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Complete List of Authors:	McEwen, Jesse; University of Northern British Columbia, NRES Graduate Program Fredeen, Art; University of Northern British Columbia, ESM Pypker, Tom; Thompson Rivers University, Faculty of Natural Resource Science Foord, Vanessa; British Columbia Ministry of Forests Lands and Natural Resource Operations Black, T. Andrew; University of British Columbia Jassal, Rachhpal; The University of British Columbia, Faculty of Land and Food systems Nesic, Zoran; The University of British Columbia, Faculty of Land and Food systems
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Carbon storage recovery in surviving lodgepole pine (*Pinus contorta* var. *latifolia)* 11 years after mountain pine beetle attack in northern British Columbia, Canada

Authors: Jesse McEwen[1], Arthur L. Fredeen[2], Thomas G. Pypker[3], Vanessa N. Foord[4], T. Andrew Black[5], Rachhpal S. Jassal[5], Zoran Nesic[5]

[1] NRES Graduate Program, University of Northern British Columbia, 3333 University Way, Prince George, BC, V2N 4Z9: mcewen@unbc.ca

[2] Ecosystem Science and Management, University of Northern British Columbia, 3333 University Way, Prince George, BC, V2N 4Z9, Canada:

[3] Faculty of Natural Resource Science, Thompson Rivers University, 805 TRU Way, Kamloops, BC, V2C 0C8, Canada

[4] British Columbia Ministry of Forests, Lands ad Natural Resource Operations and Rural Development, Prince George, BC, V2L 1R5, Canada

[5]Faculty of Land and Food Systems, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada

Corresponding Author: Art Fredeen
Email: Art.Fredeen@unbc.ca
Telephone: 250-960-5847

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Abstract

We studied the recovery of tree and stand-level C-storage in a lodgepole pine (*Pinus contorta* var. *latifolia*) forest in northern British Columbia that experienced substantial (~83%) mortality in 2006-07 (total loss by 2013 = 86%) during a severe mountain pine beetle (MPB) (*Dendroctonus ponderosae*) infestation. Earlier work suggested that this forest recovered positive annual C-storage 3 years after attack based on eddy-covariance measurements. We sought to confirm these results by examining C-storage in surviving pine trees using tree core analysis. Average growth release of surviving lodgepole pine trees was 392% (range -53% to 2326%) compared to mean decadal growth prior to MPB attack. Nearly 97% of trees underwent a growth release, considerably higher than the 15-75% reported for lodgepole pine in previous studies. Mean annual stem C-storage of the surviving trees in this study was highly correlated (r=0.88) with 10 years of annual net ecosystem productivity estimates made using the eddy covariance technique, indicating that surviving lodgepole pine remain an important part of C-recovery after MPB attack. Mean annual stem C-storage was also highly correlated (r=0.92) with the cumulative percent of downed stems ha^{-1} at the site, suggesting that increased availability of resources is likely assisting the growth release.

Key words: forest disturbance, growth release, dendrochronology, lodgepole pine, carbon storage, mountain pine beetle

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Introduction

The mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) is a bark beetle native to western North America that ranges from Mexico to central British Columbia (BC), Canada. Lodgepole pine (*Pinus contorta* var. *latifolia* Douglas) is the primary host (Safranyik and Carroll 2006). Historically, MPB populations have been cyclical, switching between low endemic populations and high epidemic outbreak levels every 12-53 years (Alfaro et al. 2003; Axelson et al. 2009, 2010). Mountain pine beetles primarily target large mature pine trees, generally leaving sub-canopy trees alive (Safranyik and Carroll 2006). Although MPB outbreaks are a natural disturbance in BC, factors such as climate change (i.e. warmer winters) and forest management practices (e.g. fire suppression and pine monocultures) are thought to have contributed to the severity of the most recent outbreak (Campbell et al. 2007, Raffa et al. 2008), with ~731 million m^3 (54% by volume) of mature pine in BC killed (FLNRORD 2016).

Forest-scale carbon balance as determined by eddy-covariance (EC) approaches in the BC central interior suggests that MPB-attacked stands can recover their C sink status within 3-5 years of first attack (Brown et al. 2012). Component-level gas-exchange measurements of photosynthesis in surviving plants (especially sub-canopy conifer and deciduous tree species) scaled up to the stand-level (Bowler et al. 2012) aligned well with the EC results of Brown et al. (2012), but direct assessment of C-storage in surviving trees was not assessed in either case. There is good evidence that natural thinning events, such as MPB-outbreaks, can lead to reduced competition for resources allowing

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surviving trees to increase their radial and vertical growth rates (Veblen et al. 1991; Dhar and Hawkins 2011; Coyle et al. 2016). Hawkins et al. (2012) and Amoroso et al. (2013) found that pine-dominated stands were able to recover volume rapidly after MPB-outbreaks as a result of significant growth release in surviving trees. Together, these findings strongly support the premise that compensatory growth of surviving trees is responsible for the rapid recovery of stand-level net ecosystem productivity (NEP) after MPB attack, providing significant stand recovery of tree volume (Alfaro et al. 2003; Hawkins et al. 2012; Pelz and Smith 2012; Amoroso et al. 2013).

Dendrochronology has been used to determine the spatial extent of historic MPB outbreaks to better understand the unprecedented nature of the recent outbreak (Jarvis and Kulakowski 2015). Through tree core analysis, radial growth before and after large disturbances such as MPB-outbreaks can be used to quantify the timing of the disturbance and the growth response of the trees (Alfaro et al. 2003; Amoroso et al. 2013) Growth release following MPB outbreaks has been observed to range from 15-75% in surviving overstory trees and up to 90% for understory trees (Axelson et al. 2009, 2010; Amoroso et al. 2013). Individual surviving trees have been observed to increase their growth by up to ~750% of the pre-outbreak radial growth rate (Amoroso et al. 2013), aiding in the rapid recovery of C-storage, tree stem volume and ecological function of a stand (Hawkins et al. 2012; Alfaro et al. 2015).

While past research suggests surviving trees can release following an MPB outbreak (Alfaro et al. 2003; Axelson et al. 2009, 2010; Amoroso et al.

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2013) we lack a clear connection of how trees of varying ages, heights and diameters will respond. Early work and conventional wisdom on growth release in lodgepole pine strongly suggests that surviving trees would weakly release, if at all, with increasing time of suppression and on poor sites (Lotan and Critchfield 1990), conditions that existed at our study site. We sought to examine this issue in more detail in MPB-impacted pine stands, that is, their potential to generate surviving tree timber production and C storage following such events.

