Changes in stand structure in uneven-aged lodgepole pine stands impacted by mountain pine beetle epidemics and fires in central British Columbia

by Jodi N. Axelson[1,2], René I. Alfaro[1] and Brad C. Hawkes[1]

ABSTRACT

We examined the development of lodgepole pine (*Pinus contorta* Dougl.) in uneven-aged stands in the Interior Douglas-fir (IDF) biogeoclimatic zone of central of British Columbia (B.C.), which are currently undergoing a massive outbreak of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB). Using historical ecological approaches, dendrochronology, and stand measurement data, we determined the roles MPB and fire disturbances have played in the ecological processes of lodgepole pine in an Interior Douglas-fir zone. We found that multiple mixed-severity fires created patchy uneven-aged stands dominated by lodgepole pine. Since fire suppression in the 20th century, multiple MPB disturbances have maintained the structural complexity of the stands and favoured regeneration of lodgepole pine in the understory despite the absence of fire, resulting in self-perpetuating multi-age lodgepole pine stands. Analysis of the stand structures remaining after multiple MPB outbreaks showed that, even with high overstory mortality, the sample stands contained several MPB-initiated cohorts, consisting of younger and smaller-diameter lodgepole pine. These surviving lodgepole pine layers, which are less susceptible to beetle, will provide important ecological legacies, and could play an important role in the mid-term timber supply chain. We concluded that, in the absence of fire, the MPB plays a more frequent role in directing stand dynamics and structure in uneven-aged lodgepole pine stands resulting in self-perpetuating complex stands in the central interior. We compared and contrasted these findings with those obtained in "even-aged" lodgepole pine stands, also in the Interior Douglas-fir zone in the southern interior, which were investigated in an earlier study.

Key words: lodgepole pine, mountain pine beetle, dendroecology, complex stands, mixed-severity fire regime

RÉSUMÉ

Nous avons étudié le développement du pin lodgepole (*Pinus contorta* Dougl.) dans des peuplements inéquiennes de la zone biogéoclimatique du sapin de Douglas de l'Intérieur dans le centre de la C.-B., qui connaissent actuellement une épidémie massive du dendroctone du pin (*Dendroctonus ponderosae* Hopkins; DP). Au moyen des historiques écologiques, de la dendrochronologie et des données mesurées des peuplements, nous avons déterminé le rôle des perturbations provoquées par le DP et les feux de forêt dans les processus écologique du pin lodgepole dans la zone du sapin de Douglas de l'Intérieur. Nous avons noté que plusieurs feux d'intensité variable ont créé des peuplements inéquiennes morcelés dominés par le pin lodgepole. Depuis le contrôle des feux de forêt au cours du XXe siècle, plusieurs perturbations provoquées par le DP ont maintenu la complexité structurale des peuplements et favorisé la régénération du pin lodgepole en sous-étage malgré l'absence de feu, ce qui a entraîné l'autoperpétuation de peuplements inéquiennes de pin lodgepole. L'analyse de la structure des peuplements en place après plusieurs épidémies de DP indique que, même avec une forte mortalité dans l'étage dominant, les peuplements échantillons contenaient plusieurs cohortes issues du DP, formées de tiges plus jeunes et plus petites de pin lodgepole. Ces strates survivantes de pin lodgepole, qui sont moins exposées au DP, constitueront un important héritage écologique et pourraient jouer un rôle important dans la chaîne d'approvisionnement à moyen terme en matière ligneuse. Nous avons conclu que, en absence de feu de forêt, le DP joue un rôle plus fréquent de redirection de la dynamique et de la structure des peuplements dans le cas des peuplements inéquiennes de pin lodgepole, ce qui engendre des peuplements complexes auto-perpétués dans le centre intérieur de la province. Nous avons comparé et mis en évidence ces résultats avec ceux obtenus dans des peuplements « équiennes » de pin lodgepole, également de la zone du sapin de Douglas de l'Intérieur situés au sud de la région Intérieur et qui avaient été étudié lors d'une recherche précédente.

Mots clés : pin lodgepole, dendroctone du pin, dendroécologie, peuplements complexes, feux de forêt d'intensité variable

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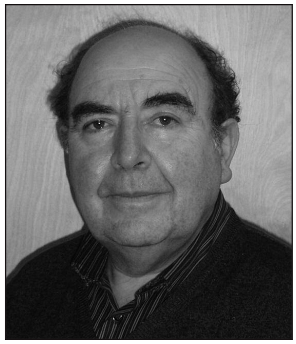

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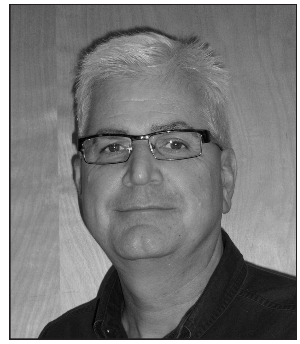

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Introduction

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) is an agent of natural disturbance, and the most important insect impacting the productivity of North American pine forests (Furniss and Carolin 1977). In western North America all pine species 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 pine species in British Columbia (B.C.) (Krajina 1969, Meidinger and Pojar 1991). In B.C. lodgepole pine covers over 14 million hectares of the forested landbase, and, in the current MPB outbreak, has affected approximately 13 million hectares of these forests (Westfall and Ebata 2008). There is a lack of specific information on stand development following MPB epidemics of the current scale (Griesbauer and Green 2006).

Earlier studies have demonstrated that MPB outbreaks play an important role in directing ecological processes and the dynamics of lodgepole pine forests (e.g., Roe and Amman 1970, Stuart *et al.* 1989, Heath and Alfaro 1990, Hawkes *et al.* 2004, Shore *et al.* 2006, Axelson *et al.* 2009). Bark beetle epidemics are viewed as stand-releasing disturbances that favour the release of existing suppressed and understory trees which then forms a new forest (e.g., Heath and Alfaro 1990, Veblen *et al.* 1991, Alfaro *et al.* 2004, Hawkes *et al.* 2004, Berg *et al.* 2006, Axelson *et al.* 2009). In the northern Rocky Mountains of the United States, MPB outbreaks exerted widespread influence upon stand succession where, in the absence of fire, lodgepole pine regeneration was superseded by the establishment of shade-tolerant species (Roe and Amman 1970). In B.C., a similar result was obtained by Heath and Alfaro (1990) and Axelson *et al.* (2009), who found that MPB outbreaks, in combination with fire suppression, accelerated successional processes in favour of shade-tolerant, or semi-tolerant, species (e.g., Douglas-fir) in even-aged lodgepole pine. In the Cariboo–Chilcotin (CC) region of central B.C., Hawkes *et al.* (2004) examined stand composition following the 1980s MPB outbreak and determined the density of advance regeneration was high and predominately made up of lodgepole pine, demonstrating the ability of pine to regenerate under its own canopy. In south-central Oregon, old self-perpetuating multi-aged lodgepole pine forests had pulses of episodic regeneration that were strongly correlated to MPB outbreaks or fire (Stuart *et al.* 1989).

In 2006, we commenced a two-year study to examine stand development and stand structure in even- and uneven-aged lodgepole pine stands in the Interior Douglas-fir (IDF) biogeoclimatic zone of B.C. Even-aged stands were selected in the southern interior in the Kamloops Forest District, and uneven-aged stands in the central interior in the Cariboo Forest District. In the even-aged stands we found that stand replacement fires initiated even-aged seral lodgepole pine stands; while subsequent multiple MPB disturbances transformed stands into forests with multiple age cohorts with increasing species diversity, each initiated by canopy-thinning by MPB (Axelson *et al.* 2009). In this previous study, historic MPB outbreaks acted as a modifier of even-aged lodgepole pine stand structure such that the reduction in stand merchantable volume from the current MPB outbreak could be mitigated by the presence and release of multi-species suppressed sub-canopy and understory cohorts. In this study, we present results from sampling uneven-aged lodgepole pine stands in the Cariboo–Chilcotin in areas with a mixed-severity fire regime and compare the impact of fire and MPB disturbances on stand structure and regeneration with our published results from even-aged stands.

