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Stand recovery and self-organization following large-scale mountain pine beetle induced canopy mortality in northern forests

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ABSTRACT

A mountain pine beetle (MPB) epidemic is currently ravaging large areas of interior British Columbia (BC) with significant implications for ecosystem services including future timber supply and community economic stability. Information is needed on future stand dynamics in areas of impacted forests that are unlikely to be salvaged logged. Of greatest concern are stands dominated by lodgepole pine (>50% timber volume). Predicting how surviving trees in these areas respond and grow and the timing and species composition of natural regeneration ingress is of critical importance for multiple forest values. We undertook a retrospective study in the Flathead Valley of southeastern British Columbia where an intense MPB epidemic peaked in 1979–1980. Our objective was to gain insight into stand recovery and stand self-organization as influenced by species-specific growth responses of different sized secondary structure trees (individual seedling, sapling, sub-canopy and canopy trees surviving the epidemic) and post-beetle regeneration dynamics. MPB mortality rates, the percent of basal area killed by beetles, varied from 42% to 100% with most stands between 60% and 80%. In general, all surviving secondary structure released but the extent of growth release exhibited species variability. Release of surviving canopy lodgepole pine trees was often dramatic and greatest in stands with high total stand MPB mortality rates. Ingress of natural regeneration was slow in the first few years after MPB attack but there was a strong pulse of recruitment 10–20 years post disturbance which then slowed considerably. Nearly 30 years after the MPB attack, the stocking and composition of the understories have changed dramatically. Overall, the occurrence of the MPB epidemic resulted in more structurally and compositionally diverse stands leading to multiple successional pathways different from those of even-age pine dominated stands. The recovery and self-organization of unsalvaged natural stands in the Flathead Valley was a complicated process. It has provided insights for future forest management in areas impacted by the current massive MPB epidemic ongoing for the past decade in western North America.

1. Introduction

The mountain pine beetle (*Dendroctonus ponderosae*) (MPB) is currently in the outbreak phase of an infestation cycle throughout much of its range in British Columbia (BC). The current epidemic, starting in the late 1990s, has now impacted over 18 million hectares of BC forest land in the interior portions of the province (Walton, 2012). The current MPB epidemic is the most significant forest management challenge BC has ever faced and has caused variable levels of damage from near complete mortality in many lodgepole pine (*Pinus contorta* var. *latifolia*)-dominated stands to partial mortality in mixed-species stands. In the central and southern interior regions of BC, the MPB epidemic has impacted just over 10 million hectares of the 22 million hectare provincial operable land base (the total area available for commercial timber harvest in all of BC). The epidemic has killed a cumulative total of 710 million m^3 of pine in the operable land base, or 53% of the merchantable pine volume in the province at the start of the infestation, and is now projected to kill approximately 57% of the pine volume by 2017 (Walton, 2012).

In response to the epidemic an aggressive salvage strategy has been implemented to harvest dead pine while it retains economic value. Targeted stands for salvage were those dominated by pine (>50% by volume). It is estimated about 5 million hectares of the operable land base are pine dominated and just over 1 million hectares were salvage logged and reforested to 2011. Depending on future harvest intensity assumptions, salvage operations may reach 1.7–2.1 million hectares by 2024, at which time the dead

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pine are no longer expected to have economic value for conventional sawmill products. Clearly, large areas of the operable land base severely impacted by the epidemic will not be logged. Information on the speed, composition and density of post-MPB regeneration combined with data on expected growth rates of trees surviving the epidemic will be of considerable importance for projecting future timber supply in the operable land base and have clear implications for community economic stability in the highly impacted areas of BC. Likewise, understanding stand recovery and self-organization in MPB-impacted forests in both the operable and non-operable land base will be important for predicting their future provision of ecosystems services such as carbon sequestration (Bowler et al., 2012), hydrological recovery (Winkler et al., 2012) and wildlife habitat (Bunnell et al., 2011).

The composition and size structure of trees surviving the epidemic is highly variable with different combinations of species and densities of understory and overstory trees that have been collectively called 'secondary structure' (Coates et al., 2006, 2009; Vyse et al., 2009; Hawkins et al., 2012). In the drier forest types of the central and southern interior, understory and sub-canopy trees that survive the epidemic are often dominated by lodgepole pine. The understory and sub-canopy trees surviving the epidemic in moister forest types or in the more northern regions of the epidemic area are primarily more shade tolerant conifer species than pine. Larger diameter trees that survive the beetle epidemic are typically of non-host species (e.g., interior spruce (*Picea glauca* × *engelmanii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), or broadleaf species).

There are two pathways for recovery of MPB attacked stands. First, impacted stands can be salvage logged, usually by clearcutting with retention, followed by planting or natural regeneration. Salvage logging prescriptions follow standard practices with predictable outcomes from a timber supply perspective. Second, and the focus of our analysis, is the recovery of MPB-impacted stands that are not salvaged logged. The timing and abundance of post-beetle natural regeneration and the growth responses of new regeneration and secondary structure in unsalvaged MPB-impacted stands is a much more complicated issue for projection than a salvage logging and planting scenario.

Astrup et al. (2008) found that recruitment of new seedlings in the early years of the current MPB epidemic in central British Columbia was patchy and poorly developed and was substantially lower than the strong pulse of regeneration observed after stand replacement wildfires in these northern forests. Likewise, Axelson et al. (2009) and McIntosh and MacDonald (2013) concluded that natural seedling recruitment following MPB outbreaks is a slow process. Furthermore, the recruitment of new regeneration after MPB-attack is quite variable across biogeoclimatic zones in British Columbia (Hawkes et al., 2004; Hawkins et al., 2012). Overall, the longer-term timing and extent of post-disturbance recruitment from seed is poorly understood in MPB-disturbed forests (Mitchell, 2005).

For the major tree species found within MPB-impacted stands there has been considerable work done on how seedlings and saplings grow as a function of their light environment (Wright et al., 1998; Coates and Burton, 1999), how rapidly growth rates of seedlings and saplings reflect their new light environment following disturbance (Wright et al., 2000), and how sub-canopy and canopy trees grow as a function of their competitive neighbourhoods (Canham et al., 2004; Coates et al., 2009; Coates et al., 2013). These studies all suggest canopy mortality of lodgepole pine will result in improved growing conditions (increased light availability and reduced belowground competition) for surviving secondary structure. Elsewhere, it has been observed that insect epidemics that rapidly kill canopy pine trees create ideal conditions for a rapid and prolonged release response of surviving trees (Baskerville, 1975; Romme et al., 1986; Thompson et al., 2007). The magnitude of the release response can be modified by factors such as tree species, age, size, condition and damage (Messier et al., 1999; Griesbauer and Green, 2006).

Even so, skepticism about the potential of secondary structure to release and grow well and help mitigate expected timber supply shortages and other ecosystems services in MPB-impacted landscapes remains strong. An effective method to acquire growth data for secondary structure after beetle attack is to undertake retrospective studies in areas attacked in the past (Heath and Alfaro, 1990). Our retrospective study examines long term species-specific growth responses of different sized secondary structure trees and post-beetle regeneration dynamics in unsalvaged natural stands after a short but severe MPB epidemic that peaked in 1979–1980 in the Flathead Valley of southeastern BC (Young, 1988). Specifically, we (a) quantify release of surviving seedlings, saplings, sub-canopy and canopy trees of different tree species, and (b) reconstruct understory recruitment dynamics after the epidemic.