Earlier studies of ours based on physiological gas-exchange data suggested that surviving pine contributed 40-50% to growing season NEP (Bowler et al. 2012; Brown et al. 2012) in the years immediately following the disturbance. In this study, we combine stand level carbon flux measurements from an EC tower with tree based growth measurements. Specifically, we use dendrochronology approaches to corroborate our earlier findings, and determine how long and by how much surviving trees are increasing their radial growth relative to environmental conditions. We hypothesized that increased C-storage in surviving pine trees following MPB-outbreak would contribute significantly to the NEP of these MPB-attacked stands.

Methods and Materials

Site Description and Experimental Design

The study area is located in central BC, Canada, ~30km southeast of Mackenzie, BC (55°06'42.6''N, 122°50'28.5"W) (Fig.1). The study site has been characterized previously in a number of publications, e.g., Brown et al. (2010,

2012) and Bowler et al. (2012). The site receives little growing season precipitation (230mm between May and September) and the soils are coarse textured with 34% coarse fragments by volume (Brown et al. 2012), allowing for rapid drainage and low water holding capacity. At the time of peak MPB attack in 2006 and 2007, the stand was dominated by ~80 year old lodgepole pine trees, with a very sparse population of subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall) and white spruce (*Picea glauca* (Moench) Voss). Overall live tree densities of trees >6.5cm DBH is 605 stems ha^{-1} (Table 1). *Vaccinium* spp., mosses and *Cladonia* spp. dominate the understory (Brown et al. 2010). Between 2006 and 2007 96.5% of the trees attacked by MPB died, with the remaining 3.5% dying by 2013 (Seip 2019 Personal Communication).

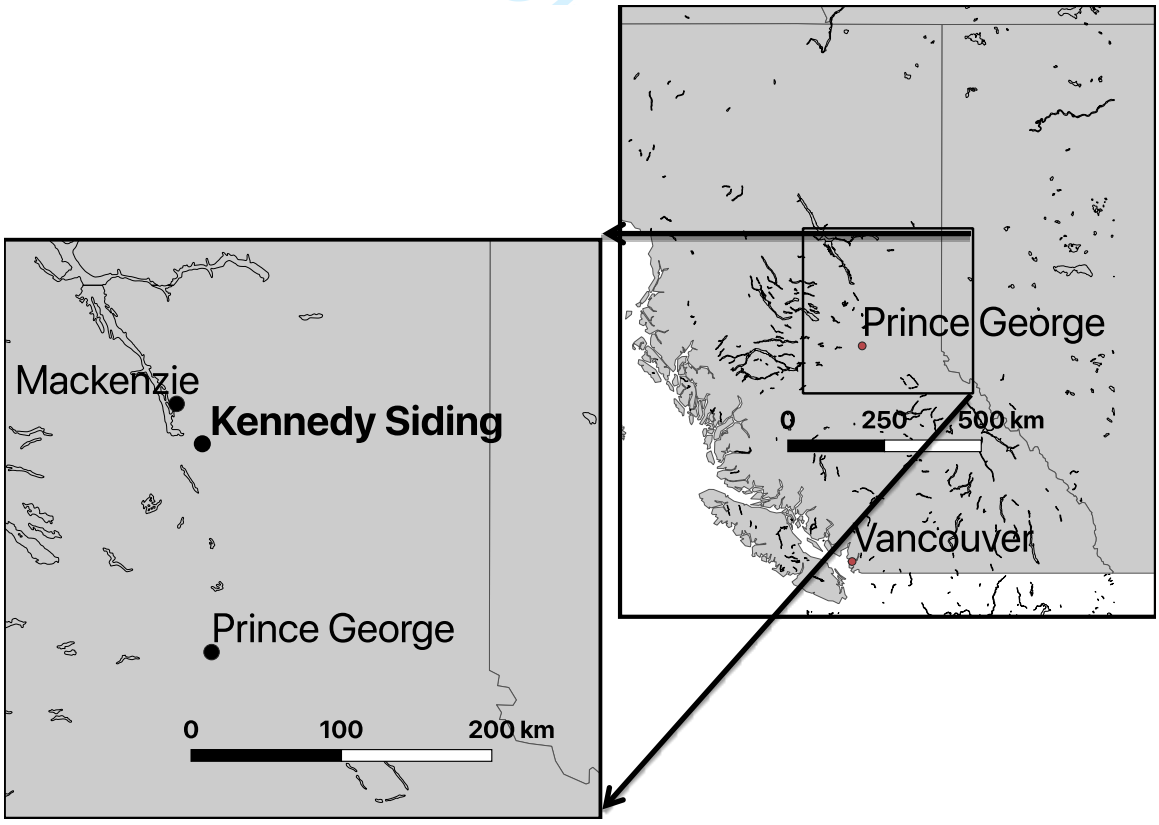


Figure 1. Map of central British Columbia (BC) region and Kennedy Siding study site relative to Prince George, BC, Canada. Contains information licensed under the Open Government Licence – Canada. Created using QGIS software.

This site has had an EC flux tower measuring CO_2 and H_2O vapour fluxes since July of 2006 (Brown et al. 2010), ~ 1 month prior to MPB attack. In 2006, plots were established to measure the annual number of downed canopy trees of MPB-attacked lodgepole pine within the EC tower footprint (Seip and Jones 2010). Together, these and other associated research conducted at the site provided a detailed picture of the changing C-balance of the site. Our study aimed to leverage and validate these data by examining the C storage in surviving trees, mostly within the perimeters of previously established MPB-killed tree fall-down plots where the history of canopy openness data was monitored. This approach has been successfully applied to a mixed conifer forest in central Maine, USA (Teets et al. 2018).

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Tree selection

Eight research plots ranging from 0.25-0.75ha were installed across the study area. Seven of the plots overlapped the 'fall-down rate' plots of Seip and Jones (2010). Briefly, their plots contained MPB-attacked trees every 20 m along random 100 m transects that have been monitored annually since 2007. In our study, we selected and flagged ten pairs of healthy surviving lodgepole pine trees (>6.5 cm in diameter at breast height (DBH) and without any major defects and intact leaders) randomly across each plot, with each pair consisting of a larger (>12 cm DBH) and a smaller (<12 cm DBH) diameter tree within 5 m of one another. This design resulted in a total of 160 experimental trees across ~450 ha of the study area within the EC flux tower operational footprint.