At the landscape level, mosaics of even- and uneven-aged lodgepole pine forests are the norm and reflect the regional disturbance history (Agee 1993). In the Cariboo–Chilcotin uneven-aged stands have been historically created and maintained by a mixed-severity fire regime (Francis *et al.* 2002, Daniels and Watson 2003), although the role of MPB was not examined. In the current outbreak, the Chilcotin Forest District has sustained the highest number of hectares impacted by MPB in B.C., with 1.5 million hectares recorded (Westfall and Ebata 2008). Currently, there is a gap in our understanding about the potential growth release of advance regeneration and establishment of seedlings, from establishment to full maturity, particularly as it relates to large scale MPB outbreaks (Griesbauer and Green 2006), especially in uneven-aged lodgepole pine stands in B.C. There are some studies that have examined the role of fire and MPB disturbances on uneven aged lodgepole pine stand dynamics in the U.S. (e.g., Stuart *et al.* 1989). In this study we used a case-study approach by selecting a small number of stands in the Cariboo–Chilcotin to conduct in-depth dendroecological analyses to determine the role of fire and MPB disturbances, and their interaction, on stand dynamics in uneven aged lodgepole pine stands in central B.C. Reconstruction of detailed stand histories requires the collection of large numbers of increment cores and bole sections of live and dead trees and intense laboratory preparation to conduct tree-ring measurements. The large number of tree-ring measurements required in studies of this nature, and the need for cross-dating each sample, does not allow a large number of stands to be sampled in the field. However, the case-study approach provides in-depth understanding of ecosystem processes and serves as a basis for ecosystem modeling.

The objectives of this study are similar to those in Axelson *et al.* (2009), except they target uneven-aged lodgepole pine stands as compared to even-aged stands reported in Axelson *et al.* (2009):

1. To determine the impacts of the current MPB outbreak on stand structure and composition in the IDFdk4 of the Cariboo–Chilcotin (CC) after multiple MPB outbreaks.
2. To determine how historic fire and MPB disturbances interacted to shape the present day structure of these forests.

Methods

Study area

The study area was located in low-elevation forests of the Cariboo–Chilcotin region, in central B.C. Pre-screening of suitable stands was initiated using Geographic Information System (GIS) and BC Ministry of Forestry and Range maps, which included information on forest cover types, age classes and biogeoclimatic zones. Stands had to meet three criteria to be considered for sampling: 1) lodgepole pine as a leading species, 2) located in the dry cool (dk) Interior Douglas-fir (IDF) biogeoclimatic (BEC) zone, and 3) with an overstory estimated to be at least 80 years old. Three stands were selected in the IDFdk4, located between the communities of Alexis Creek (52°5′N, 121°16′W) and Tatla Lake (51°53′N, 124°35′W) (Fig. 1).

The IDF zone has a continental climate, characterized by warm, dry summers, a long growing season and cool winters (Hope *et al.* 1991), and occupies the lee side of the Coast, Cascade and Purcell Mountains (Hope *et al.* 1991). Forests in the IDF tend to be a combination of interior Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and lodgepole pine, where pine is a common successional species, and, along with trembling aspen (*Populus tremuloides* Michx.), is a widely distributed seral species throughout the zone (Lloyd *et al.* 1990; Hope *et al.* 1991). The IDFdk4 occupies the gently rolling landscape and the western portions of the Plateau are strongly affected by the Coast Mountains rainshadow, where total annual precipitation near Tatla Lake is 338 mm (Steen and Coupé 1997). The IDFdk4 is the coldest biogeoclimatic unit of the IDF zone in B.C. and is climatically transitional from the IDF to the cold dry (cd) Sub-Boreal Pine Spruce (SBPS) zone (Steen and Coupé 1997). Stands were sampled in the summer of 2007.

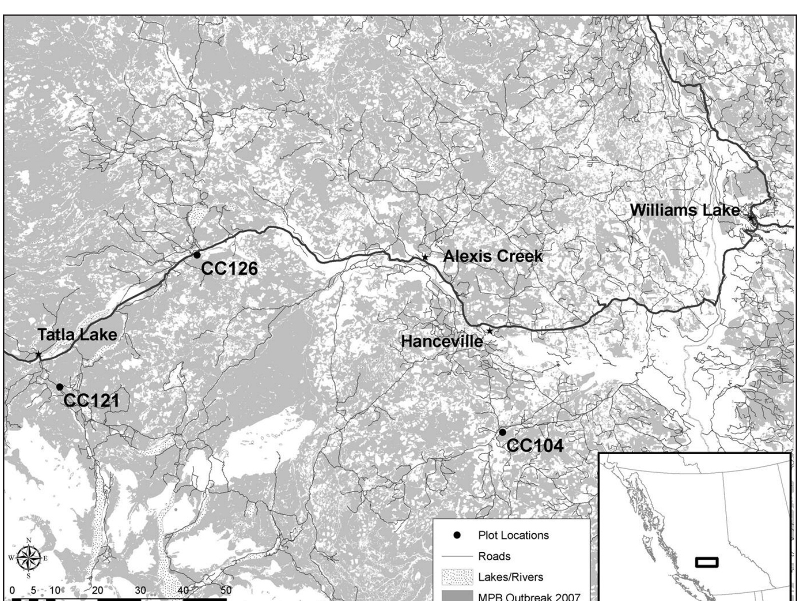

Fig. 1. Location of three uneven-aged stands of lodgepole pine sampled in the Interior Douglas-fir (IDFdk4) biogeoclimatic subzone located in the Cariboo–Chilcotin, B.C.

Field sampling

We employed systematic random sampling to select four fixed area sub-plots (5.64-m radius or 0.01 hectare in area) 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. All live and dead overstory trees (defined as trees ≥1.37 m tall) 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 grey attack (trees killed by MPB two 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 m and <1.37 m tall), which were numbered, identified to species and measured for diameter at ground height (DGH; 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).

Dendroecological sampling

To reconstruct in-depth stand histories we conducted increment core and disc sampling of select trees in each sub-plot from as many size classes as possible. Increment core samples were collected from live trees, at breast height, from a variety of DBH classes in each sub-plot. In addition, we extracted increment cores from the largest and presumably oldest trees in the stand to obtain the longest (i.e., oldest) chronologies possible. Trees were cored at breast height, a common procedure in forestry, though we do recognize that these samples underestimate true ages by about 5 to10 years. Disc samples were obtained from smaller trees (<7 cm DBH) at breast height and also at the tree base (root collar) to develop an age correction factor for trees sampled at breast height. Destructive samples were also collected at the tree base for the advance regeneration layer to date this cohort.

To extend the tree chronologies beyond the period recorded by the living trees in the plots, and to determine year of death, we obtained a targeted sampling (i.e., we obtained samples outside the plots) of coarse woody debris (CWD) (≥7 cm DBH). 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 samples decreases farther back in time.

Fires and sub-lethal MPB attacks can leave a permanent record in the form of scars on the tree bole. To determine past fire and MPB attack history, recorded as scars on the tree bole, we targeted the sampling of scarred trees, live or dead, by walking through each stand. Full discs or wedges were collected from as many specimens as could be located in each stand.

Dendroecological analyses

All wood samples were processed using standard dendrochronology methods (Stokes and Smiley 1968). Samples were scanned and measured using WinDendro™ (v.2002a; Regent Instruments 2003[3]), 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 were standardized with the program ARSTAN (Cook and Holmes 1986) to produce a mean ring-width chronology. To standardize the measurement series we used a horizontal line through the mean, as this procedure retains the 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). Tree-ring chronologies were developed for lodgepole pine in each stand.

Using scar characteristics we were able to identify the year in which a fire or MPB attack occurred (Mitchell *et al.* 1983, Stuart *et al.* 1983) (Fig. 2). Scars that could not be identified as either fire or MPB origin, possibly due to mechanical or animal damage, were classified as "other".

Under epidemic conditions MPB preferentially kill the largest trees in the stand, and under intense MPB pressure this can result in mortality of a large portion of the overstory within a stand (Safranyik *et al.* 1974). Trees not killed by MPB often sustain a prolonged period of accelerated growth after the outbreak, which is referred to as a growth release. The tree-ring program JOLTS (Holmes 1999) 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, Axelson *et al.* 2009).

