



## Survival and growth of residual trees in a variable retention harvest experiment in a boreal mixedwood forest

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### ABSTRACT

Long-term sustainability of forest resources is in question given wide-spread use of conventional clear-cut silviculture. In response, variable retention (VR) harvest has been increasingly promoted as a landscape-based approach to enhance sustainability by maintaining biodiversity and other ecosystem functions in managed forests. Although the success of the VR approach depends on post-harvest stand dynamics, little is known about growth and mortality of residual trees after harvest and how such trees respond to interactions between amount of retention and tree or site level covariates. We use data from three censuses distributed over a 10-year period of the main merchantable species to study the effects of retention level (i.e., percent of trees retained), mixedwood cover type, tree species, and three tree or terrain covariates (tree stem diameter, percent live crown, and soil wetness) on survival and growth of residual trees in a retention harvest experiment in NW Alberta, Canada. Both mortality and growth of residual trees were negatively related to retention levels. During the first five-year period after harvest, effects of retention levels on mortality were more evident for white spruce (*Picea glauca*) than for *Populus* spp., but effects on growth were weaker for white spruce. Tree mortality decreased through time following VR harvest for all species and in most cover types, while trends in tree growth varied by species. During the second five-year period after harvest, growth of residual *Populus* spp. had decreased from high levels observed in the first period. In contrast, growth of residual white spruce was greater in the second five-year period than in the first period. After the original harvest, re-entry of stands for additional harvest focused mainly on hardwoods may be economically rewarding and ecologically justified, depending on the overall objectives for retention. The positive effect of increased retention level on tree survival was strongest for trees with larger diameter and longer crowns. Thus, retention patches are a management option to protect large trees and trees with greater crown length when retaining such trees is a management goal.

### 1. Introduction

Forests are important for the supply of wood and fiber; however, the ecological sustainability of conventional clear-cut silvicultural systems has been questioned in relation to a broader appreciation of forest values (Bliss, 2000; Lindenmayer et al., 2012). Variable retention harvest (VR) that retains single trees and/or forest patches at the time of harvest is increasingly employed with the aim of maintaining biodiversity and other ecosystem functions (Fedrowitz et al., 2014; Franklin et al., 1997; Spence, 2001).

In VR systems, retained trees provide wildlife habitat, store carbon, and influence future regeneration and succession. Thus, an understanding of post-harvest growth and mortality of retained trees, under various retention prescriptions, is critical to assessing success of the VR approach. Although impacts of boreal retention harvests on biodiversity

have been investigated for many taxa, including understory plants, invertebrates, and vertebrates (e.g., Gandhi et al., 2004; Lance and Phinney, 2001; Macdonald and Fenniak, 2007; Moses and Boutin, 2001), relatively little is known about post-harvest growth and mortality of residual trees, and how these processes are influenced by interactions among amount of retention and site and tree level covariates, particularly for the western Canadian boreal mixedwood (see Bose et al., 2014a; Prévost et al., 2010; Prévost and Dumais, 2014; Smith et al., 2016 for results from eastern Canada).

The boreal forest is the largest terrestrial biome on Earth and also the major forest biome in which the VR model is currently practiced (Fedrowitz et al., 2014; Gustafsson et al., 2012). Several studies from the boreal zone have demonstrated enhanced growth rates and elevated mortality of retained trees after partial harvest (Bose et al., 2014a; Prévost et al., 2010; Rosenvald et al., 2008; Solarik et al., 2012).

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However, post-harvest responses could vary considerably among species, levels of retention, and study areas. For example, enhanced growth of trembling aspen (*Populus tremuloides*) was significant only in the lower retention treatment (< 1/3 retention vs. no effect on > 2/3 retention) applied in a boreal mixedwood forest in northwestern Quebec, Canada (Bose et al., 2014a). In contrast, diameter growth of residual trees increased linearly with partial harvest intensity in a trembling aspen–conifer mixed stand in southeastern Quebec (Prévost et al., 2010). Improved understanding of such effects could be used in planning harvests that are fiber efficient and contribute to biodiversity conservation and recovery.