2. Methods

2.1. Study area

The study area was located in the Flathead Valley, a term used to identify a large system of drainages in the southeastern corner of BC that eventually join up and flow into Flathead Lake in Montana (Young, 1988). The dominant area of sampling was approximately 60 km southeast of Fernie, BC. The Flathead Valley is in the Dry Cool subzone (MSdk) of the Montane Spruce biogeoclimatic zone, about 1500 m above sea level (Meidinger and Pojar, 1991). The MSdk experiences a continental climate (mean annual temperature of 3–5 °C) with cold, snowy winters (mean coldest month temp of −9.4 °C) and short, warm summers (mean warmest month temp of 15.6 °C) with 151 frost free days per year. Mean annual precipitation is 750 mm (May–September 275 mm) with annual winter snowfall of 342 cm (Lloyd et al., 2006). Lodgepole pine, interior spruce, subalpine fir, Douglas-fir, and western larch (*Larix occidentalis*) are the dominant coniferous tree species.

The Flathead Valley experienced a number of fires in the early 1900s with the largest occurring in 1936 resulting in the establishment of extensive lodgepole pine stands (Young, 1988; Barrett et al., 1991). Since 1945 there have been no significant fires in the Flathead Valley. An intense MPB epidemic started in the Flathead Valley in 1976, peaking in 1979–1980, and then abruptly ended in 1981, likely due to severe winter temperatures (Young, 1988). At the time of the epidemic the forest profile of the Flathead Valley was one dominated by pine forests 40–60 years old, but it also contained pockets of mature pine that had survived the earlier fires (Young, 1988).

2.2. Field sampling

In the fall of 2007, we sampled a total of 22 stands that encompassed a range of surviving secondary structure and pine mortality from the 1976–1981 MPB attack. The boundaries of the epidemic location were well documented and selection of sample stands was based on old maps of the epidemic area. We sampled stands with mesic soil moisture and nutrient conditions that had clear evidence of prior MPB mortality. Stands with evidence of other disturbances or unaccounted mortality were avoided. We specifically sought out stands with variability in surviving secondary structure species composition and MPB mortality rates (expressed as percent total stand mortality or percent pine mortality, Table 1). There was, however, no attempt to place stands into different attack intensity categories. Our objective was to have a balanced sample of stands

Table 1
Year of mountain pine beetle attack, pre- and post-attack basal area (m^2 per hectare), percentage total stand and lodgepole pine basal area mortality, current and post-attack basal area growth, and current understory tree density (stems per hectare) for all trees <7.5 cm DBH at the 22 sample sites.

Site	Attack year	Pre-attack basal area	Post-attack basal area	Percentage basal area dead at attack		Present basal area	Post-attack basal area growth	Understory trees
				Total	Lodgepole pine			
1	1980	52.2	21.1	59.6	65.4	46.1	25	23,720
2	1979	48.6	23.4	51.9	78.7	51.0	27.6	1000
3	1980	55.6	15.4	72.3	78.5	32.7	17.3	3480
4	1980	57.7	11.8	79.5	89.2	26.5	14.7	1800
5	1978	52.6	27.0	48.6	41.8	44.7	17.7	6160
6	1979	49.5	18.6	62.4	64.7	35.3	16.7	1560
7	1980	42.2	6.9	83.8	83.5	14.5	7.6	6840
8	1980	56.6	16.4	71.0	80.5	40.7	24.3	10,200
9	1980	35.0	6.3	82.1	68.3	16.4	10.1	4200
10	1980	54.1	30.6	43.5	65.7	51.5	20.9	3920
11	1980	46.3	19.1	58.7	69.7	34.1	15	440
12	1979	43.5	12.3	71.7	71.6	29.8	17.5	1400
13	1980	40.9	17.6	57.1	81.8	34.4	16.8	4000
14	1980	58.4	20.7	64.5	62.2	35.2	14.5	5200
15	1980	44.8	20.3	54.7	66.2	34.6	14.3	2120
16	1979	30.7	0.0	99.9	99.9	4.0	4	400
17	1979	39.9	11.7	70.8	68.9	24.8	13.1	1520
18	1980	29.9	11.4	61.9	61.9	19.8	8.4	1680
19	1980	33.4	5.0	85.1	84.0	7.8	2.8	1280
20	1980	50.4	25.0	50.4	51.2	50.1	25.1	680
21	1980	29.0	11.0	61.9	71.2	27.3	16.3	920
22	1979	43.7	25.2	42.3	51.1	44.3	19.1	1560

that had MPB mortality rates of 40 to 90% total stand mortality (Table 1). These stand mortality rates bracket mortality rates seen in the current epidemic ongoing in central BC. Once a stand was selected we picked a random point in the polygon and from that point a random transect direction was selected and 5 plots, spaced 50 m apart, were sampled for a total of 110 plots in the 22 stands.

Each plot consisted of two nested plots. The larger outer plot had a 7.98 m radius and the smaller inner plot a 3.99 m radius. In the larger plot we recorded tree species and diameter at 1.3 m (DBH) of all live trees taller than 1.3 m and DBH of all MPB killed pine trees. In the smaller inner plot the species and height of all live trees (5 cm or taller) was recorded. An increment core was taken at 1.3 m from all live trees larger than 7.5 cm DBH within the inner plot to document radial growth rates. Smaller live trees (seedlings and saplings) within the inner plot were destructively sampled. We obtained radial growth data and age estimates from a disc taken at the base of smaller trees. Sample sizes for cored and cut trees, by species and tree size class (overstory trees, saplings and seedlings), are found in Table 2.

2.3. Laboratory procedures

All increment core samples and tree base discs were sanded following standard dendrochronological methods (Stokes and Smiley, 1968). The MPB growth signal was very clear, with cored trees showing consistent growth releases associated with the peak timing of the MPB attack. Cores and cross-sections were visually cross-dated and ring-width series were measured on a Velmex bench to the nearest 0.001 mm. All ring-width series cores were statistically cross-dated using the program COFECHA (Holmes 1986, Grissino-Mayer, 2001) and with the help of existing master chronologies developed within the study area (Daniels, unpublished chronologies). Ring-width series of young seedlings (<20–25 years) that did not cross-date statistically and/or presented low correlation coefficient values were visually cross-dated.

Table 2
Sample sizes by tree species and tree size class. Overstory trees are >7.5 cm DBH; saplings are 1.3 m tall to 7.5 cm DBH; and seedlings are less than 1.3 m tall.

Species	Canopy trees	Saplings	Seedlings
Lodgepole pine (Pl)	332	46	19
Subalpine fir (Bl)	26	30	21
Interior spruce (Sx)	51	27	4
Douglas-fir (Fd)	22	23	13
Western larch (Lw)	25	3	0
Total	456	129	57

2.4. Analyses

Using the MPB epidemic maps, tree ring data from surviving living trees and DBH data for MPB killed trees we estimated year of attack, living and dead basal area and total basal area at the time of MPB attack. MPB killed trees were still solid, largely on the ground, with obvious beetle galleries present. Based on these estimates, at each site, we calculated the percent of total stand basal area and lodgepole pine killed as well as basal area recovery to fall of 2007, or almost 30 years post-peak beetle attack (Table 1).