Results

Current stand structure

Stands sampled in the Chilcotin consisted of open-canopy, uneven-aged and multi-cohort stands of lodgepole pine with scattered aspen that had active infestations of MPB (Fig. 3). Stand diameter and height distributions of live and dead trees indicated significant departures from normality (Shapiro-Wilk test, $p < 0.05$), with distributions skewed to the left (Fig. 4) with a reverse-J shape, where a larger number of trees occurred in the smaller diameter and height classes (Fig. 4). Both distributions showed several peaks indicating the presence of a layered forest structure. The exception to this was stand 121, where the distribution was skewed to the left but did not have a reverse-J shape, indicating that trees were more uniformly distributed (Fig. 4).

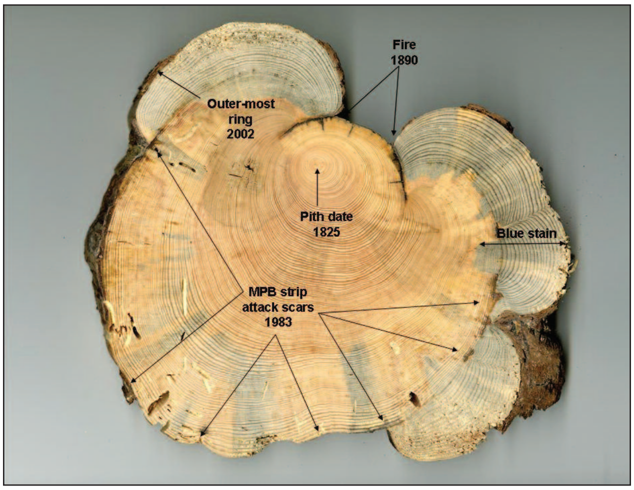

Fig. 2. Example of lodgepole pine lower bole section used to date past fire and mountain pine beetle (MPB) disturbances. This tree had a pith date of 1825; a single fire scar indicating a surface fire in 1890, MPB strip scars in 1983, and a successful MPB attack (with blue-stain fungus) in 2002 killing the tree (original in color).

Fig. 3. An uneven-aged lodgepole pine stand in the Interior Douglas-fir (IDFdk4) biogeoclimatic subzone located in the Cariboo–Chilcotin, B.C. Red-needled overstory lodgepole pine (background) has been killed by mountain pine beetle (MPB) as part of the current outbreak. The fallen lodgepole pine trees (foreground) were killed during the MPB outbreak in the early 1980s. Opening of the canopy and sub-canopy following the 1980s outbreak allowed the establishment of lodgepole pine seedlings and release of advance regeneration that created understory layer in the foreground.

[3]http://www.regentinstruments.com/

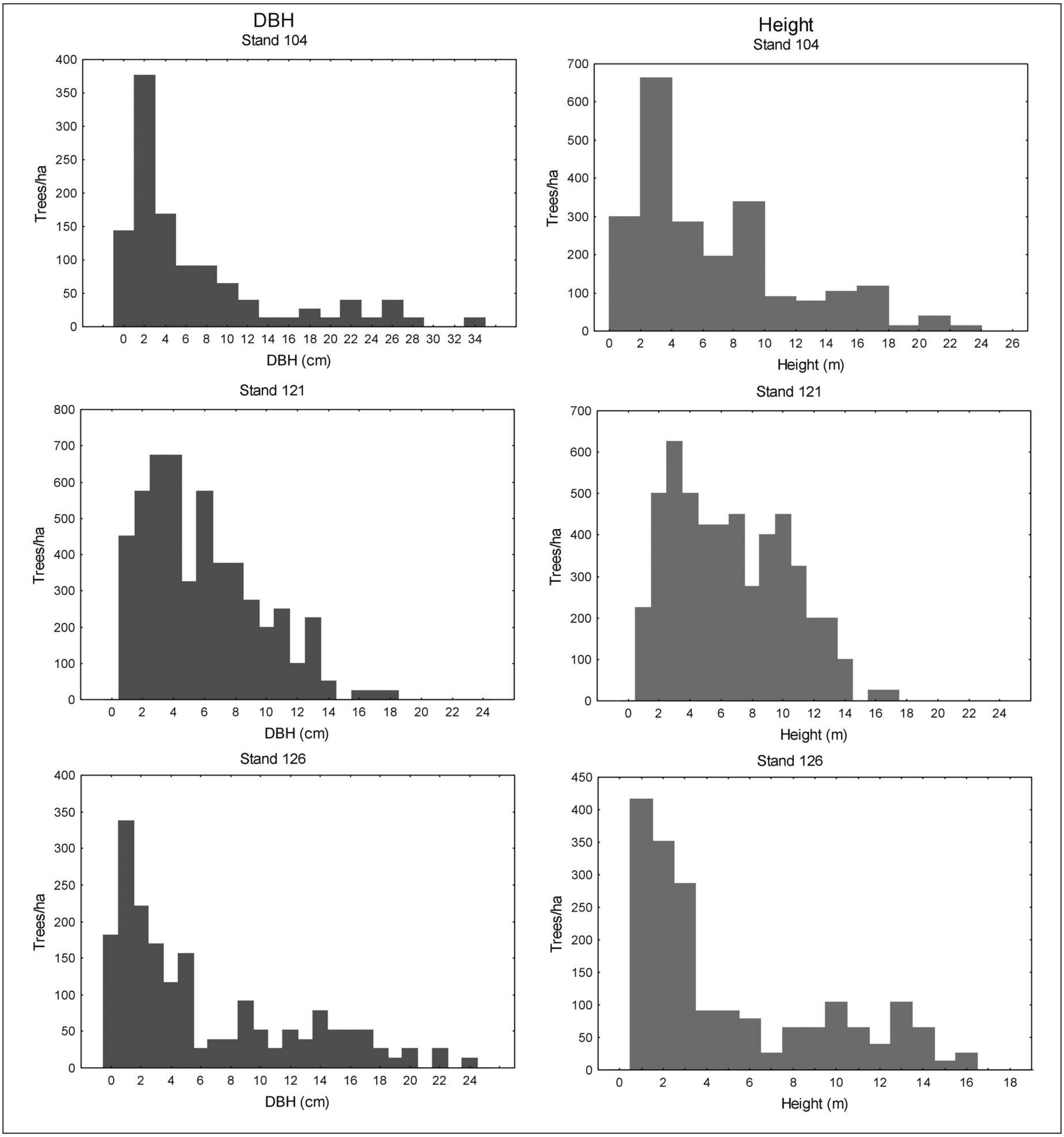

Fig. 4. Histograms of all live and dead lodgepole pine diameter-at-breast height and total height for stands 104, 121 and 126 sampled in the Interior Douglas-fir (IDFdk4) biogeoclimatic subzone located in the Cariboo–Chilcotin, B.C.

In the canopy, live tree density ranged from 278 to 1675 stems/ha, and average DBH and height was roughly 10.5 cm and 10 m tall, respectively (Table 1). The canopy was 100% lodgepole pine in stands 121 and 126, with 23% aspen in stand 104 (Table 1). In the sub-canopy, live tree density ranged from 825 to 1400 stems/ha, and was more variable than the canopy based on standard error of the mean (Table 1). Sub-canopy DBH and height ranged from 2.4 cm to 2.9 cm and 2.6 m to 5.8 m, respectively (Table 1). Lodgepole pine dominated the live sub-canopy although stands 104 and 126 had aspen as a secondary species at 50% and 26%, respectively (Table 1).

In the canopy, dead lodgepole pine density ranged from 225 to 513 stems/ha, with DBH and height ranging between 11.5 cm to 19.6 cm and 11.2 m to 13.6 m, respectively (Table 2). No dead secondary species were present in the canopy. Dead tree density in the sub-canopy ranged between 125 to 1875 stems/ha with DBH and height from 2.7 cm to 3.3 cm and 2.9 m to 4.2 m, respectively (Table 2). Stands 104 and 126 had aspen as a secondary species ranging between 20% and 29% of the total dead stems (Table 2). The proportion of dead trees that were killed by MPB ranged from 70% to 83% in the canopy and 0% to 20% in the sub-canopy (Table 2).

Table 1. Live canopy and sub-canopy tree density, diameter at breast height, height, live proportion of total tree density and species composition, for stands sampled in the Cariboo–Chilcotin, B.C.