157 **Radial growth**

158 The radial growth of all experimental trees was monitored across the
159 growing seasons of 2017 and 2018 using permanent plastic dendrometer bands
160 (Model D1, UMS GmbH, München) installed on May 29th and 30th, 2017 at the
161 1.3-m height from the ground level (DBH) (Pélissier and Pascal 2000). Initial
162 diameter measurements were made in May 2017 and final measurements in fall
163 of 2018 were used in combination with annual radial growth increments obtained
164 from dendrochronology for tree volume increment calculations (see below).

165 **Height growth**

166 Height measurements were taken at the same intervals as dendrometer
167 measurements in 2017 and 2018 using a laser hypsometer (Forestry Pro, Nikon,
168 Tokyo) with an accuracy of +/- 20 cm. To reduce measurement error, four
169 measurements were taken for each tree at each sampling period and averaged.
170 Where possible, tree-height measurements were made at ~1 tree length from the
171 experimental tree base (Rodriguez et al. 2014).

172 **Dendrochronology**

173 To obtain a history of radial growth, all 160 sample trees were cored in
174 May of 2018 with 40 x 0.43 cm diameter 3-threaded increment borers (Haglöf,
175 Sweden) perpendicular to the vertical axis of the tree to obtain representative
176 ring widths (Alfaro et al. 2003). To maximize the number of tree rings, tree cores
177 were taken as close to ground level as possible (~30 cm) and were cored
178 through or as close to the pith as possible. To account for uneven radial growth
179 on all sides of the tree, two cores from each sample tree were taken at ~ 90°

from one another on the widest and narrowest diameter axes. Immediately following extraction, cores were placed in plastic straws; both ends of the straw were taped shut, labeled, and then stored in Ziploc® bags. All cores were placed in a freezer (-18^{o}C) until they were processed.

Tree cores were processed following techniques of Stokes and Smiley (1968). In summary, tree cores were mounted onto blocks of wood using wood glue with the tracheid openings facing upwards. The cores were sanded gradually beginning with 120 grit sandpaper followed by finer grits until all cores had been sanded with 600-grit paper to ensure a smooth flat surface that would allow all rings to be identified clearly. Once all decadal rings were manually marked on cores with a pen, they were scanned into WinDENDRO (Density 2012, Regent Instruments Inc, Saint-Foy). All cores from a plot were correlated to determine missing rings using the program COFECHA (Tree-Ring Lab, Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York). COFECHA identified the best cores for accurately cross dating to the remaining cores. Annual ring width of the 2 orthogonal cores were averaged for each tree.

Growth release and tree stem C-storage

The percent growth release method used in our study mimicked past work by Axelson et al. (2009) and Amoroso et al. (2013) who used the percent change in ring widths to determine release. Growth release of surviving lodgepole pine trees was determined by first computing the annual increases in tree stem volume (ATSV) using Smalian's formula [1] (Plank and Cahill 1984). It was selected over other formulas (e.g. Huber's) because we were only able to

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measure the stem diameters at the bottom of live trees. Smalian's equation is also the standard equation used in BC (Ministry of Forests Lands and Natural Resource Operations 2011).

[1] $ATSV = [(\pi r_2^2/2)H_2 - (\pi r_1^2/2)H_1]/(t_2 - t_1)$

ATSV = Annual tree stem volume increase (m^3 yr)

H_1, H_2= Average height of experimental trees by size class in the initial (H_1) and subsequent (H_2) year of sampling (m)

r_1, r_2 = Average radii of experimental trees by size class in the initial year (r_1) and subsequent year of sampling (r_2) (m)

t_1, t_2 = sampling times (difference is 1 yr)

The tree heights for the previous 20 years were estimated using an average height to diameter ratio for all 2018 trees with reliable heights and diameters, similar to Wonn et al. (2001). Sample tree heights were calculated by multiplying tree diameters by the height to diameter ratio of 77:1 determined for lodgepole pine trees at the site. Pearson's correlations were used to determine any potential relationships between the stem C-storage over the past decade calculated from dendrochronology data and values of both EC NEP and the percentage of MPB-attacked canopy trees that had fallen in each year. If there was a significant correlation, a linear regression was performed to determine the predictive power of each independent variable. Growth release was compared using an average increase in volume from the decade prior to peak attack (1997-

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226 2006) compared with the average volume increase in the decade after peak
227 attack (2007-2016).

228 ***Surviving pine C-storage***

229 Annual tree stem carbon (ATSC) was calculated using a published
230 specific weight (444 kg dry wood m^{-3}: Singh 1984) and C density (0.5032 kg C
231 (kg dry wood)$^{-1}$: Lamlom and Savidge 2003) for lodgepole pine [2].
232 [2] ATSC = 1,000 ATSV M D

233 ATSC = Annual tree stem C increase (g C yr^{-1})

234 ATSV = Annual tree stem volume increase (m^3 yr^{-1})

235 M = Specific weight of lodgepole pine (kg dry wood m^{-3})

236 D = C-density of lodgepole pine (kg C (kg dry wood)$^{-1}$)

237

238 In order to compare annual tree stem C (ATSC) to EC NEP values, we
239 also measured the density of small and large surviving lodgepole pine trees from
240 all eight experimental plots. The tree density for each of the 8 study plots were
241 determined using five circular 10 m radius density plots distributed at 50-m
242 intervals along a linear transect using a random compass bearing. Numbers of
243 large (>12 cm DBH) and small (<12 cm and >6.5 cm DBH) surviving trees were
244 evaluated separately in each subplot. Trees on the edge of the plots were
245 counted if >50% of the stem was inside the plot. Site level average stand
246 densities for large and small trees were calculated using all of the tree density
247 subplots from each of the eight research plots and transformed to a per hectare
248 basis for area-based C-storage as above. To reduce edge effects, plots were a

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minimum of two tree lengths from cut-blocks or roads (Hawkins et al. 2012). Area-based C-storage increase was calculated by multiplying mean ATSC for small and large lodgepole pine trees by the mean plot-level densities of small and large sample trees which ranged from 350 to 1019 and 70 to 261 stems ha^{-1}, respectively [3].