Master ring-width chronologies were developed for each site by standardization using the program ARS41_win (Cook and Krusic, 2006). Standardization is a process that removes the long-term variations from a time series of measured tree-ring properties by dividing the actual measurements by those predicted from a statistically derived equation. For this study, standardization was performed by fitting the observed data to a horizontal line passing through the mean ring width of the series. This method detects past outbreak events better than other standardization models (Veblen et al., 1991; Kitzberger et al., 2000). Species-specific master chronologies were developed for each site by combining all trees of a species so as to represent their average growth. The chronologies were later used to study the response of the surviving overstory trees as a consequence of the outbreak.

We calculated percent-growth change for individual trees according to the technique of Nowacki and Abrams (1997). Percent-growth change for a year is equal to $(M_2{-}M_1)/M_1$, where M_1 represents the average growth over the prior 10 years and M_2 represents the average growth over the subsequent 10 years. It represents positive (releases), negative (suppression) and no significant changes. A 10-yr span for radial-growth averaging was selected since it tends to average out short-term growth responses related to climate, while capturing growth changes associated with canopy disturbance (Leak, 1987; Nowacki and Abrams, 1997).

Release and suppression events were identified for each tree based on the raw ring width measurements, and the criteria used were: high release (suppression) for >100% growth change; medium release (suppression) for 50–100% growth change, and low release (suppression) for < 50% growth change (increase/decrease) in radial growth. For each tree we recorded the magnitude of the growth release or suppression, when the event was initiated, and the number of series in which no significant release (suppression) was recorded after the MPB attack.

Analyses were performed using simultaneously the ARS41_win (Cook and Krusic, 2006) and JOLTS (Holmes, 1999) programs. The ARS41_win program calculated only release events in raw series of tree-rings based in changes in percent-growth. We set running mean window of 10 years and percent-growth change following the criteria defined above. The JOLTS program was used to calculate not only release events but also suppression in radial growth. This program calculates the occurrence, coincidence and span of growth releases and suppressions. Again, we used a running mean window of 10 years and growth change factors for the change from pre- to post- event related to the criteria expressed above (factors 1.05, 1.5, 2 related to >50%, 50–100% and >100% growth change, respectively). As the magnitude of the release and suppression responses (percent-growth change) could vary given different tree size-classes, we analyzed the association between radial growth responses and the diameter at the time of the MPB attack reconstructed from ring-width measurements.

For all cross-sections, ring-width series were used to determine number of years since germination as the difference between the pith date and the year of sampling (2007). We then reconstructed the time of establishment of all understory seedlings and saplings by species, summarized in 5-year age classes. At each site, the ring widths of seedlings and saplings that were at least 10 years older than the year of MPB attack were used to assess the post-outbreak percent growth change using the same approach described previously (Nowacki and Abrams, 1997).

3. Results

3.1. Overstory composition, mortality and recovery

Our analysis indicated one stand in the Flathead Valley was attacked by the mountain pine beetle (MPB) in 1978 and all remaining stands were attacked in 1979–80 (Table 1). Just before the epidemic hit the Flathead Valley, the basal area of our sample stands averaged 45.2 m^2 ha^{-1} (Table 1). The proportion of pine killed in the Flathead Valley averaged 70.7% (ranged from 41.8% to 99.9%) (Table 1). The total stand basal area killed in the epidemic was slightly lower at 65.2% (Table 1) reflecting, on average, the relatively small contribution of other tree species to total stand basal in the lodgepole pine dominated stands we sampled. Stand basal area was reduced to an average of 16.2 m^2 ha^{-1} immediately post-beetle attack (Table 1).

In fall 2007, almost 30 yrs post-MPB attack, total stand basal area averaged 31.1 m^2 ha^{-1}. This represented an average increase of 14.9 m^2 ha^{-1} since attack and a recovery of 68.8% of the stand basal area pre-beetle attack. Individual stands varied from 4 to 51 m^2 ha^{-1} in 2007 (Table 1). Nearly 30% of stands had recovered to basal area values similar to those before the attack. Stands with the greatest proportion of total stand basal area killed exhibited the poorest basal area recovery (e.g., sites 7, 9, 16, and 19) (Table 1).

Lodgepole pine retained clear dominance in 41% of the stands but other species such as interior spruce, western larch and Douglas-fir increased their relative dominance and had became dominant almost 30 yrs after the attack in 23% of the stands (e.g., sites 2, 3, 10, 12, and 13). In all these latter cases the species gaining dominance were those of second importance in the stands before the canopy mortality (Table 3). In addition, species that were a minor component, or even absent before the attack, later became important elements of stand composition in 32% of stands.

3.2. Overstory tree growth response

Growth responses of the surviving overstory trees were variable among the Flathead Valley stands with differences in how individual species reacted to the stand conditions post-MPB (Fig. 1

Table 3
Overstory stand composition pre- and post-attack (fall 2007) by species as a percentage of the total basal area (m^2 per hectare) and percent understory composition post-attack for the 22 sampled sites. Species codes are in Table 1.

Site	Overstory pre-attack					Overstory post-attack					Understory				
	Pl	Bl	Sx	Fd	Lw	Pl	Bl	Sx	Fd	Lw	Pl	Bl	Sx	Fd	Lw
1	88.6	6.3	5.1	0	0	59.0	19.8	21.2	0	0	0.5	95.3	4.2	0	0
2	63.5	0.3	36.2	0	0	36.0	5.3	58.7	0	0	76.0	8.0	12.0	4.0	0
3	85.7	1.1	13.2	0	0	40.9	6.3	52.8	0	0	16.2	42.5	39.1	1.1	1.1
4	90.1	4.6	5.3	0	0	48.3	0	26.7	0	25.0	2.2	55.6	42.2	0	0
5	97.9	0	2.1	0	0	92.9	0	7.1	0	0	43.5	24.7	28.6	1.9	1.3
6	91.7	0	0.1	8.1	0	89.2	0	1.0	9.8	0	12.8	7.7	7.7	71.8	0
7	99.6	0	0.4	0	0	83.2	0	0	16.8	0	34.9	22.7	5.2	36.6	0.6
8	85.5	5.7	8.5	0.3	0	44.9	32.2	19.3	3.6	0	10.5	56.3	4.7	28.5	0
9	100	0	0	0	0	100	0	0	0	0	8.4	1.9	89.7	0	0
10	61.0	0	0	32.3	6.7	35.1	0	0	50.1	14.8	4.1	7.1	1.0	87.8	0
11	98.2	0	0	0	1.8	92.8	0	0	0	7.2	27.3	54.5	0	9.1	9.1
12	87.2	0.1	0	0	12.8	50.0	1.1	0	0	48.8	38.5	38.5	20.5	2.6	0
13	67.7	0	0.2	0.4	31.7	30.8	0	1.5	1.0	66.7	58.0	37.0	3.0	2.0	0
14	92.1	3.7	2.8	0.8	0.5	80.3	8.5	6.4	3.4	1.3	2.3	89.2	7.7	0.2	0
15	81.9	0	1.1	0	16.9	64.4	0	5.8	0	29.8	52.7	34.5	10.9	1.9	0
16	97.6	0	2.4	0	0	100	0	0	0	0	50.0	10.0	0	40.0	0
17	75.9	0	24.1	0	0	76.4	0	23.6	0	0	12.8	17.9	69.2	0	0
18	100	0	0	0	0	100	0	0	0	0	13.6	15.9	11.4	59.1	0
19	100	0	0	0	0	100	0	0	0	0	21.9	50.0	3.1	21.9	3.1
20	100	0	0	0	0	100	0	0	0	0	41.2	35.3	5.9	5.9	11.8
21	92.1	0	0	7.9	0	86.1	0	0	13.9	0	0	39.1	17.4	39.1	4.3
22	83.8	0	0	1.2	15.1	70.5	0	1.0	3.0	25.5	26.2	21.4	35.7	11.9	4.8

displays individual graphs for sites 1–22). In general, the growth performance of surviving trees depended on both the proportion of the lodgepole pine killed and the proportion of pine in each stand. Across all sites 62%, 30% and 8% of the surviving overstory pine trees had a positive, negative or neutral growth response, respectively. In general, pine growth release was best at sites that experienced high mortality rates (e.g., sites 4 and 16) and poorest at sites with low mortality rates (e.g., sites 1, 5, 14, 15 and 22). These trends for pine were, however, not entirely consistent (e.g., sites 2 and 20 for somewhat opposite growth responses) suggesting local stand and neighbourhood conditions were likely both important for determining growth responses of surviving overstory pine trees.