Stand no.	Live tree density (stems/ha) (std error)	Live proportion of total density (%)	Live DBH[a], cm (std error)	Live height[a], m (std error)	Live proportion of non-pine species[b] (%)
		Canopy[c]			
104	325 (116)	38	10.2 (0.63)	9.5 (0.60)	23 At
121	1675 (287)	47	10.1 (0.28)	10.4 (0.27)	0
126	278 (32)	43	11.8 (0.72)	9.3 (0.60)	0
		Sub-canopy[c]			
104	825 (268)	79	2.9 (0.19)	3.6 (0.24)	50 At
121	1400 (227)	43	2.9 (0.19)	5.8 (0.35)	0
126	1363 (380)	92	2.4 (0.15)	2.6 (0.10)	26 At

[a]Average values and standard error.
[b]Species abbrev: At = Trembling aspen.
[c]Canopy is defined as ≥1.37 m tall and ≥7 cm DBH, and the sub-canopy as ≥1.37 m tall and <7 cm DBH.

Table 2. Dead canopy and sub-canopy tree density, diameter at breast height, height, live proportion of total tree density and species composition for stands sampled in the Cariboo–Chilcotin, B.C.

Stand no.	Dead tree density (stems/ha) (std error)	Dead proportion of total density (%)	Proportion of dead lodgepole pine killed by MPB (%)	DBH[a], cm (std error)	Height, m (std error)	Dead proportion of non-pine species[b] (%)
			Canopy[c]			
104	513 (97)	62	83	19.6 (1.4)	13.6 (0.67)	0
121	225 (75)	53	70	11.5 (1.2)	11.2 (1.2)	0
126	375 (72)	57	83	15.2 (0.80)	11.5 (0.51)	0
			Sub-canopy[c]			
104	213 (13)	21	0	2.9 (0.33)	3.5 (0.30)	29 At
121	1875 (193)	57	0	3.3 (0.17)	4.2 (0.22)	0
126	125 (66)	8	20	2.7 (0.39)	2.9 (0.31)	20

[a]Average values and standard error.
[b]Species abbrev: At = Trembling aspen.
[c]Canopy is defined as ≥1.37 m tall and ≥7 cm DBH, and the sub-canopy as ≥1.37 m tall and <7 cm DBH.

Table 3. Live advance regeneration and seedling density, diameter-at-ground-height (DGH), height, proportion of non-pine species for stands sampled in the Cariboo–Chilcotin, B.C.

Stand no.	Live tree density (stems/ha) (std error)	DGH[a], cm (std error)	Height, m (std error)	Non-pine species[b] (%)
		Advance Regeneration[c]		
104	2183 (545)	0.75 (0.46)	0.73 (0.29)	47 At
121	200 (122)	0.56 (0.18)	0.58 (0.10)	0
126	4800 (1900)	0.95 (0.07)	0.62 (0.02)	11 At
		Seedlings[c]		
104	700 (176)	–	–	43 At
121	1825 (910)	–	–	0
126	4300 (1560)	–	–	2 At

[a]DGH = mean diameter-at-ground-height.
[b]Species abbrev: At = Trembling aspen.
[c]Advance regeneration defined as <1.37 m tall and ≥0.30 m tall; seedlings defined as <0.30 m tall.

As expected, MPB-related mortality of lodgepole pine was higher in the larger DBH classes while the highest live tree density occurred in the lower DBH classes (Fig. 5). The most common cause of lodgepole pine mortality in the smaller DBH classes was predominately self-thinning (Fig. 5). Self-thinning was most evident in stand 121, which had the highest density in the lower DBH classes, where the mortality was all attributed to other causes (Fig. 5).

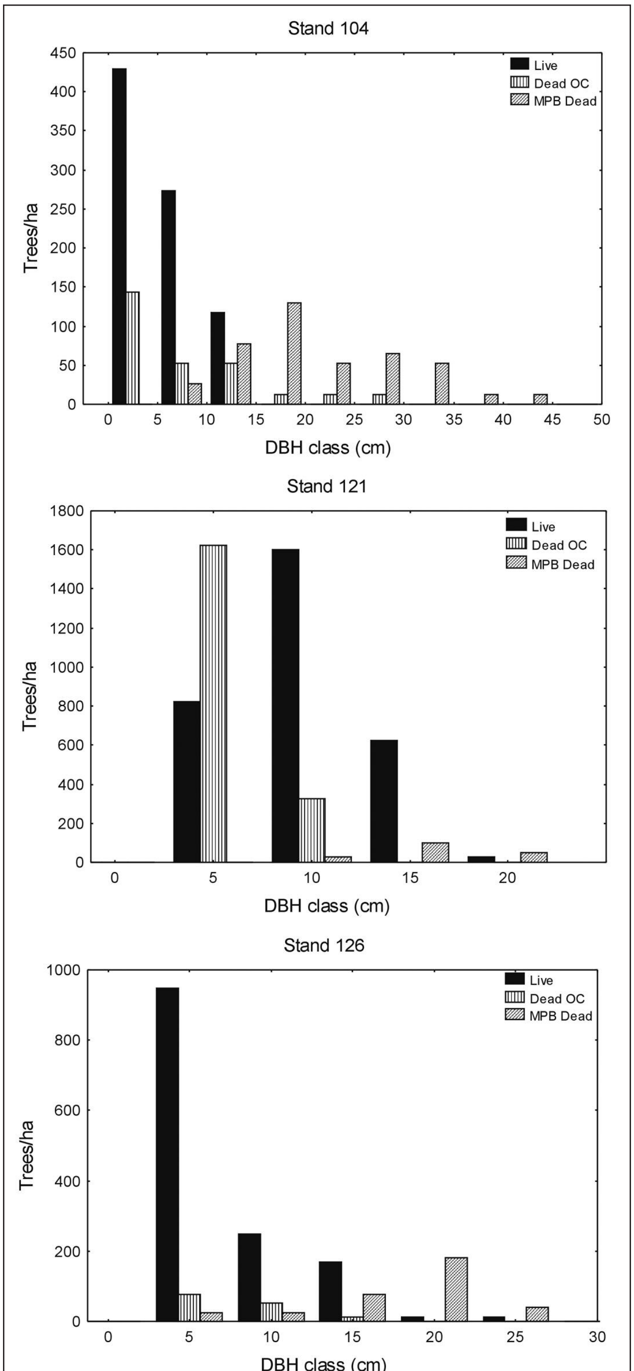

Fig. 5. Distribution of canopy and sub-canopy lodgepole pine by diameter-at-breast height (DBH) class and tree status for stands 104, 121 and 126 sampled in the Interior Douglas-fir (IDFdk4) biogeoclimatic subzone located in the Cariboo–Chilcotin, B.C. Tree status included Live, Dead OC (Other causes) (OC included mortality other than Mountain Pine Beetle (MPB)), and MPB Dead (included green (current), red and grey attacked lodgepole pine)

Advance regeneration density ranged from 200 to 4800 stems/ha, and diameter at ground height (DGH) and height ranged from 0.56 cm to 0.95 cm and 0.58 m to 0.73 m, respectively (Table 3). Seedling (only live seedlings tallied) density ranged from 700 to 4300 stems/ha (Table 3). Species composition was similar for advance regeneration and seedlings, where the leading species was lodgepole pine while aspen was secondary ranging from 15% to 19% (Table 3).

Dendroecological stand histories

Tree-ring analysis of tree increment cores and discs from the canopy, sub-canopy, and advance regeneration cohorts indicated past dates of tree establishment, mortality, and growth release for sample stands.

Canopy and sub-canopy establishment

Based on fire scar analysis, five fire events were recorded in stand 104 (Fig. 6a), five in stand 121 (Fig. 7a) and four in stand 126 (Fig. 8a). No fire scars were identified after 1911 in any of the three stands sampled. Mountain pine beetle strip attack scars were recorded in the 1910s to 1920s for stand 121 (Fig. 7a) and in the 1940s for stand 126 (Fig. 8a); while no MPB strip attack scars were found in stand 104 (Fig. 6a). An 1842 fire was recorded in all three stands, although, based on tree-ring analysis, this fire did not result in the establishment of the current canopy or sub-canopy (Figs. 6b to 8b).

In stands 104 and 126, lodgepole pine in the canopy and sub-canopy established over a period of a hundred years (Table 4), with no distinct pulses (Figs. 6b and 8b), suggesting that fires were of mixed-severity type, i.e., ground fires that crown in portions of the landscape, leaving many surviving trees. Stand 121 had a fire in 1911 that initiated lodgepole pine regeneration over a two-decade period, which now forms the canopy and sub-canopy of the present stand. The regeneration initiated by this fire indicates that fire severity was higher than those fires occurring in stands 104 and 126, possibly a stand replacement fire (Fig. 7a and 7b; Table 4).