Several unanswered questions about the fate of retention trees are important both for understanding forest function and improving management. For instance, previous studies suggest a general pattern in post-harvest growth, i.e., a short lag period immediately after harvest is followed by a gradual increase up to a peak that gives way to a period of reduced growth toward pre-harvest rates (Bose et al., 2014a; Smith et al., 2016). Yet, little is known about how this pattern may vary among species or stand types. Although site factors such as soil wetness contribute to variation in tree growth and mortality (e.g., Hogg et al., 2005), few studies have examined growth and mortality of trees remaining after partial harvest in relation to such factors (Solarik et al., 2012). Models that simultaneously incorporate harvest effects, intrinsic tree characteristics, and extrinsic environmental factors could improve understanding of post-harvest stand dynamics.

In addition, understanding interactions between partial harvest treatments and other covariates would facilitate tests of hypotheses about drivers of tree growth and mortality. For example, it has been widely shown that size-based asymmetric competition for resources affects tree mortality and growth (Metsaranta and Lieffers, 2008; Schwinning and Weiner, 1998). Thus, we expect to see different effects of harvest intensity on the performance of trees based on their relative size. In this study, we hypothesized that interaction between stem diameter and harvest treatments would affect tree growth and mortality. Specifically, the reduction of competition at lower retention levels should benefit smaller trees more than larger trees because smaller trees suffer more from competition in unharvested forests (Smith et al., 2016). Likewise, mortality should be reduced for smaller trees with reduced competition. This could counteract increased post-harvest mortality, especially if windthrow mortality is the dominant part of post-harvest mortality.

The EMEND (Ecosystem Management Emulating Natural Disturbance) experiment in northwestern Alberta (Volney et al., 1999) is among the largest and longest-running experiments assessing ecological consequences of partial harvest to different retention levels, and is providing critical information to guide sustainable management of boreal forests (Gustafsson et al., 2012). In this paper, we expanded upon previous work about mortality of residual trees at EMEND (Solarik et al., 2012) to examine the effects of retention level, tree level characteristics, site wetness, and their interactions on both post-harvest tree growth rates and survival probability across species and cover types. The data analyzed here are from a dispersed retention treatment where retained trees were chosen according to a consistent prescription and relatively evenly distributed in space (see *Materials and methods*). Specifically, our study focused on the following two objectives: (1) model growth rates and survival probabilities over 10-years following partial harvest using retention level, tree diameter, tree crown length, site wetness, and potential interactions between retention level and the other covariates, and (2) better understand variation in post-harvest growth and survival responses among species and cover types.

## 2. Materials and methods

### 2.1. Study site

The EMEND experimental site is located on the boreal mixedwood

plain, approximately 90 km northwest of Peace River, Alberta (56°46'13"N, 118°22'28"W) with elevation ranging from 677 to 880 m asl. Data collected 1981–2010 at a nearby weather station (Eureka River, 56°29'N, 118°44'W) give a mean annual precipitation of 440 mm with 65% of this occurring during the growing season from May to September. Mean annual temperature is 0 °C, with a January mean of –16.9 °C and a July mean of 15.0 °C (Environment Canada, 2013). EMEND includes approximately 1000 ha of treated compartments embedded within a c. 24 km<sup>2</sup> forested landbase. Forests at EMEND fall into four cover types according to the proportions of dominant overstory trees: (1) deciduous-dominated stands (DD), which have > 70% deciduous trees (mainly trembling aspen and balsam poplar (*Populus balsamifera*)) in the canopy, (2) deciduous stands with coniferous understory (DU), as in DD but with understory of white spruce (*Picea glauca*) at least 30% as tall as canopy at the time of harvest, (3) mixed-wood stands (MX), which have both deciduous and coniferous components comprising 40–50% of the canopy trees, and (4) coniferous-dominated stands (CD), which have > 70% coniferous trees (mainly white spruce) in the canopy. Stand age within each of the four cover types was relatively homogenous and the mean age of DD, DU, MX, and CD stands when the harvests were applied was ~80, 80, 100, 125 years, respectively (Spence and Volney, 1999). A summary of pre-treatment stand structure for each cover types can be found in Table 1. Experimental compartments (each c. 10 ha in size) were established in previously unmanaged natural stands in the summer of 1998, and during the winter of 1998–99, a set of harvest treatments was applied across these compartments. Retention levels (percentage of retained stems) within compartments were set at 10%, 20%, 50%, 75%, and 100% (unharvested control), and three replicate compartments for each retention level were distributed over three blocks in each of the four cover types (Fig. S1). Mean post-harvest tree densities for these retention levels were 238, 368, 431, 658, and 1068 living trees per ha with diameter at breast height (DBH) ≥ 5 cm, respectively. Retention harvesting was conducted using north-south facing 5-m-wide machine corridors that alternated with 15-m-wide retention strips. All trees within machine corridors and a prescribed proportion of trees within retention strips were harvested to achieve experimentally desired levels of dispersed retention. A 75% retention level was created by only machine corridors through compartments. Lower retention levels were achieved by harvesting additional trees, strictly in the order encountered and regardless of species, from the retention strips at the following ratios: 1:2 (cut:left) for 50% retention, 3:1 for 20% retention, and 7:1 for 10% retention (see Work et al., 2010 for fuller account of design).