Subalpine fir overstory trees had the highest positive release with 69% of the trees having a positive growth response (23% and 8% negative or neutral). Surprisingly, interior spruce had fewer positive release trees (55%) than lodgepole pine (27% and 18% of spruce were negative or neutral). In general, subalpine fir and spruce performed best in stands with high pine mortality. Spruce overstory trees showed diameter growth releases immediately after the outbreak at most sites (e.g., sites 1, 3, 15 and 17) whereas subalpine fir exhibited a slower and less clear response (sites 1, 8 and 14). Interestingly, in some cases the strong positive growth response by spruce was associated with stands with poor pine release (e.g., sites 1 and 15). Douglas-fir and western larch had the poorest release among the overstory trees (at 41%, 18% and 41%

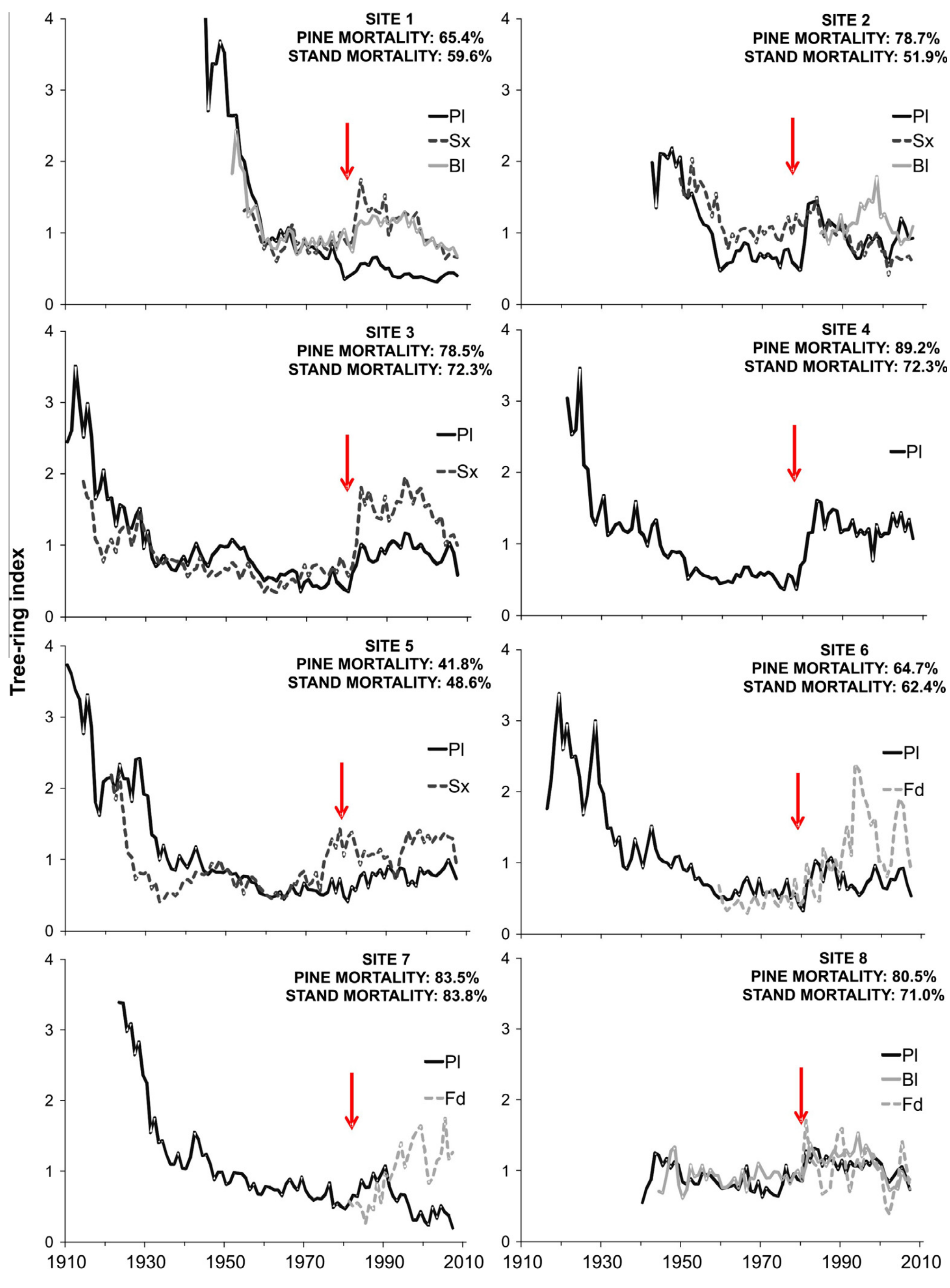

Fig. 1. Ring-width mean chronologies for secondary structure currently >7.5 cm DBH by species for sites 1–22. Ring-width series were standarized using a horizontal line passing through the mean of each series. Vertical arrows indicate year of attack. Species codes are in Table 2.