Partial mortality of the lodgepole pine canopy by MPB reduces the canopy cover, which can facilitate tree regeneration through increased light and soil moisture availability (Coates and Hall 2005). Sub-canopy establishment for lodgepole pine was extremely prolonged occurring from the late-1800s to the mid-1970s and for aspen during the late-1960s to the early-1990s (Table 4). There were distinct pulses of sub-canopy tree establishment (Figs. 6b to 8b); especially in the 1980s for stands 104 and 126 (Figs. 6b and 8b). Sub-canopy establishment often coincided with historic MPB outbreaks as indicated by MPB scar dates (Figs. 6a and 8a) and periods of growth release in the tree ring record (Figs. 6c to 8c, see below). In addition to tree ring evidence, historic MPB outbreaks have also been documented during these periods by insect overview surveys (Wood and Unger 1996).

Historic mountain pine beetle outbreaks based on tree-ring analysis

Stand-wide growth releases were detected in each stand (Figs. 6c to 8c; Table 5). Growth releases were recorded by surviving lodgepole pine trees after fire events in the early portion of the record in each stand (Figs. 6c to 8c), and also after documented MPB outbreaks in the 1930s and 1980s (Figs. 6c to 8c; Table 5)

(Wood and Unger 1996). In addition, MPB-induced growth releases were recorded in stands 104 and 126 in the late-1950s to the 1960s (Fig 6c and 8c; Table 5) after smaller, more localized MPB infestations across the central interior during this time (Wood and Unger 1996). The proportion of sampled trees releasing in each stand was between 15% and 45%, with releases lasting between eight and 25 years (Table 5). The interval between consecutive releases, calculated from the start of one release to the start of the next release within a stand, averaged 17 years and ranged from 12 to 43 years (Table 5). The interval between releases is considered a surrogate for the interval between MPB outbreaks (Axelson *et al*. 2009).

Tree mortality dates from coarse woody debris

Dating of the coarse woody debris (CWD) (≥7 cm DBH) provided individual tree mortality dates and disclosed synchronous periods in which multiple tree mortality occurred. Tree mortality dates coincided with canopy and sub-canopy tree-ring release periods during periods of recorded MPB outbreaks (Wood and Unger 1996). Tree mortality dates occurred primarily from the 1960s to present, with tree mortality coinciding with the 1980s outbreak in all three stands (Figs. 6d to 8d). Multiple tree mortality in the 1980s was followed by periods of growth release in the remaining live canopy and sub-canopy (Figs. 6c to 8c), which in turn was followed by establishment of advance regeneration (Figs. 6e to 8e). A limitation of the CWD analysis is that sample depth decreases over time since the old CWD is not datable using dendrochronological methods because of the advance stages of rot; thus, the mortality record for each stand is incomplete, covering only the last 60 to 80 years.

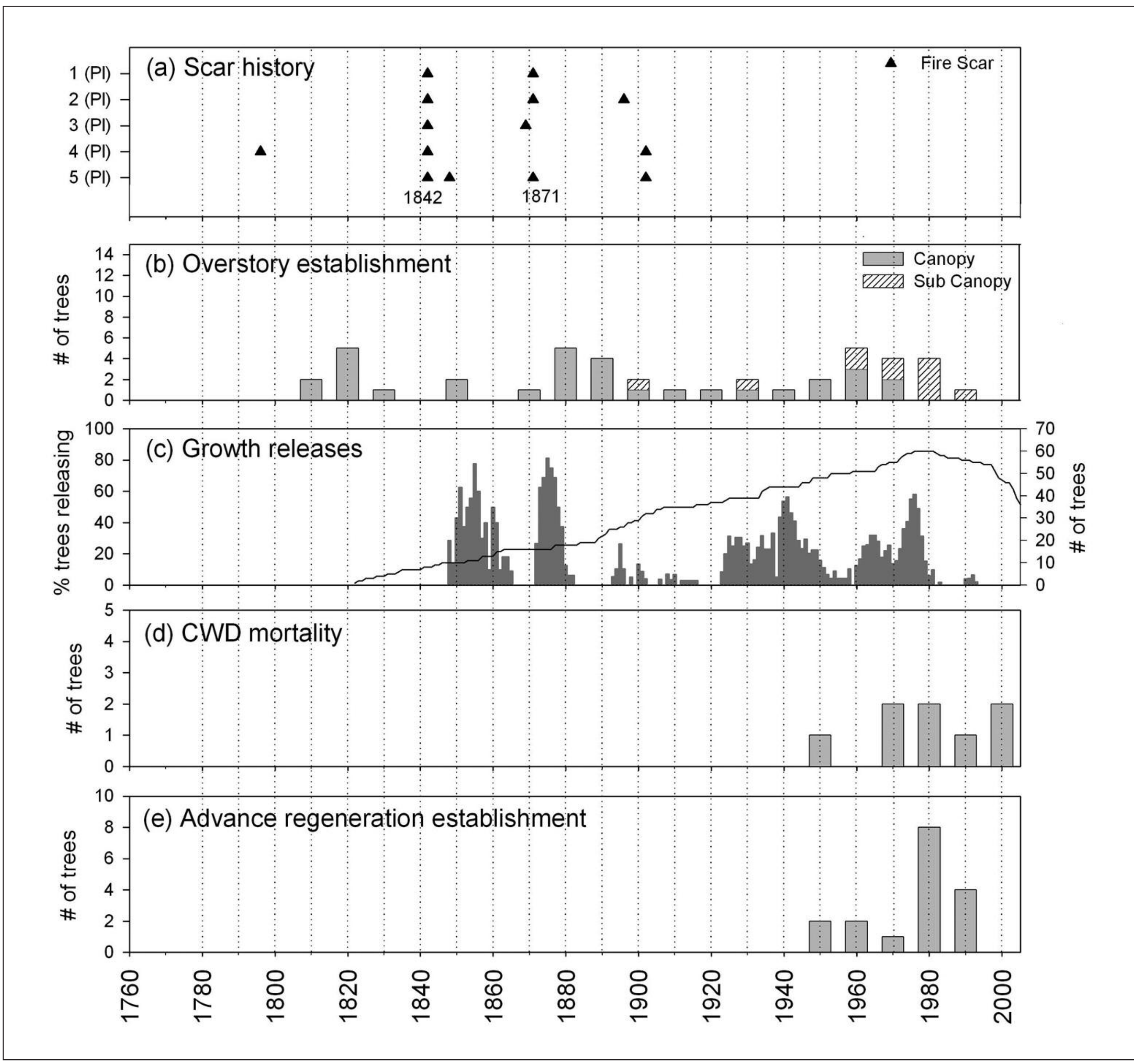

Fig. 6. Disturbance history of stand 104: **(a)** Fire scar dates; **(b)** approximate establishment date of the overstory; **(c)** Proportion of lodgepole pine showing growth releases in a given year (left axis), and sample depth (right axis); **(d)** year of death for coarse wood debris; and **(e)** date and number of advanced regeneration.

Establishment of advance regeneration

The advance regeneration in the understory originated following MPB-induced tree mortality in the 1980s (Figs. 6d to 8d) in a process similar to what triggered the recruitment of the sub-canopy trees (Figs. 6e to 8e). Advance regeneration establishment was facilitated by the canopy gaps created by MPB-induced mortality in the canopy (Fig. 3).

Discussion

Using a case study approach we determined the role of fire and MPB disturbances in the ecology of lodgepole pine in even-aged stands in southern B.C. (Axelson *et al.* 2009), and in this study, in uneven-aged stands in the IDFdk4 zone of the Cariboo–Chilcotin (CC) region of central B.C.

In this study, detailed tree-ring analysis suggest that, historically, the CC forests have been maintained by a combination of frequent low- to moderate-severity and infrequent high-severity (stand-replacement) fires and repeated MPB outbreaks varying in severity. Mixed-severity fires primarily thin lodgepole pine stands from below, killing mainly the small-diameter trees (Agee 1993), while MPB outbreaks primarily thin from above, killing large-diameter-canopy trees (Safranyik 2004). The historic fire and MPB disturbance regime has resulted in complex multi-aged lodgepole pine stands (Fig. 3), with some of the current-canopy lodgepole pine trees having both fire and MPB strip scars (Fig. 2).