### 2.2. Tree survival and growth

Six permanent plots (2 × 40 m each) were randomly located 40 m or more from the edges of each compartment in mid-late summer 1998 before harvest treatments were applied. All plots were oriented perpendicular to the machine corridors so as to include equivalents of two 5-m-wide machine corridors and two 15-m-wide retention strips. All living trees in these permanent plots with DBH ≥ 5 cm were tagged and measured, and most plots were re-visited in 1999 (to establish post-

**Table 1**  
A summary of pre-treatment compartment-level stand structure for the four cover types.

Cover type	Basal area (m <sup>2</sup> /ha)		DBH (cm)		Maximum height (m)		90% quantile of tree height (m)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
DD	35.34	1.56	23.37	0.94	28.91	0.57	25.40	0.23
DU	47.30	1.47	21.09	1.16	29.13	1.02	25.59	0.77
MX	45.50	1.76	26.65	1.80	33.10	0.74	28.97	0.85
CD	45.15	2.84	26.36	1.31	32.19	0.71	28.64	0.48

harvest survival), and all were fully re-censused in 2003 and 2008. This paper deals with the fates of trees still living after harvest in 1999 in these plots or in replacement plots (12.5% of all plots) that were established and measured after harvest to accommodate changes to compartment boundaries made at harvest. In each of these assessments, the status of each tree was assessed as alive, standing dead, or fallen dead. Tree DBH, height to the base and top of the live crown were also recorded during all censuses. As the starting point for analyses, measurements made on trees tagged in 1998 were used for plots that did not change location, but these variables were measured in early 1999 for residual trees in the replacement plots established post-harvest.

Survival status and annual diameter growth rate of retained trees were calculated for both the first (1998–2003) and second (2003–2008) five-year post-harvest periods using the census data described above. Growth rates were calculated only for trees that were alive throughout each five-year interval. There were 131 (9.2%) and 122 (9.4%) trees in the first and second five-year periods, respectively, for which data suggested negative or zero growth rates. To account for potential bias due to separating these non-positive growth rates, we performed two analyses. First, the observations with non-positive growth rates were excluded from the growth analyses. Second, we added a small number (0.2 cm/year) to all growth rates and redid the growth analyses using all observations. The two methods showed similar results, so we report the results from the first method in the main text with the results from the second method presented in the Appendix (Tables S1–S4).

### 2.3. Tree characteristics and site wetness

We used tree DBH and percent live crown (PLC = crown length/tree height  $\times$  100, where crown length was the difference between the heights to base and top of live crown) at the beginning of each five-year interval as intrinsic factors to model tree survival and growth. PLC is an indicator of tree vigor and has been identified as an important predictor of tree growth and mortality (D'Amato et al., 2011; Wilson and MacLean, 2015).

We also used a cartographic depth-to-water-table (DTW) index derived from LiDAR (Light Detection and Ranging) data as an extrinsic environmental factor (White et al., 2012). Murphy et al. (2011) showed that the LiDAR-derived DTW was more closely related to soil drainage, soil type, vegetation type, and a variety of soil properties than the widely used terrain wetness index (TWI, Moore et al., 1991). Furthermore, in the EMEND area, Hiltz et al. (2012) found that DTW accounted for 68% of variation in a field-assessed soil moisture-based vegetation index. It was also positively related to pre-harvest forest productivity and usefully predicted forest regrowth after partial harvest (Nijland et al., 2015). Using a LiDAR-derived DTW map available for EMEND (resolution 1.0 m; initiation threshold 4 ha; White et al. 2012), we extracted the set of values for each  $2 \times 40$  m tree plot and used the mean DTW for the 80 m<sup>2</sup> area in analyses of tree survival and growth. LiDAR data for the EMEND area, acquired on 15 August 2008, were provided by Alberta Environment and Sustainable Resource Development (White et al., 2012).