[3] SLSC = ATSC d / 10,000

SLSC = Annual stand level stem carbon increase (g C m^{-2})

ATSC = Annual tree stem C increase (g C yr^{-1})

d = stand density of small or large trees (stems ha^{-1})

Statistical analyses

All data were tested for normality before parametric tests were performed. When data were not normal, the data was transformed to obtain normality, if data was not normal after transformation, non-parametric tests were used. Statistical analyses were conducted using SPSS (V.24 IBM Corporation, Armonk, New York). An alpha of 0.05 was used to determine significance level for all statistical tests. Percent C-storage release data were not normally distributed (Komogorov-Smirnov test for normality) and therefore, the data were cube root transformed. Following the transformation the data was normally distributed (p=0.2), however, two outliers (547b and 521b) were removed following the transformation, because upon further inspection, it was found that among the 5 that did not release, tree 521b was the only tree with a damaged leader, and tree 547b appeared to have an 8-year delay in release (2016 and 2017 ring widths were

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twice that of the previous 10 years) suggesting there was some other factor affecting its growth rate (an immediate response or one year delay was normal across the site).

Growth release can be affected by multiple variables. Therefore, an ANOVA was used to determine if tree age class, size class, or plot location, affected C-storage. Surviving trees fell into one of four age classes: young (>60 yrs, n=14), mature (60-79 yrs, n=21), old (80-99 yrs, n=104), and very old (>100 yrs, n=21) and one of two size classes: small (<12 cm DBH) or large (>12 cm DBH).

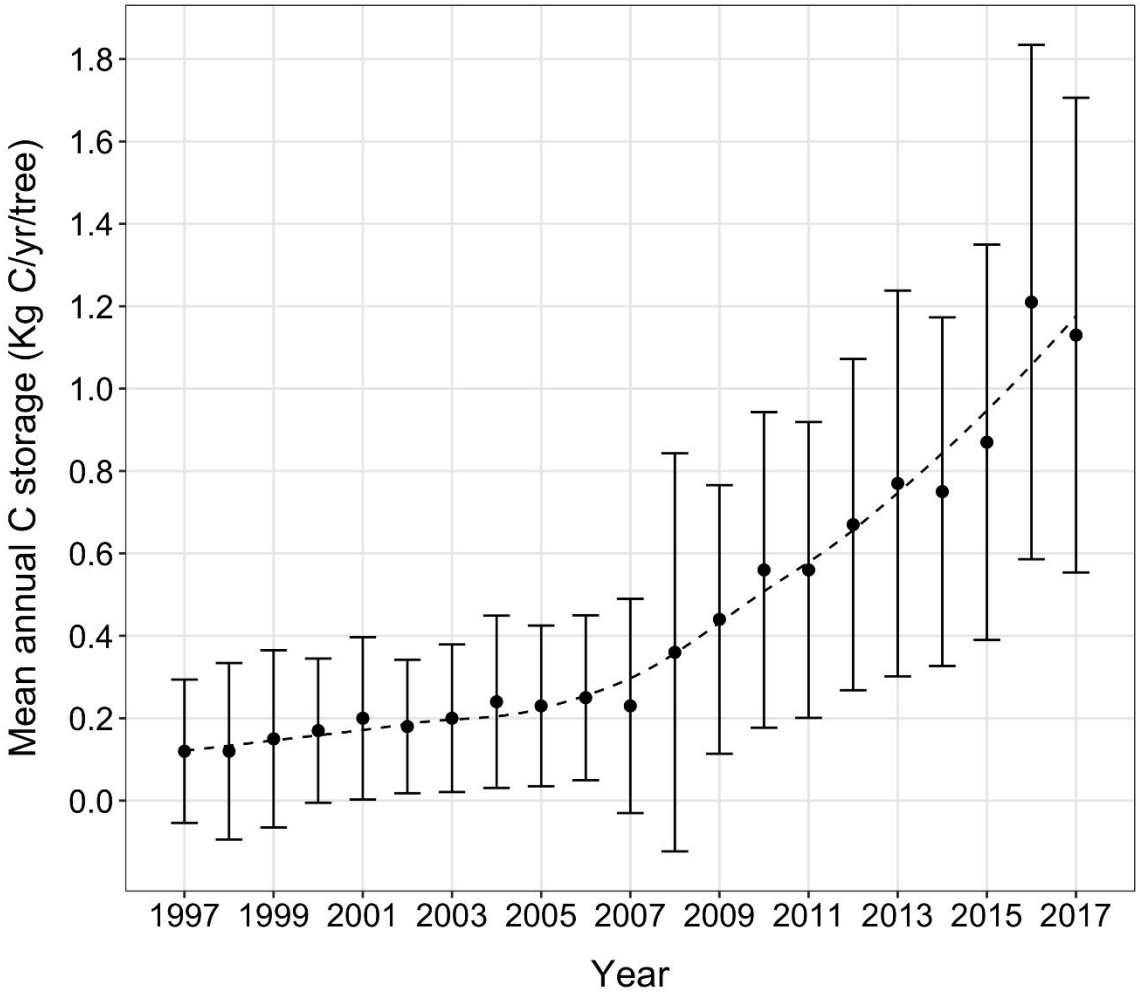
Results

Growth release of surviving trees post-MPB attack

Annual C-storage

Following a 1-2 year lag after MPB-attack which peaked in 2006 and 2007, the mean annual C-storage of surviving trees steadily increased from an average of 0.186 kg C $tree^{-1}$ yr^{-1} between 1997-2006 to a peak of 1.21 kg C $tree^{-1}$ yr^{-1} in 2016 and a slight decline to 1.13 kg C $tree^{-1}$ yr^{-1} in 2017, 10 and 11 years after the peak MPB attack year, respectively (Fig. 2). Mean annual C-storage was significantly and highly elevated post-attack for small, large and combined tree size classes (i.e.10-year average pre-attack versus 10-year average post-peak attack) using paired t-tests ($p<0.001$).