Tree-ring analysis of tree cores and fire scars indicated that fires were first recorded in the early 1700s (older samples were

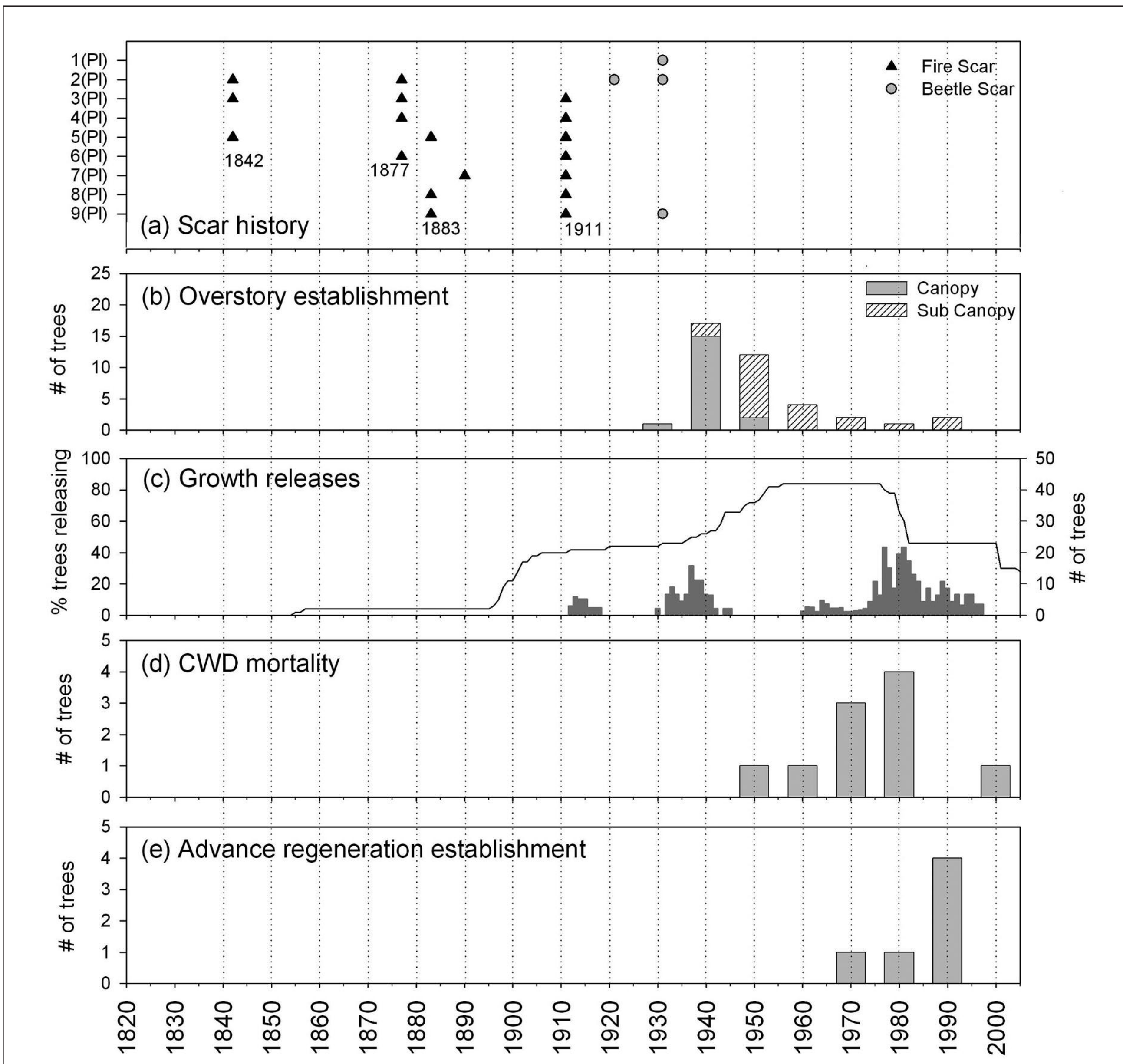

Fig. 7. Disturbance history of stand 121: **(a)** Fire and mountain pine beetle strip attack scar dates; **(b)** approximate establishment date of the overstory; **(c)** Proportion of lodgepole pine showing growth releases in a given year (left axis), and sample depth (right axis); **(d)** year of death for coarse wood debris; and **(e)** date and number of advanced regeneration.

not available), persisting throughout the 1800s, and then no longer occurring in sampled stands after the early 1900s (Figs. 6a to 8a). A similar fire history has been identified in other fire history studies in the CC (BCMFR 1995, Blackwell *et al.* 2001, Francis *et al.* 2002, Iverson *et al.* 2002, Daniels and Watson 2003, Hawkes *et al.* 2005).

In recent decades, there has been a reduction in the area burned for interior forests dominated by lodgepole pine, which was partly attributed to the start of forest fire suppression in B.C. (Taylor and Carroll 2004), and in the absence of fire during most of the 20th century, the main disturbance agent in the CC stands has shifted to MPB. Recurrent MPB outbreaks in the CC region have caused variable levels of mortality across the landscape (Hawkes *et al.* 2004), which in turn has affected the strength and duration of canopy and sub-canopy growth release. Growth releases of surviving lodgepole pine after MPB occurred in all three stands following the documented 1930s and 1980s outbreaks (Wood and Unger 1996), and in stands 104 and 126 during a smaller outbreak in the 1950s (Figs. 6c and 8c; Table 5). The strength and duration of growth releases detected in the canopy and sub-canopy are similar to other studies of MPB outbreaks in

