole pine stands; while subsequent multiple MPB disturbances have transformed stands into forests with multi-stories and multiple age cohorts, initiated by repeated canopy thinning.
- In the long term, the impacts of MPB mortality on the overstory will be alleviated by the presence of a sub-canopy, and to a lesser extent, the advance regeneration layers which will form reasonably well stocked forests in the future.

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