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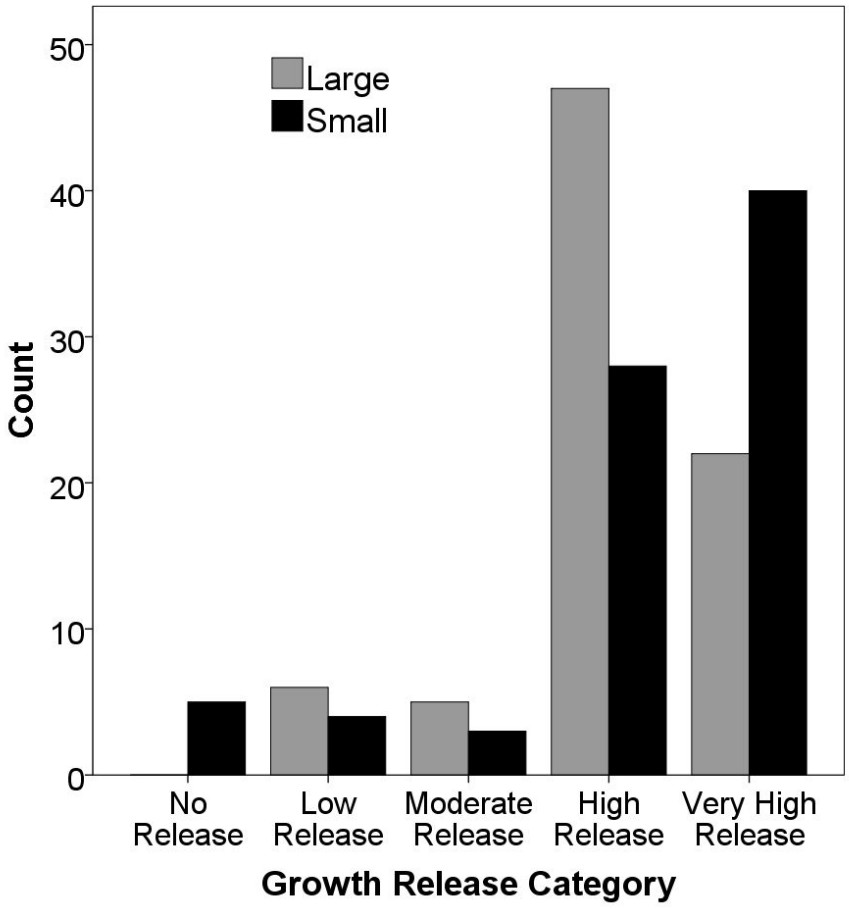


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295 Figure 2 . Mean annual C-storage (kg C tree^{-1} yr^{-1}) of lodgepole pine trees from
296 1997-2017 based on dendrochronology of the lodgepole pine trees surviving
297 MPB peak attack years of 2006 and 2007. Error bars indicate +/- 1 SD.

298 The growth release response of the pine trees were placed into 4
299 categories: low (0-50%), moderate (50-100%), high (100-400%), and very high
300 (>400%; Fig. 3) based on the distributions observed at the site. Smaller trees
301 were more commonly in the very high range of growth release than larger trees
302 (Fig. 3). Most sampled trees (155 out of 160) experienced release, with 62
303 having very high release (small=40, large=22), 75 high release (small=28,

304 large=47), 8 moderate release (small=3, large=5) and 10 with low release
305 (small=4, large=6;Fig. 3). Five trees did not release (small=5; Fig. 3). The overall
306 average change in C-storage for all trees was +392%, with a range of -53% to
307 +2326%.



308

Figure 3 . Lodgepole pine wood volume growth release category (no release (<0%), Low (0-50%), Moderate (Mod., 50-100%), High (100-400%) and very high (>400%) after MPB attack in large (>12cm DBH: grey) and small (<12cm DBH: black) surviving trees.

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310 **Stand Characteristics and radial growth release**

311 Mean age of small (85 ± 17 years) and large (88 ± 15 years) trees were
312 not significantly different. As a result, it was not surprising that there was no
313 significant effect of age-class (young <60, mature 60-79, old 80-99 and very old
314 >99) on the growth release of surviving lodgepole pine (One-way ANOVA;
315 p=0.239). The youngest tree sampled was 43 years of age and the oldest tree
316 sampled was 127 years of age, however, regenerating seedlings resulting from
317 the MPB attack were not sampled because all were well below the diameter cut-
318 off for small trees. While not significant, the young trees had the smallest
319 average growth release (236 %) and the very old trees had the largest average
320 growth release (496 %) (Table 1).
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Table 1. Percent growth release of mean annual wood volume of all plots, age classes and size classes in the 10 years prior to MPB-outbreak versus the 10 years following MPB-outbreak. Blank cells had no trees present in that plot and age class.

	Mean annual wood volume growth release (%)								
	Age Class				**Size Class**		**Overall**	**Stand Density (stems ha^{-1} >6.5cm DBH)**	**Basal Area (m^2 ha^{-1})**
Plot	**Young <60**	**Mature 60-79**	**Old 80-99**	**Very-Old >99**	**Large >12cm**	**Small <12cm**		**Large** Small	
1	462.21	322.15	705.69	-	433.35	838.62	635.98	**127** 485	**1.77** 2.62
2	-	190.17	150.00	117.56	148.84	149.46	149.15	**70** 1019	**0.80** 6.07
3	-	-	540.70	567.17	461.68	659.42	560.55	**191** 280	**3.18** 2.03
4	170.06	157.54	454.58	-	291.10	415.14	353.12	**242** 197	**4.45** 1.41
5	160.52	-	274.25	362.52	234.21	300.38	267.29	**261** 426	**4.29** 3.18
6	213.62	544.43	366.59	-	243.55	433.42	338.48	**248** 414	**4.51** 3.13
7	569.74	402.80	399.45	598.92	337.77	519.73	428.75	**88** 350	**1.24** 2.03
8	-	229.15	478.99	-	317.19	490.89	404.04	**70** 369	**0.97** 2.39
Overall	236.78	299.87	410.72	496.22	308.46	475.88	392.17	**162** 443	**2.47** 2.93

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Growth release was significantly correlated with the size class of the surviving lodgepole pine trees (small <12 cm DBH versus large >12 cm DBH) (Welch's ANOVA; p=0.043). Smaller trees had a significantly greater increase in annual C-storage than the larger trees. Indeed, smaller trees underwent a larger proportional release (476%) than larger trees (308%) when compared to the overall average of 392% growth release across all trees (Table 1). In absolute terms, large trees increased from an average of 0.30 kg C yr^{-1} $tree^{-1}$ between 1997-2006 to 0.93 kg C yr^{-1} $tree^{-1}$ between 2007-2016. By comparison, small trees increased from 0.07 to 0.33 kg C yr^{-1} $tree^{-1}$ over the same periods, respectively. However, there are 443 stems ha^{-1} of small trees and 162 stems ha^{-1} of large trees. Therefore, overall contributions to site level carbon storage was similar between large and small trees.