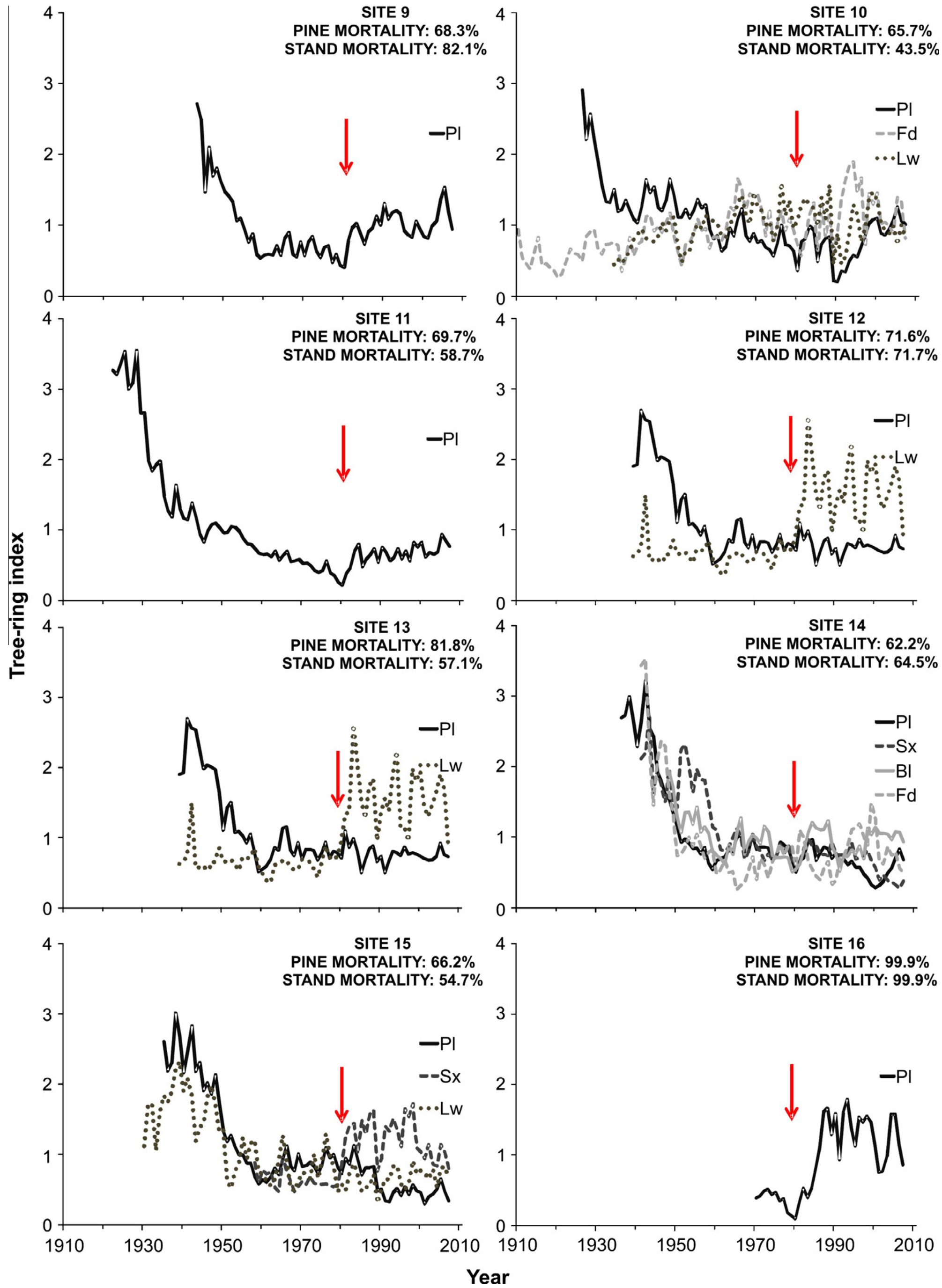

Fig. 1 (*continued*)

and 48%, 40% and 12% positive, negative or neutral growth, respectively).

Initial tree diameter had no clear influence on the growth response of the surviving secondary structure, although, depending on species, the highest positive growth changes took place when trees were smaller than 20 cm diameter (Fig. 2). The correlation values between diameter at the year of attack and percent-growth change were low and not significant and negatively correlated for Douglas-fir, spruce and larch (*r* values were lodgepole pine: 0.06; subalpine fir: 0.29; Douglas-fir:-0.08; interior spruce: −0.12; western larch: −0.28). No strong pattern of release (positive values) or suppression (negative values) related to a particular tree size was found (Fig. 2). Growth suppression responses after MPB attack were not affected by tree species or size (Fig. 2).

3.3. Understory establishment and growth

Understory tree species composition prior to the beetle attack varied considerably in pine-leading Flathead Valley stands (Fig. 3, left-hand bars). Nearly 30 years later, the stocking and composition of the understories changed dramatically in all but a few of the stands (Fig. 3, right-hand bars). Before the epidemic hit the Flathead the understories of the stands averaged 781 trees ha^{-1}; by 2007 the understory density averaged 3038 trees ha^{-1}. The composition of the post-attack regeneration varied greatly among the Flathead stands (Fig. 3, Table 3). For example, understory regeneration in about 22% of stands was dominated by a single species, whereas two to five species were commonly present at the rest of the sites. Subalpine fir and interior spruce dominated, but all

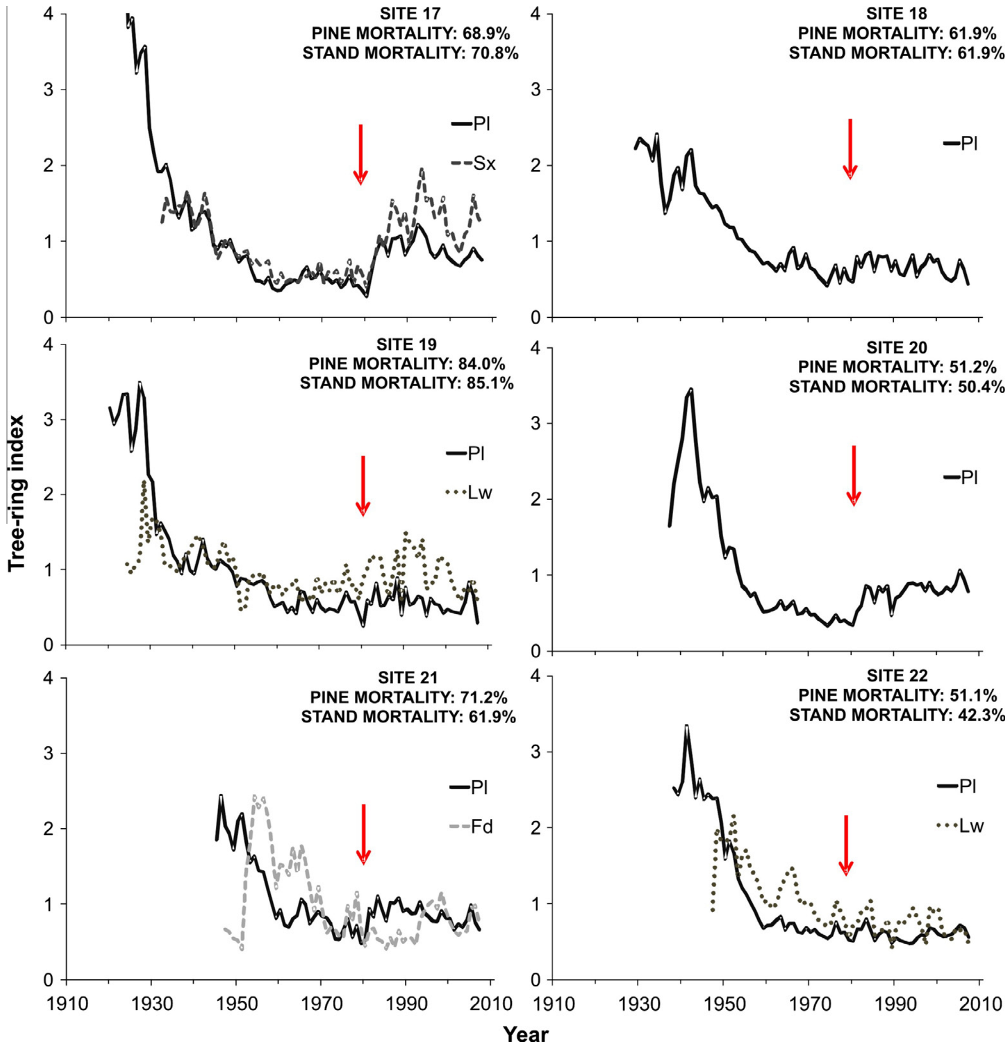

Fig. 1 (*continued*)

species were able to establish and survive under the MPB-damaged canopies (Figs. 3 and 4). New tree regeneration was slow in the first few years after MPB attack (255–524 trees ha^{-1}), however, there was a strong pulse of recruitment 10–20 years post disturbance (868–1013 trees ha^{-1}) which then slowed considerably at almost all sites around the year 2000, or about 20–22 years post-MPB attack (Fig. 4). Due to continuous recruitment over time, 85% of the new regeneration remains shorter than 1.3 m tall almost 30 years post-beetle attack. The tallest trees were 10–16 m tall and accounted for less than 1% of all trees.