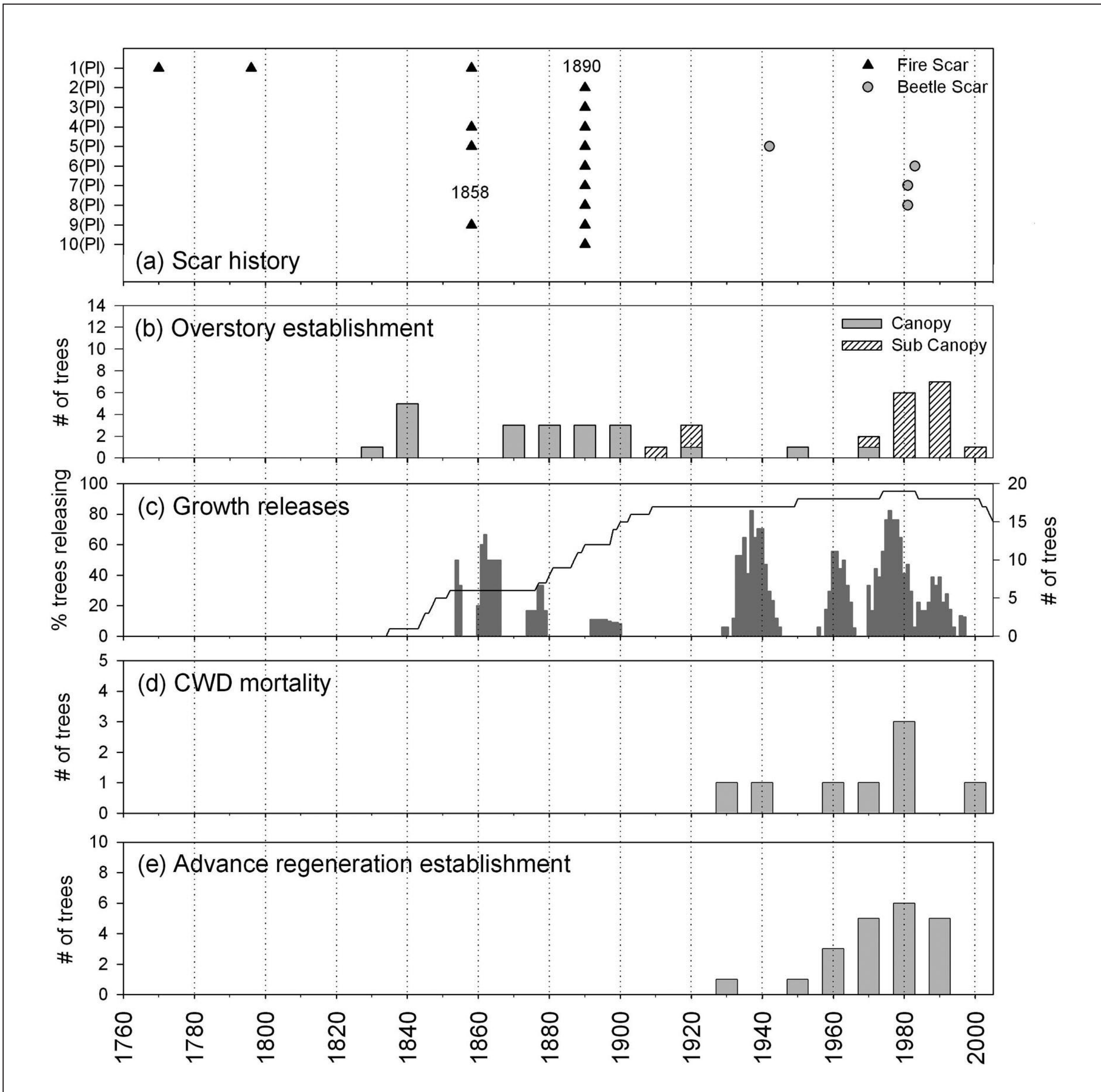

Fig. 8. Disturbance history of stand 126: **(a)** Fire and mountain pine beetle strip attack scar dates; **(b)** approximate establishment date of the overstory; **(c)** Proportion of lodgepole pine showing growth releases in a given year (left axis), and sample depth (right axis); **(d)** year of death for coarse wood debris; and **(e)** date and number of advanced regeneration.

Table 4. Tree age and establishment statistics for the canopy and sub-canopy for stands in the Cariboo–Chilcotin, B.C.

Stand no.	Species	Median age at ground height[a]	Median date of origin[b]	Range (min–max)
		Canopy[c]		
104	Lodgepole pine	116	1891	1813–1963
121	Lodgepole pine	71	1936	1929–1946
126	Lodgepole pine	130	1877	1825–1964
		Sub-canopy[c]		
104	Lodgepole pine	62	1945	1892–1970
	Trembling aspen	29	1978	1977–1979
121	Lodgepole pine	64	1943	1921–1962
126	Lodgepole pine	65	1942	1895–1974
	Trembling aspen	31	1977	1969–1991

[a]Age corrected for canopy trees cored at breast height. Correction factor derived from sub-canopy trees collected at ground-height.
[b]Tree origin based on corrected age.
[c]Canopy is defined as ≥1.37 m tall and ≥7 cm DBH, and the sub-canopy as ≥1.37 m tall and <7 cm DBH.

Table 5. Growth release dates, proportion of samples releasing, duration and interval between releases attributed to mountain pine beetle in overstory (canopy and sub-canopy) lodgepole pine in the Cariboo–Chilcotin, B.C.

Stand no.	Release dates[a]	% of trees releasing	Duration of release (years)	Interval between consecutive releases[b]
104	1924–1949	28.7	25	–
	1950–1969	15.4	19	26
	1970–1982	25.4	13	23
121	1932–1942	16.0	10	–
	1975–1995	20.6	20	43
126	1932–1945	44.9	13	–
	1958–1966	34.8	8	26
	1970–1994	38.0	24	12
Mean		**28.0**	**16.5**	**26**

[a]Growth release defined as a 25% increase in radial growth over a 10-year period recorded by a minimum of ≥10% of samples.
[b]Interval is calculated from the start of one release to the start of the next release.

B.C. (Heath and Alfaro 1990, Taylor *et al.* 2006, Campbell *et al.* 2007, Axelson *et al.* 2009). In this study, tree-ring analysis indicates that the multiple MPB outbreaks since the early 1900s have continued to maintain complex uneven-aged lodgepole pine stands without mixed-severity fires influencing stand structure and age.

Growth releases in surviving canopy and sub-canopy trees in this study, and in Axelson *et al.* (2009), were accompanied by periods of lodgepole pine regeneration (Fig. 6b to 8b; Table 4). This is consistent with studies in the western United States (Gara *et al.* 1985, Stuart *et al.* 1989, Mitchell and Preisler 1998), which have shown that the structure of lodgepole pine forests in central and southern Oregon was uneven-aged, with distinct episodic pulses of regeneration strongly correlated to MPB outbreaks and fire. In our CC stands the lodgepole pine sub-canopy mainly established after the 1930s MPB outbreak and the advance regeneration after the 1980s outbreak.

While mortality of canopy lodgepole pine by the MPB has been found to favour mainly the establishment of advance regeneration by shade-tolerant tree species (e.g., Roe and Amman 1970, Heath and Alfaro 1990, Axelson *et al.* 2009), Griesbauer and Green (2006) reported that shade-intolerant species, such as lodgepole pine and trembling aspen, were found as advance regeneration in uneven-aged lodgepole pine stands on edaphically limiting sites (Stuart *et al.* 1989, Williams *et al.* 1999, Kneeshaw *et al.* 2002, Hawkes *et al.* 2004, Daintith *et al.* 2005). In our study, the predominance of lodgepole pine in the sub-canopy, advance regeneration and seedling cohorts (Fig. 3) is consistent with Hawkes *et al.* (2004), who also found multi-age and size structures existed as a result of lodgepole pine being able to regenerate under its own canopy. In our study, the sub canopy and advance regeneration averaged 65 and 30 years old, respectively. Stem densities of the advance regeneration cohort ranged from 200 to 4800 stems/ha and seedling densities ranged from 700 to 4300 stems/ha (Table 3). Coates (2006) found that advance regeneration (five to 20 years old) densities from 1200 to 2000 stems/ha resulted in adequately stocked stands, and Koch (1996) found that seedling density of 3000 stems/ha resulted in adequate stocking. The results of these two studies suggest that our sample stands fall within the range of adequate stocking. The amount of lodgepole pine growth release found after MPB outbreaks by Murphy *et al.* (1999), Axelson *et al.* (2009) and in our study indicates that there is a potential for CC lodgepole pine sub-canopy and advance regeneration to play an important role in reducing the falldown in mid-term timber supply by reducing the time required for stand volume recovery. The growth release of surviving lodgepole pine may also reduce the need for restoration or artificial regeneration.

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References

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, DC. 493 p.

Alfaro, R., R. Campbell, P. Vera, B. Hawkes and T. Shore. 2004. Dendroecological reconstruction of mountain pine beetle outbreaks in the Chilcotin Plateau of British Columbia. *In* T.L. Shore, J.E. Brooks and J.E. Stone (eds.). Mountain Pine Beetle Symposium: Challenges and solutions. pp. 245–256. Natural Resources Canada, Canadian Forest Service, Pac. For. Centre, Victoria, BC. Inf. Rep. B.C.-X-399. 287 p.

Axelson, J., R. Alfaro and B. Hawkes. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. Forest Ecology and Management 257(9): 1874–1882. doi: 10.1016/j.foreco.2009.01.047.

Berg, E., D. Henry, C. Fastie, A. De Volder and S. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. Forest Ecology and Management 227: 219–232

Blackwell, B., R. Gray and K. Iverson. 2001. Fire Management Plan Churn Creek Protected Area. Report submitted to B.C. Parks, Cariboo District. Williams Lake, BC.

[BCMFR] British Columbia Ministry of Forests and Range. 1995. 1994 Forest, Recreation, and Range Resource Analysis. B.C. Ministry of Forests, Public Affairs Branch, Victoria, BC. 308 p.

Campbell, E., R. Alfaro and B. Hawkes. 2007. Spatial distribution of mountain pine beetle outbreaks in relation to climate and stand characteristics: A dendroecological analysis. Journal of Integrative Plant Biology 49(2): 168–178.

Cook, E. and R. Holmes. 1986. User's manual for program ARSTAN. *In* R.L. Holmes, R.K. Adams and H.C. Fritts (eds.). Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin. pp. 50–56. University of Arizona, Tucson, AZ. Chronology Series, VI.

Coates, K.D. 2006. Silvicultural approaches to managing MPB damaged stands: Regeneration and mid-term timber supply. Presentation at the Northern Silviculture Committee Winter Workshop: Silviculture tactics to lessen the downfall. Prince George, BC. January 16–18, 2006.