Location was significantly related to the growth release of surviving lodgepole pine (One-way ANOVA; p<0.001). Post hoc Tukey HSD tests revealed that several significant differences occurred between plots, i.e. plot 2 had significantly less release than plots 1, 3, 7, and 8; plot 5 also had statistically less release than plots 1 and 3. Plot 2 experienced the smallest growth release (149%) whereas plot 1 experienced the greatest growth release (636%; Table 1).

Interactions between age, size and stand location on radial growth

There was no significant interaction between all factors (age class, size class and stand location) on growth release at the site (p=0.479). However, the interaction between size and age class was significant (p=0.007). The

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interactions between site and size class, as well as site and age class, were not significant (p=0.639 and p=0.765, respectively).

Mean annual carbon storage and climate

Pearson correlations were used to determine if mean annual C storage (kg C $tree^{-1}yr^{-1}$) in surviving lodgepole pine trees was related to climate variables in the 10-years before (1997-2006) and 10-years after MPB attack (2007-2016). A strong positive correlation was found between annual ring width and growing season precipitation (mm) (r = 0.639), annual precipitation (mm) (r = 0.601) and annual maximum temperature (°C) (r = 0.578). Annual radial growth was moderately and positively correlated with growing season maximum temperature (r = 0.492). Strong negative correlations were found between annual radial growth and growing season minimum temperature (r = -0.734) and annual minimum temperature (r = -0.645), respectively. Together, these correlations suggest that warm and wet years resulted in better growth than cool years, thus explaining much of the variation in annual ring width pre and post attack. However, a paired t-test found that mean annual precipitation and temperature were not significantly (p=0.917 and p=0.082, respectively) different in the 10 years pre and post peak MPB attack. Thus, interannual climate variables can help explain the interannual variation in ring widths in the decade before and after MPB-attack, but, the mean decadal climatic conditions pre and post outbreak cannot explain the notable growth increases that occurred post-attack.

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Net Ecosystem Productivity

A strong and significant ($p = 0.001$) positive Pearson correlation ($r = 0.877$) was observed between lodgepole pine annual stem C-storage and NEP as measured by the EC flux tower (Meyer et al. 2018). Linear regression analysis of the same variables also resulted in a strong correlation ($R^2 = 0.77$, $p = 0.001$; Fig. 4).

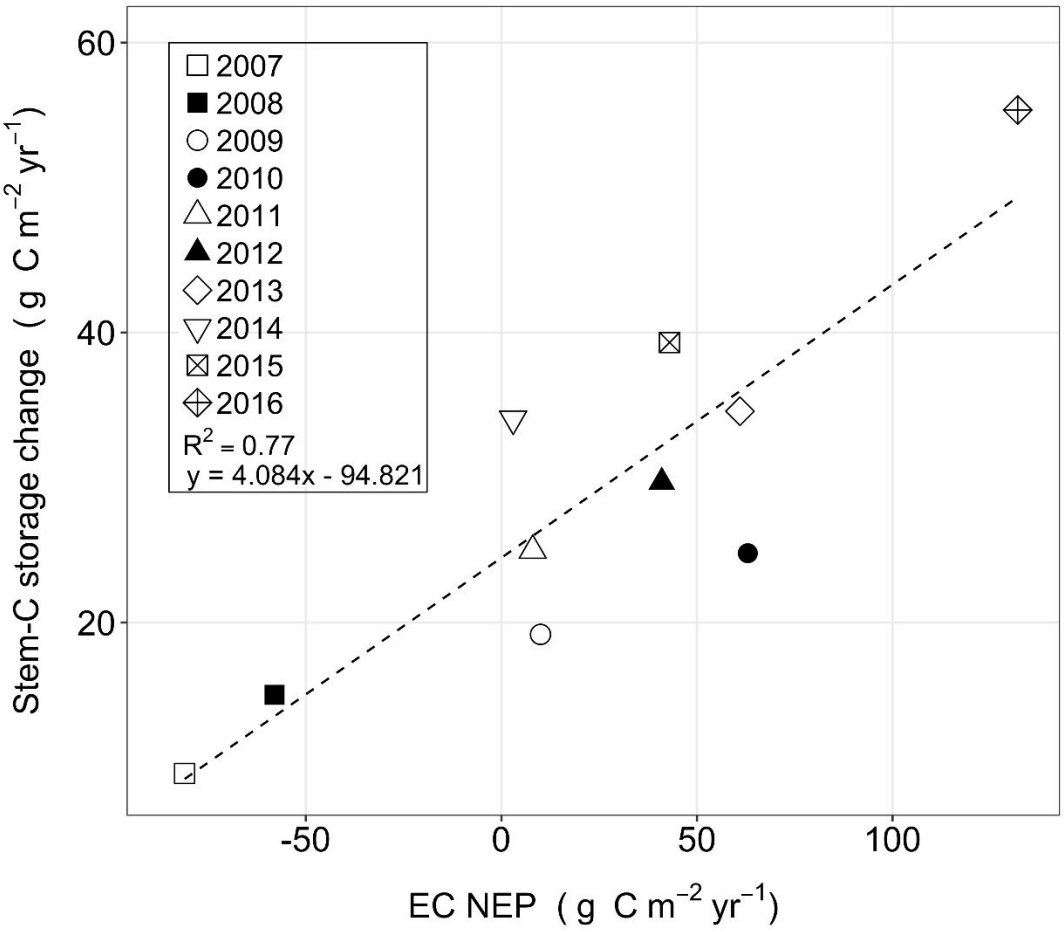
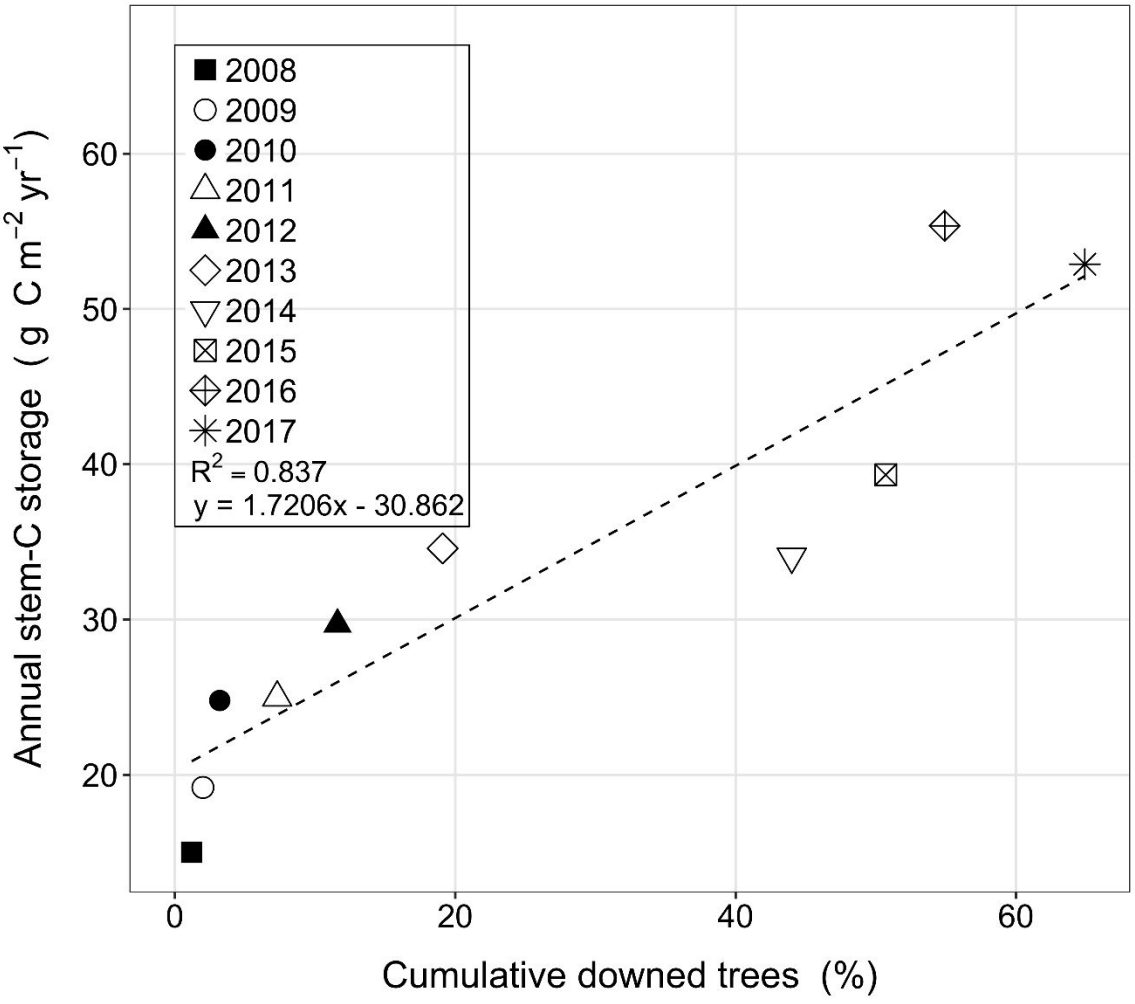