### 2.4. Statistical analyses

We used mixed effect models to examine how survival probability and growth rate of trees were affected by retention level, time period, and the covariates (DBH, PLC and plot DTW). Binomial errors with a logit link function (i.e., logistic regression) were used to model tree mortality (1 = alive, 0 = dead), while normal regression with Gaussian error structure was used to model log-transformed diameter growth rate. Two sets of models were fitted for tree growth and survival. In the first set (analysis 1), tree species were modeled in addition to retention level, time period, and the three covariates as fixed effects. In contrast, the second set (analysis 2) included cover type in addition to retention level, time period, and the three covariates as fixed effects. The nested

structure of the dataset was accounted for by including random effects of plot within compartment within cover type. In the second set of models, species were also treated as a random effect crossed to the nested error structure. To further evaluate factors affecting status of dead trees (i.e., standing dead vs. fallen), we also conducted similar analyses on the status of dead trees (1 = standing, 0 = fallen) as done for tree survival using the logistic model. DBH and DTW were log-transformed to normalize their highly right-skewed distributions. Finally, retention level, PLC, and the log-transformed values of DBH and DTW were mean-centered and scaled to unit variance (Table S5) before calculating interaction terms.

For each analysis of survival and growth, we compared 10 candidate models, ranging from a simple random effect model with an intercept (i.e., mean effect), to a mixed model adding the fixed effects of the tree characteristics, and more complex models considering different combinations of interactions among retention level, time period, species/cover type, and other covariates (Table S1). The Akaike Information Criterion (AIC) was used to identify the best model. Marginal  $R^2$ , which describes the proportion of variance explained by the fixed factors, and conditional  $R^2$ , which describes the proportion of variance explained by both the fixed and the random factors, were also calculated for all models (Nakagawa and Schielzeth, 2013). Selected models were then used to assess the effect of different factors on the response variables using type III tests (Singmann et al., 2015). Parameters of all models were estimated using the lme4 package (Bates et al., 2015) in R version 3.1.2 (R Core Team, 2014). To demonstrate the effect of interactions, simple slopes (Aiken and West, 1991) were calculated and relationships between response variables and retention level were plotted with potentially interacting variables fixed at several different values.