Stand composition post-MPB attack was considerably more diverse than prior to the attack (Table 3, Fig. 4). On a few sites, lodgepole pine has maintained dominance by regenerating in the understory but on most sites, a shift in species composition has occurred with the shade tolerant subalpine fir and interior spruce representing more than 50% of the current understory trees.

Understory tree species density was low in the studied stands prior to MPB attack. All tree species, however, with the exception of western larch (Table 2), were present in sufficient quantities to allow us to quantify species-specific post-beetle understory growth response (Fig. 5). Understory subalpine fir trees had the best release (90% positive, 8% negative and 2% neutral) followed by interior spruce (81%, 13% and 6%). Understory Douglas-fir, unlike their overstory counterparts, exibited good release (75% positive, 22% negative and 3% neutral). Pine understory trees were next at 66% positive, 29% negative and 5% neutral. Western larch saplings and seedlings, like overstory larch, had exibited poor growth responses (33% positive and 67% negative). Excluding larch, seedlings and saplings of all species exhibited significant growth releases in the 10 years following the MPB outbreak (Fig. 5).

Saplings, in general, had the best growth responses (300–400%) compared to seedlings (100–300%), particularly for Douglas-fir (Fig. 5). In general, growth suppression in seedlings and saplings were most common in the light demanding species (lodgepole pine, Douglas-fir and western larch), presumably when found in local neighbourhoods with high overstory survival.

4. Discussion

4.1. Self-organization of Flathead Valley stands

The forests in the Flathead Valley regenerated as even-aged lodgepole pine or pine-dominated mixed stands following stand replacing fires in the early 1900s (Barrett et al., 1991). Lodgepole pine trees dominated the overstory and larger diameter classes of these cohorts along with some scattered Douglas-fir and western larch trees. More shade tolerant species such as interior spruce and subalpine fir, if present, occupied smaller diameter classes and sub-canopy positions as a result of differences in the initial

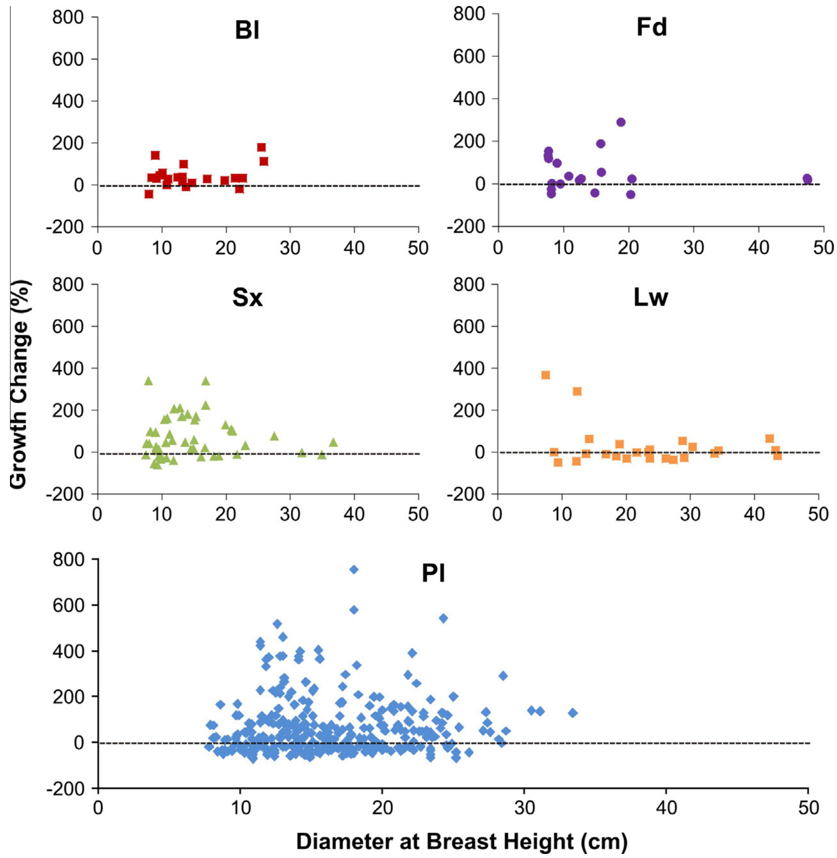

Fig. 2. Growth change percent for secondary structure currently >7.5 cm DBH by species and diameter at breast height at time of the outbreak. Species codes are in Table 2.

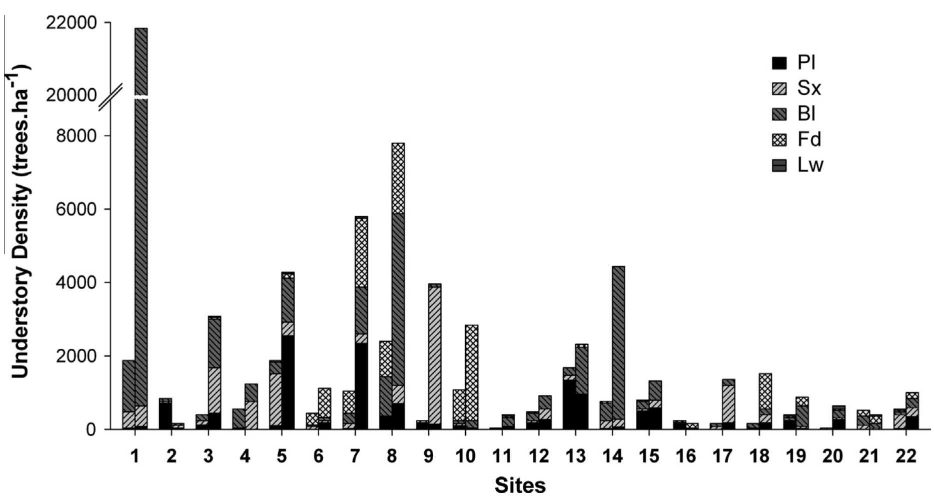

Fig. 3. Understory density by species for sites 1–22. Left and right-hand bars represent cumulative understory establishment (trees 7.5 cm DBH and smaller) prior and post-attack (fall 2007), respectively. Attack dates are in Table 1. Species codes are in Table 2.

growth rates of the species (Johnson and Fryer, 1989) leading to stratified pine-dominated stands. A striking characteristic of these stands at the time of our survey, and presumably prior to the 1979–80 peak of the mountain pine beetle (MPB) epidemic, was their exceptional good health (very low incidence of pine stem rusts, galls or mistletoe) and their relatively young age. Pine stem rusts, galls and mistletoe are a major forest health problem in pine forests throughout British Columbia (BC) (Woods et al., 2010). Another unique feature of the area was the lack of dead, dying or suppressed trees in the sample stands at the time of assessment suggesting that stems surviving the beetle epidemic remained healthy some 30 years later. The Flathead stands appeared resilient and capable of self-organization after the beetle epidemic. This capacity to recover is similar to findings after other earlier MPB epidemics in BC (Heath and Alfaro, 1990; Axelson et al., 2009) and in the US Rocky Mountains (Romme et al., 1986; Pelz and Smith, 2012).