Figure 4 . Correlation between annual (g C m^{-2}) stem-C storage change for lodgepole pine trees surviving a mountain pine beetle (MPB) attack versus Eddy Covariance derived Net Ecosystem Productivity (NEP) for the same MPB-attacked lodgepole pine stand near Mackenzie, British Columbia, Canada.

391 The growth release of surviving pine trees after MPB attack was strongly
392 correlated with the percent of dead canopy trees that had fallen down. A
393 Pearson correlation between stem C-storage change from dendrochronology
394 data and cumulative percent downed trees was strongly positive and significant
395 (R^2 = 0.837, p=<0.001). Linear regression analysis of these two variables
396 indicated a strong positive relationship (R^2 = 0.837, p=<0.001; Fig. 5).



397

398 Figure 5 . Correlation between annual tree stem volume change in surviving
399 lodgepole pine trees (g C m^{-2}) versus cumulative percent of downed (attacked

and dead) pine trees for an MPB-attacked stand near Mackenzie, British Columbia, Canada.

Discussion

Growth release

Understanding how the C-balance of lodgepole pine stands recovers after MPB-outbreaks and similar disturbances is critical in guiding future management of these stands. Conventional wisdom on growth release in lodgepole pine after silvicultural thinning or disturbance was that it is diminished with increasing time of suppression and on poorer sites (Lotan and Critchfield 1990), conditions that both existed at our study site. Contrary to the pre-1990 studies, the growth release of suppressed trees at our site (11 years after peak MPB attack) were impressive by any standards (trees having a growth change of -53% to +2326% of pre-attack levels, averaging +392%), but particularly so given the advanced age of the suppressed trees (mean age of >85 years) and on a site with very poor edaphic attributes and a low growth potential. By comparison, Amoroso et al. (2013) observed a growth response of surviving lodgepole pine trees ranged that was lower (-75% to +750% of pre attack levels) following a MPB-outbreak in 1979-1980 in the Flathead Valley of southeastern BC. However, it should be noted that the Flathead Valley surviving pine trees were in competition with other tree species, which was not the case at our study site where pine was predominant.

Past research (Axelson et al. 2009, Amoroso et al. 2013) demonstrated that stands with >70% MPB mortality showed a more substantial growth release

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423 than stands with <70% mortality. Supporting these findings, the high mortality
424 rate (>70%) at our study sites was associated with a high percentage of trees
425 releasing (96.9%) and a high average release of 392%. Our results were also in
426 general alignment with EC measurements of NEP at this site (Brown et al. 2012;
427 Fig. 4) and scaled-up leaf-level gas-exchange results of Bowler et al. (2012).
428 Together, they suggest that surviving pine trees are a major part of ecosystem C-
429 storage recovery after attack.
430

431 **Effects of stand characteristics and environmental factors on ring widths**

432 Size class was expected to affect the growth release and C-storage
433 increase of surviving trees. Smaller trees were expected to have a higher
434 percent release, on the assumption that they were likely younger trees, and
435 therefore more likely to respond to release. However, we also suspected that
436 larger trees should still have a higher C-storage increase as larger trees store
437 more C per unit of radial growth. Smaller trees were not younger than larger
438 trees indicating that they likely had more competitive growing conditions than
439 larger trees before the outbreak. Both were able to respond to decreased
440 competition; however, smaller trees had a higher percent growth release than
441 larger trees (476% vs 308%). Even though smaller trees had a larger percent
442 release, their post-outbreak mean annual ring-width of 0.917 mm was less than
443 the larger tree mean annual ring-width of 1.503 mm. Overall, the effect of
444 diameter class on percent release was significant, with the smaller trees having a
445 greater percent release, contrasting with Amoroso et al. (2013) who found no