## 3. Results

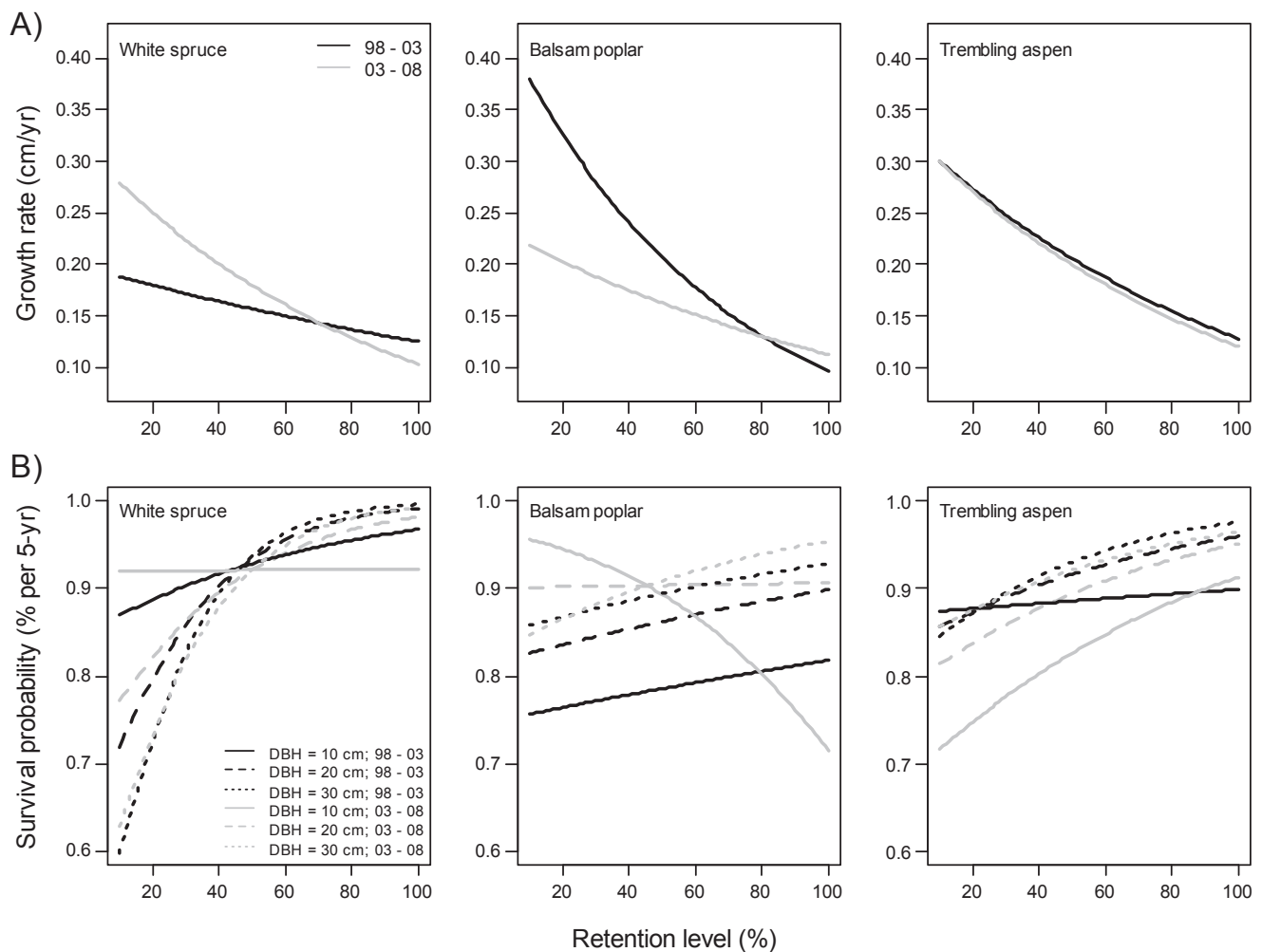
### 3.1. Post-harvest survival and growth of residual trees

Mortality and growth rates of residual trees were inversely related to retention level in both time periods (i.e., 1998–2003 and 2003–2008) (Fig. S2). Overall mortality rate for the sites with the lowest retention levels (10–20% retention) was, on average,  $\sim 4.0\%$  year<sup>-1</sup> and  $\sim 3.0\%$  year<sup>-1</sup> in the first and second five-year periods, respectively, as compared to  $1.3\%$  year<sup>-1</sup> in the controls. The highest mortality rate of  $6.9\%$  year<sup>-1</sup> was observed for trembling aspen during the second five-year period under 20% retention. Although background mortality rates were lower in spruce than trembling aspen, the effect of partial harvest was greater for white spruce, especially in the first five-year period where the probability of spruce mortality was 6.8 and 11.8 times greater, respectively, at retention levels of 10% and 20% than in controls.

Average diameter growth rates for trees in the lowest retention levels were  $0.29$  cm year<sup>-1</sup> and  $0.36$  cm year<sup>-1</sup> in the first and second five-year periods, respectively as compared to a background rate of  $0.15$  cm year<sup>-1</sup> in the controls. Growth release of residual trees was strongest for balsam poplar, for which growth rate increased to as much as  $0.48$  cm year<sup>-1</sup> in comparison to the background rate of  $\sim 0.16$  cm year<sup>-1</sup> in unharvested control compartments (Fig. S2).

### 3.2. Influence of retention level on tree survival and growth

Retention level was included in all of the most supported growth and survival models (Table S6) and increased retention always showed a negative effect on tree growth and a positive effect on tree survival (Tables S7 and S8). However, the magnitude of the effect varied across species, cover types, and time periods. For example, retention level had a stronger effect on tree growth for *Populus* species than for white spruce in the first five-year period (Table S7; Fig. 1A), although the background growth rate, as defined by control compartments, was higher for spruce than *Populus* spp. ( $t = 2.29$ ,  $P = 0.011$ , Fig. S2).