The details of the recovery of forests in the Flathead Valley following the MPB epidemic depended on memory (stand history pre-beetle), the percent of the stand killed by MPB, the species-

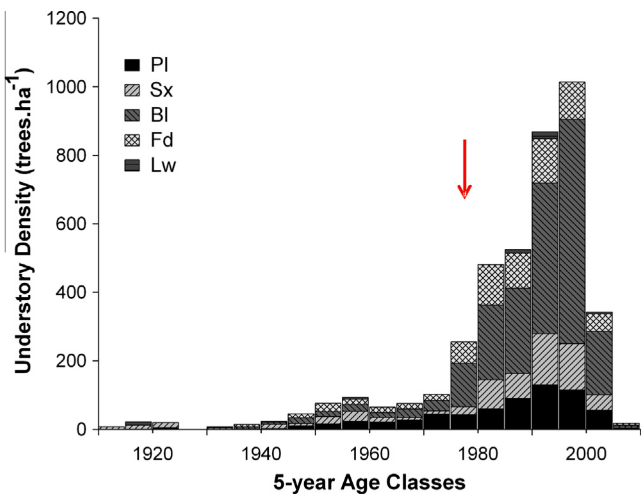

Fig. 4. Understory density (trees 7.5 cm DBH and smaller) by species in 5-year age classes averaged across the 22 study sites. The vertical arrow indicates the year at which the outbreak peaked in the study area. Species codes are in Table 2.

specific release dynamics of surviving individual overstory and understory trees and the subsequent ingress and growth of post-beetle natural regeneration. These factors, often in unique combinations, lead to near or full recovery of stand basal area 25–30 years after the attack in nearly 30% of the stands in the Flathead Valley. These rapid recovery rates are similar to rates reported for other forests after insect canopy mortality events (Baskerville, 1975; Romme et al., 1986; Thompson et al., 2007; Pelz and Smith, 2012). These stands were generally those with the lowest proportions of total stand basal area killed and with the highest component of non-pine species. These secondary species (subalpine fir and interior spruce primarily) that responded well were an important part of the stocking after the attack in stands with near complete recovery.

4.2. Overstory tree responses

Interestingly, individual tree growth responses, especially for lodgepole pine, were often poorest in stands with the best overall recovery of stand basal area. In stands with relatively low total stand basal area mortality (<70%) individual canopy pine trees had a low proportion of growth releases and a relatively high proportion of growth suppressions. These results for pine are similar to those of Axelson et al. (2009) where, on average, no more than thirty percent of the lodgepole pine trees sustained growth releases after beetle attacks. In other Flathead stands, where the total stand basal area mortality was near 70% or higher, overstory lodgepole pine trees exhibited significant tree level growth response after the attack that contributed to stand-level recovery. In most cases the surviving pine trees exhibited radial growth releases higher than 50%. Moreover, other species accompanying pine in these stands also increased their radial growth rates, likely benefited by the decreasing competition from the overall high MPB mortality rate. Yet, in the high mortality stands, these positive individual responses have not yet lead to a recovery of the total stand basal area.

Even though there remains much skepticism about the release capacity of mature lodgepole pine, overall, individual canopy pine trees released well across all sample stands in the Flathead Valley, similar to that reported for mature pine after partial cutting (Whitehead et al., 2007). More than 60% of the surviving overstory pine trees exhibited a positive radial growth response and pines with diameter growth increases greater than 100% were found in almost all sampled stands. These results parallel those of Smith et al. (2012) who found that over half of surviving overstory pine trees had accelerated growth rates following a MPB outbreak in Colorado. Other studies also reported increased growth for surviving lodgepole pine after MPB (Romme et al., 1986; Heath and Alfaro, 1990). Ultimately, the response of the surviving overstory pine trees was strongly influenced by the degree of mortality occurring at each site and how subsequent neighbourhood dynamics (Gratzer et al., 2004), or the specific composition and size of surrounding trees competitively interact with each surviving pine tree. Although difficult to quantify, small differences in stand- and neighbourhood-level mortality may be important for release success of surviving overstory pine trees.

Overstory Douglas-fir and western larch, also light-demanding species, exhibited erratic responses in radial growth after the beetle attack. The superior performance of lodgepole pine could be due to it being better adapted to the harsh climate and poor glaciofluvial soils found in the dry cool subzone (MSdk) of the Montane Spruce zone that dominates the Flathead Valley (Meidinger and Pojar, 1991; Lloyd et al., 2006). In contrast, the poorer growth response of Douglas-fir and western larch that we observed may be due to climatic stress. Other studies have reported good growth responses of Douglas-fir after canopy mortality events (Cole and Amman, 1980; Heath and Alfaro, 1990; Hawkes et al., 2004).

Overstory subalpine fir (70%) and to a lesser extent interior spruce (55%) also released well after the MPB-attack as reported in other studies (Cole and Amman, 1980; Hawkes et al., 2004; Smith et al., 2012). Suprisingly though, growth responses of subalpine fir and spruce were of lower magnitude than those of lodgepole pine yet again pointing to the overall good health of the pine at the time of the MPB epidemic. The relatively poor performance of spruce may be due to the effect of soil resources on competitive interactions between pine and spruce. In northern BC forests, lodgepole pine neighbours had a much stronger net negative effect on interior spruce radial growth on lower soil fertility sites (Coates et al., 2013) such as found throughout the Flathead Valley.

Other studies have found that the size of a tree at time of release affects its potential to release (Hawkes et al., 2004; Smith et al., 2012) but our results were inconsistent. We did not find a pattern between growth responses and tree size for subalpine fir, Douglas-fir or western larch. Interior spruce growth release was more variable at smaller diameters. Lodgepole pine exhibited little variation in the response at small and large diameters but higher variability at medium sizes. We conclude that individual tree growth response was more closely related to the degree of overstory mortality, species and condition, as well as interspecific tree-to-tree competition, than to tree size.

4.3. Understory dynamics

It is important to understand the dynamics and growth potential of suppressed understory seedlings and saplings as they may become an important component of post-MPB attack stands. We found that understory establishment prior to the beetle attack varied considerably across the sampled sites. Only a few sites had well developed understories of subalpine fir and interior spruce with lesser densities of Douglas-fir or lodgepole pine. These pre-beetle understory trees were mostly suppressed individuals from the same cohort as the overstory.