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446 significant relationship. However, Amoroso et al. (2013) found that trees less the
447 20 cm DBH at attack had higher releases, commensurate with our study site
448 release as all surviving trees had diameters less than 20 cm.
449 Higher stand densities may affect the release of the remaining trees. In
450 our study, stand location was found to significantly affect the growth release.
451 Stand densities varied among the eight plot locations (Table. 1). The two stands
452 that had the highest tree densities (plots 2 and 5) experienced significantly less
453 release relative to other plots. The greater stand densities likely resulted in a
454 higher degree of competition for resources. This suggests that post-outbreak
455 stand density is a major variable affecting growth release of surviving trees.
456 Changes in precipitation and temperature is not likely sufficient to explain the
457 increase in C storage post MBP attack. We found that years with increased
458 summer precipitation and temperature correlated with increase carbon storage.
459 Increases in precipitation is important because trees at this site are likely water
460 limited because of the very coarse textured soils. Mean annual precipitation and
461 temperature in the 10 years pre and post attack were not significantly different.
462 Pre and post peak MBP attack mean annual precipitation averaged 601 and 550
463 mm, respectively. Mean annual temperature averaged 3.30^{o}C and 3.42^{o}C pre
464 and post peak attack respectively. The lack of a coordinated increase in
465 precipitation and temperature decreases the likelihood that the post attack
466 increase in C storage in surviving trees was primarily the result of shift toward
467 more favourable weather.

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As hypothesized, we found a strong positive relationship between EC NEP measurements and C-storage change of surviving tree stems indicating that these trees are important in aiding the recovery of NEP after the most recent MPB attack. Annual C-storage of surviving lodgepole pine trees was expected to be an important contributor to EC NEP measurements at this site (Bowler et al. 2012; Brown et al. 2012). In years with low tree growth, NEP at the site was negative (Fig. 4). This supports the predictions of Bowler et al. (2012) and Brown et al. (2012) that surviving trees are a major contributor to NEP at our site. While we did observe a relatively strong correlation between NEP and tree C-storage (Fig. 4; R^2=0.77) across years in our stand, some of the variation we did observe in our relationship could have been related to shifts of carbon allocation to radial growth in subsequent years as observed by Teets et al. (2018) in mixed conifer forests in central Maine, USA.

If C-storage is a management goal, surviving trees should be retained on site following salvage harvests to minimize overall C-losses. It is likely that surviving trees from other disturbances such as spruce beetle outbreaks, forest fires or any disturbance that has surviving trees would have a similar response. For example, Whitehead et al. (2007) saw an increase in tree growth rate following a thinning of ~45% of the volume from multiple lodgepole pine stands.

Annual C-storage and time since attack

At our site, both EC NEP and tree carbon storage change were initially low, then steadily increased. As with past research, the initial response was slow as the change in canopy conditions can lead to increased wind damage (Chen et

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491 al. 1992; Garber et al. 2011) and photodamage (Harrington and Reukema 1983;
492 Lovelock et al. 1994; Jones and Thomas 2004). However, the competition for
493 light and other resources should decrease as overstory trees blocking sunlight
494 and consuming resources die and fall down thereby opening the canopy (Coates
495 and Hall 2005). As trees expand their root network to access increased water
496 resources and adapt to increases in light availability, the remaining live trees
497 should increase in growth, thus aiding in recovery of annual C-storage (Coates
498 and Hall 2005).

499 Similar to Coates and Hall (2005), we found a strong relationship between
500 annual stem C-storage and the cumulative percent of downed trees over the 11
501 post MPB outbreak years. Increased nitrogen availability resulting from litter fall
502 and reduced competition from attacked trees may have improved tree growth.
503 Romme et al. (1986) found that stands with minimal understory growth
504 experienced delayed release following a MPB attack. In addition, Rhoades et al.
505 (2013) demonstrated that following MPB attack, streamflow nitrogen did not
506 change, contrasting greatly with timber harvesting where a 400% increase in
507 nitrogen discharge was observed. This suggests that in an MPB-attacked forest
508 system, remaining vegetation can remove newly available nitrogen. In a system
509 with limited understory vegetation, as is the case at our sites, the surviving trees
510 would then be the main beneficiaries of elevated resources such as nitrogen. The
511 delayed growth response to increased nutrient availability in surviving trees at
512 our study sites could have resulted from delays in needle fall and decomposition
513 as well as gradual shifts in resource-partitioning and tree allometry (i.e. from root

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514 to shoot). In addition, other resources such as sub-canopy light levels are need
515 to be considered.

516 In addition to expected increases in belowground resources following
517 forest canopy loss, so too are the increases in aboveground resources, such as
518 understory light levels. For example, light transmittance in southern BC interior
519 lodgepole pine forests were found to increase from 27% in the green attack
520 phase to 49% in the grey attack phase after the most recent MPB-epidemic
521 (Winkler et al. 2012). Coates and Hall (2005) predicted that an even greater
522 increase in canopy transmittance would occur following fall-down of snags as
523 stems and small branches can block a significant amount of light. Hence, the
524 delay in growth response that we observed in understory pine trees were
525 undoubtedly due to the time required for the surviving trees to take advantage of
526 increased light and other resources following the multi-year canopy tree death
527 and gradual fall-down of lodgepole pine that occurred after the MPB attack in
528 British Columbia.

529 **Conclusions**

530 The results of this study confirm the expectations of Bowler et al. (2012)
531 and Brown et al. (2012), that surviving lodgepole pine are a major contributor to
532 stand-level NEP and C-sequestration. Annual stem C-storage in surviving trees
533 was found to have a significant positive relationship with both annual NEP and
534 cumulative percent of downed MPB-attacked pine trees since time of attack. The
535 extent of release in 43-127 year-old pine trees with an average release of nearly
536 400% was somewhat surprising. This study corroborates other work at our site

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and across BC, that C storage is recovering rapidly in pine forests after MPB-attack, in large part through release and rapid growth of suppressed understory lodgepole pine trees.

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