**Fig. 1.** Estimated effects of interactions between retention levels and different covariates (Species and Time for growth; Species, Time, and DBH for survival) on survival and growth of retained trees in the EMEND experiment. In each panel, conditional relationships between annual growth rate (A) or five-year survival probability (B) and the retention level are shown for different values of the interacting covariates, while other variables were controlled at their means.

In most analyses, the effect of retention level on survival declined with time (Figs. 1B and 2B, C). However, the temporal trends for the effect of retention level on tree growth differed between white spruce and *Populus* spp. (Table 2; Fig. 1A). With an one unit (SD, ~30%) decrease in retention level, the growth rate of white spruce increased by 13% and 29% in the first and second periods respectively, while the growth rate of balsam poplar increased 38% and 21%, respectively.

Analyses of the status of dead trees showed that the probability a dead tree would remain standing (versus falling) was significantly higher at higher retention levels (Tables 3 and S9). This suggested that blowdown was a significant cause of mortality for the lower retention levels.

### 3.3. Influence of tree characteristics on tree survival and growth

Tree survival and growth were positively related to DBH in all analyses (Tables S7 and S8). Positive interaction between retention level and DBH was retained in the survival models (Tables 2 and 3), suggesting that the effect of retention level on tree survival is greater for larger than smaller trees (Figs. 1B and 2B).

PLC positively affected tree survival and growth in all analyses (Tables S7 and S8). Significant interaction between retention level and PLC was retained in the survival model in analysis 2 (Table 3), suggesting that PLC influence the effect of retention level on tree survival (Fig. 2C). Analyses of the status of dead trees demonstrated that at

lower retention levels the likelihood that dead trees remained standing was negatively related to their PLC when they were alive (Fig. S3), underscoring that blowdown was a significant factor in post-harvest stand dynamics.

### 3.4. Influence of site wetness on tree survival and growth

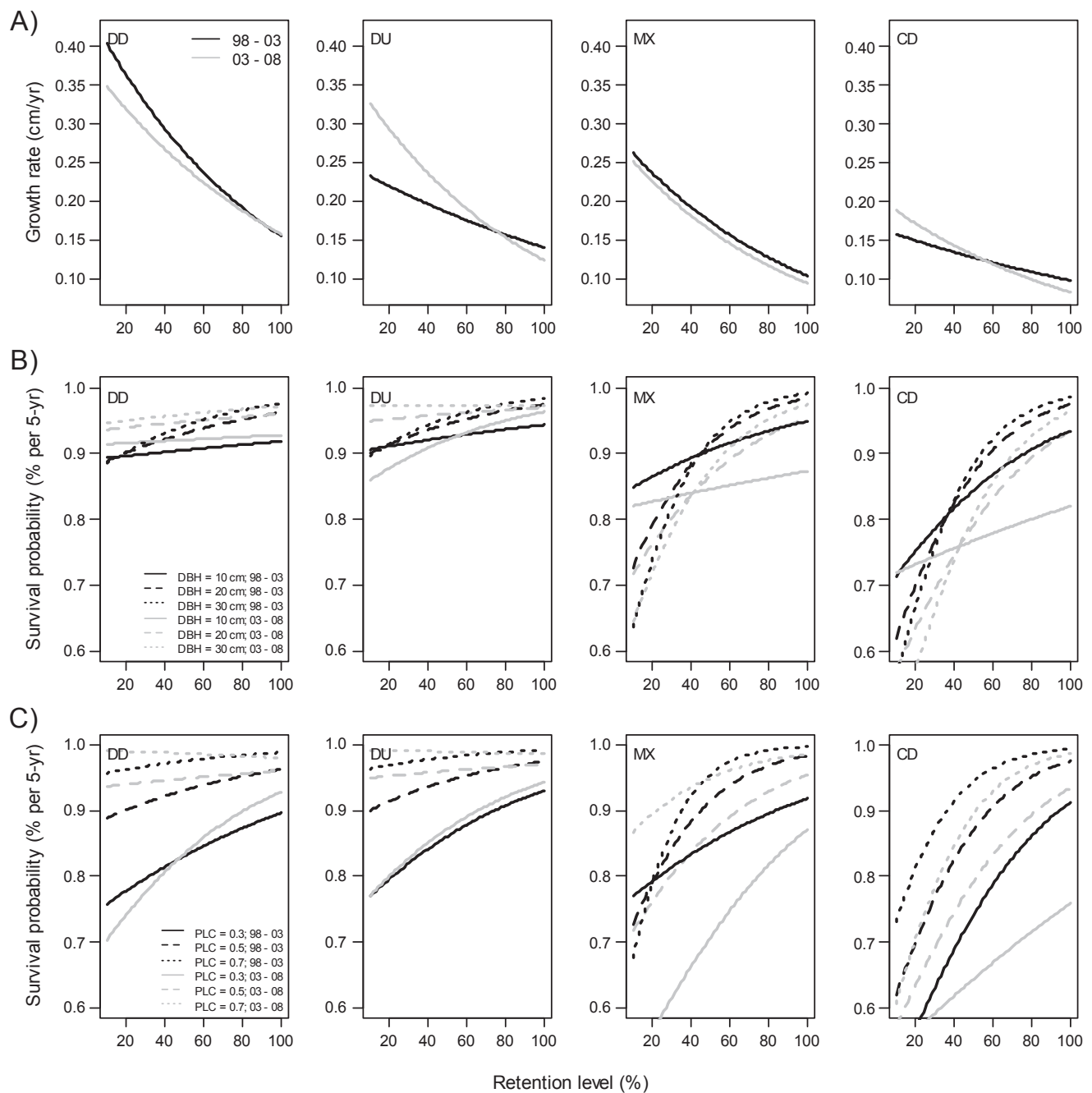
Depth-to-water as measured by the LiDAR-derived model did not significantly affect either tree growth or survival in any analysis (Tables 2 and 3).