Coates, K.D. and E.C. Hall. 2005. Implications of alternative silvicultural strategies in mountain pine beetle damaged stands. Bulkley Valley Center for Natural Resources Research and Management, Smithers, BC. Technical Report for Forest Science Program Project Y051161.

Daintith, N.M., M.J. Waterhouse and H.M. Armleder. 2005. Seedling response following partial cutting in lodgepole pine forests on caribou winter range in west-central British Columbia. The Forestry Chronicle 81: 409–417.

Daniels, L.D. and E. Watson. 2003. Climate–fire–vegetation interactions in Cariboo Forests: a dendroclimatic analysis. Report to Forest Innovation and Investment, Forest Research Program, Vancouver, BC.

Francis, S., S. Skinner, M. Gallagher and C. Marion. 2002. Characterizing fire regimes: fire history research in the SBPS and SBS Biogeoclimatic zones of the Cariboo Forest Region, a Report for the Lignum Ltd. IFPA. Report prepared for Lignum Ltd. by Applied Ecosystem Management Ltd., Williams Lake, BC. 164 p.

Furniss, R. and V. Carolin. 1977. Western forest insects. United States Department of Agriculture, Miscellaneous Publication No.1339. 654 p.

Gara, R.I., W.R. Littke, J.K. Agee, D.R. Geiszler, J.D. Stuart and C.H. Driver. 1985. Influence of fires, fungi, and mountain pine beetles on development of a lodgepole pine forest in south-central Oregon. *In* D.M. Baumgartner (ed.). Lodgepole pine: the species and its management. Symposium Proceedings, May 8–10, 1984, Spokane, WA, and May 14–16, 1984, Vancouver, BC. pp. 153–162. Washington State University Conferences and Institutes, Pullman, WA.

Griesbauer, H. and S. Green. 2006. Examining the utility of advance regeneration for reforestation and timber production in unsalvaged stands killed by the mountain pine beetle: Controlling factoring and management implications. BC Journal of Ecosystems Management 7(2): 81–92.

Hawkes, B., S. Taylor, C. Stockdale, T. Shore, R. Alfaro, R. Campbell and P. Vera. 2004. Impact of mountain pine beetle on stand dynamics in British Columbia. *In* T.L. Shore, J.E. Brooks and J.E. Stone (eds.). Mountain pine beetle symposium: challenges and solutions. October 30–31, 2003. pp. 177–199. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Information Report B.C.-X-399. 287 p.

Hawkes, B., S. Taylor, C. Stockdale, T. Shore, S. Beukema and D. Robinson. 2005. Predicting mountain pine beetle impacts on lodgepole pine stands and woody debris characteristics in a mixed severity fire regime using PrognosisBC and the Fire and Fuels Extension. *In* L. Lagene, J. Zelnik, S. Cadwallader and B. Hughes (eds.). Mixed Severity Fire Regimes: Ecology and Management, November 17–19, 2004. pp. 123–135. Washington State University Coop Extension Service, The Association for Fire Ecology, Pullman, WA. Vol. AFE MISC03.

Heath, R. and R. Alfaro. 1990. Growth response of a Douglas-fir/lodgepole pine stand after thinning of lodgepole pine by the mountain pine beetle. Journal of the Entomological Society of British Columbia 87: 16–21.

Holmes, R. 1983. Computer assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43: 69–78.

Holmes, R. 1999. Program JOLTS. Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ. unpublished.

Hope, G., W. Mitchell, D. Lloyd, W. Erickson, W. Harper and B. Wikeem. 1991. Chapter 10: Interior Douglas-fir Zone. *In* D. Meidinger and J. Pojar (eds.). Ecosystems of British Columbia. pp. 153–166. B.C. Ministry of Forests Special Report Series 6. Research Branch, Victoria, BC. 330 p.

Iverson, K., R. Gray, B. Blackwell, C. Wong and K. MacKenzie. 2002. Past fire regimes in the Interior Douglas-fir, Dry Cool subzone, Fraser variant (IDFdk3). Report to Lignum Ltd. Williams Lake, BC. 112 p.

Kneeshaw D.D, H. Willians, E. Nikinmaa and C. Messier. 2002. Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting. Canadian Journal of Forest Research 32: 255–65.

Krajina, V. 1969. Ecology of forest trees in British Columbia. Ecology of Western North America 2: 1–146.

Koch, P. 1996. Lodgepole pine in North America-Part I: Background. Forest Products Society, Madison, WI. 343 p.

Lloyd, D., K. Angrove, G. Hope and C. Thompson. 1990. A guide to site identification and interpretation for the Kamloops Forest Region. British Columbia Ministry of Forests.

Meidinger, D. and J. Pojar (compilers and editors). 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Special Report Series No. 6.

Mitchell, R., R. Martin and J. Stuart. 1983. Catfaces on lodgepole pine – fire scars or strip kills by the mountain pine beetle? Journal of Forestry 81: 589–601.

Mitchell, R. and H. Preisler. 1998. Fall rate of lodgepole pine killed by the mountain pine beetle in central Oregon. Western Journal of Applied Forestry 13: 23–26.

Mitchell, R., H. Preisler and K. Haiganoush. 1991. Analysis of Spatial Patterns of Lodgepole Pine Attacked by Outbreak Populations of the Mountain Pine Beetle. Forest Science 37(5): 1390–1408.

Murphy, T.E., D.L. Adams and D.E. Ferguson. 1999. Response of advance lodgepole pine regeneration to overstory removal in eastern Idaho. Forest Ecology and Management 120: 235–244.

Roe, A. and G. Amman. 1970. The mountain pine beetle in lodgepole pine forests. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT. Research Paper INT-71. 23 p.

Rubino, D. and B. McCarthy. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia 21(3): 97–115.
Safranyik, L. 2004. Mountain pine beetle epidemiology in lodgepole pine. *In* T.L. Shore, J.E. Brooks and J.E. Stone (eds.). Mountain Pine Beetle Symposium: Challenges and Solutions. October 30–31, 2003, Kelowna, British Columbia. pp. 33–40. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399. Victoria, BC. 298 p.
Safranyik, L., D. Shrimpton and H. Whitney. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Environment Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Forestry Technical Report 1. 24 p.
Shore, T., L. Safranyik, B. Hawkes and S. Taylor. 2006. Effects of the mountain pine beetle on lodgepole pine stand structure and dynamics. *In* L. Safranyik, and B. Wilson (eds.). The Mountain Pine Beetle: A Synthesis of Biology, Management and Impacts on Lodgepole Pine. pp. 95–114. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. 304 p.
Steen, O. and R. Coupé. 1997. A field guide to forest site identification and interpretation for the Cariboo Forest Region. B.C. Ministry of Forests, Victoria, BC. Land Management Handbook. No. 39. 358 p.
Stokes, M. and T. Smiley. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, IL. 73 p.
Stuart, J., J. Agee and R. Gara. 1989. Lodgepole pine regeneration in an old, self-perpetuating forest in south central Oregon. Canadian Journal of Forest Research 19: 1096–1104.
Stuart, J., D. Geiszler, R. Gara and J. Agee. 1983. Mountain pine beetle scarring of lodgepole pine in south-central Oregon. Forest Ecology and Management 5: 207–214.
Taylor, S. and A. Carroll. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in B.C.: A historical perspective. *In* T.L. Shore, J.E. Brooks and J.E. Stone (eds.). Mountain Pine Beetle Symposium: Challenges and solutions. pp. 41–51. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. Inf. Rep. B.C.-X-399. 287 p.
Taylor, S., A. Carroll, R. Alfaro and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. *In* L. Safranyik and B. Wilson (eds.). The Mountain Pine Beetle A Synthesis of Biology, Management and Impacts on Lodgepole Pine. pp. 67–94. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. 304 p.
Veblen, T., K. Hadley, M. Ried and A. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology 71(1): 213–231.
Westfall, J. and T. Ebata. 2008. 2008 Summary of forest health conditions in British Columbia. Pest Management Report Number 15. British Columbia Ministry of Forests and Range, Victoria, BC.
Williams, H., C. Messier and D.D. Kneeshaw. 1999. Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine. Canadian Journal of Forest Research 29: 222–231.
Wood, C. and L. Unger. 1996. Mountain pine beetle: A history of outbreaks in pine forests in British Columbia, 1910 to 1995. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. 61 p.