With few exceptions, all stands with advance regeneration exhibited growth releases of the understory trees after the outbreak and all species but western larch experienced a positive growth response. Responses levels depended on the number of surviving trees after the attack, the proportion of trees killed and

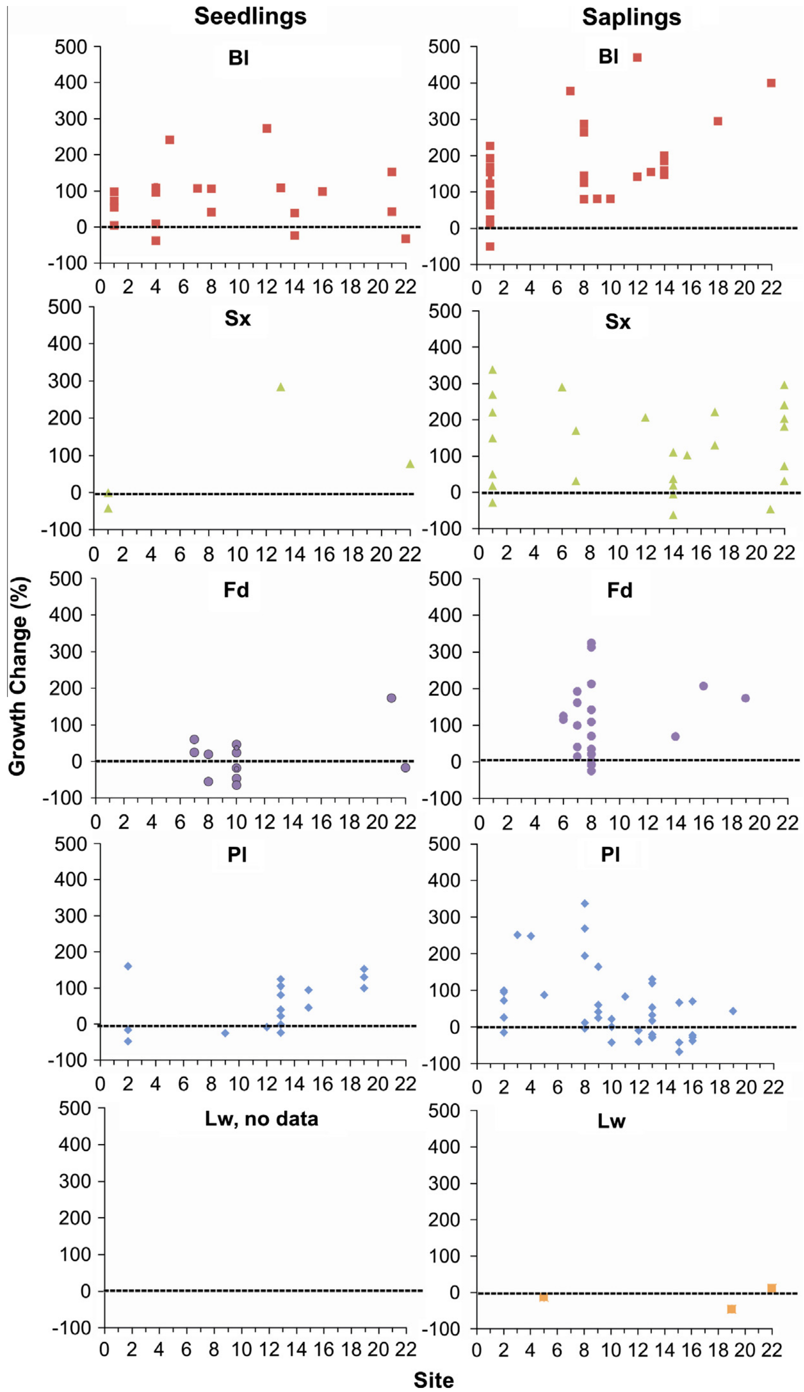

Fig. 5. Growth change percent (radial growth) responses of seedlings (<1.3 m tall trees) and saplings (1.3 m tall to 7.5 cm DBH) by species for the 22 study sites. Species codes are in Table 2.

the species composition. Smith et al. (2012) reported increasing radial growth rates for sub-canopy lodgepole pine, Engelmann spruce and subalpine fir following the 1980s beetle outbreak in northwestern Colorado. Similarly, overstory mortality after a mountain pine beetle outbreak permitted accelerated growth of small Douglas-fir and spruce pole-sized trees and seedlings in stands in southern British Columbia (Hawkes et al., 2004).

We found tree species that were a minor stand component before the MPB attack had increased their relative dominance and became important elements of stand composition almost 30 years after the attack as a result of enhanced growth. Hawkes et al. (2004) also found a gradual shift after MPB attack towards shade-tolerant species in the co-dominant and dominant tree layers.

Understory recruitment post-MPB was successful in all sampled stands demonstrating the importance of this component to the overall recovery of forests after MPB attack. While slow in the first decade following the MPB attack, as reported in other studies (Astrup et al., 2008; McIntosh and Macdonald, 2013), strong pulses of recruitment were evident 10–20 years post disturbance. The number and composition of the post-attack regeneration varied greatly among sites probably reflecting local availability of seed sources and substrate availability (LePage et al., 2000). Overall, shade tolerant subalpine fir and interior spruce dominated understory recruitment as previously reported (Astrup et al., 2008; Axelson et al., 2009; Diskin et al., 2011; Hawkins et al., 2012; Pelz and Smith, 2012). Yet, species with low-to-moderate shade tolerance, such as lodgepole pine and Douglas-fir, were also able to recruit (see also, Hawkes et al., 2004; Nigh et al., 2008; Axelson et al., 2009; Collins et al., 2010). Two to five regenerating species were common in most sample stands – only 22% of the stands had a single regenerating species. As a result the present stand composition in the Flathead Valley is considerably more diverse than prior to the attack.

5. Conclusions

Our study and the existing literature report broadly similar results for release of surviving trees after a natural disturbance event such as the MPB that rapidly kills canopy trees. Even so, it must be recognized that British Columbia is exceptionally varied climatically and the MPB epidemic has affected a huge range of environments. The types of growth responses reported in this study cannot necessarily be expected to be consistent with all other studies or be applicable to all site and stand conditions. For example, on nutrient-rich soils in a milder climate we would expect higher growth rates of Douglas-fir, interior spruce and subalpine fir relative to lodgepole pine. Alternatively, if the lodgepole stand was over mature at the time of beetle attack we would expect poorer growth responses for surviving pine trees.

Overall, the occurrence of MPB attacks in pine dominated stands resulted in more structurally and compositionally diverse stands leading to multiple successional pathways different from those of even-age pine dominated cohorts (Axelson et al., 2009; Diskin et al., 2011; Hawkins et al., 2012). Stand composition and structure have changed dramatically compared to before the attack. It is expected that the abundant seedlings and saplings now present in the understory will rapidly start merging with sub-canopy trees as most understory trees presented high levels of radial growth release after the attack. Such uneven-aged stands with variable but generally low densities of mature trees are considered to be less susceptible to future mountain pine beetle outbreaks (Axelson et al., 2010) and provide opportunities for mitigating the effects of salvage logging on ecological processes (Lindenmayer et al., 2008) and critical timber supply shortages forecast in the mid-term for many BC management units impacted by the MPB (B.C. Ministry of Forests and Range, 2007).The recovery and future growth of unsalvaged natural stands, therefore, represents a much more complicated issue than projection of planted units after clearcut salvage, however, the variability in stand structure provides a greater opportunity for a broader range of silvicultural systems. We need, however, a better understanding of the specific characteristics of individual trees to predict the response and the degree of the response, including suppressed time, diameter, and percent live crown. History and tree condition would certainly influence the growth response of the trees as their surrounding environment changes after beetle-caused mortality.

Forests are dynamic social-ecological systems with interactions and feedbacks between climate, disturbance and management (Seidl et al., 2012). Promoting resilient and adaptable forests will require taking a systems view of forest management in contrast to more traditional approaches (Messier et al., 2013). In an increasingly uncertain world, forest management needs to shift to an emphasis on adaptability and self-organization. Our retrospective study of an older MPB epidemic has provided concrete evidence of the multiple factors involved in self-organization and recovery of forest productivity and structure that can be used to broaden management options for western North American forests currently impacted by a massive MPB epidemic ongoing for the past decade.

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