## 4. Discussion

We analyzed data from a large variable retention harvest experiment in western Canada to explore how partial harvest affects post-harvest tree survival and growth, and how effects may be influenced by tree characteristics and site wetness. While we demonstrated consistent increases in tree mortality and growth rates with declining retention level, responses varied across species, cover types, and intrinsic tree characteristics. The LiDAR derived site wetness index was not a useful predictor of tree growth or survival in our study.

### 4.1. Effects of retention levels

Although absolute mortality rate was lower for white spruce than



**Fig. 2.** Estimated effects of interactions between retention levels and different covariates (cover type and time for growth; species, time, DBH, and PLC for survival) on survival and growth of retained trees in the EMEND experiment. In each panel, conditional relationships between annual growth rate (A) or five-year survival probability (B & C) and the retention level are shown for different values of the interacting covariates, while other variables are controlled at their means. DD = deciduous-dominated stands; DU = deciduous stands with coniferous understory; MX = mixed-wood stands; CD = coniferous-dominated stands.

trembling aspen across all retention levels (Fig. S2), the partial harvest affected white spruce more than *Populus* spp., especially during the first five-year period (Fig. 1). This reflected higher absolute mortality rates of *Populus* spp. in old-growth mixedwood forests (Peterson and Peterson, 1992) and higher rates of windthrow for spruce at lower retention levels (i.e., across all cover-types: 10.5% and 5.5% in the first and second five years' post-harvest, respectively, for 10–20% retention as compared to 0.4% and 0% in control compartments). These higher rates of blowdown in white spruce can be attributed to the shallower root systems and higher drag coefficients reflecting the larger crown in this species. Blowdown is likely to be amplified during winter storms, given the 'sail effect' of both the larger crowns and that white spruce generally has greater maximum height than other species co-occurring

in the study area (Solarik et al., 2012). Our results contrast with those from eastern Canada where partial harvest increased mortality of hardwoods but did not affect conifers (Prévost et al., 2010). The study in eastern Canada was conducted in younger (< 65 years) deciduous-dominated stands in which spruce trees were smaller than in our study, and this likely resulted in lower mortality rates compared with spruce studied here (Solarik et al., 2012). Our finding that retention level had weaker effects on mortality in stands with a deciduous overstory (Fig. 2B) and stronger effects on mortality of larger white spruce trees (Fig. 1B) support this possibility.

*Populus* species responded more strongly to harvest with positive growth than did white spruce supporting previous findings that shade-intolerant *Populus* species are less competitive than spruce in mature

**Table 2**

Analysis of variance table for growth and survival models summarizing type-III tests for significance in analysis 1. A linear mixed-effects model, with random effects of plot within compartment within cover type, was fit for annual diameter growth rates. Generalized linear mixed-effects models with the same random effect were fit for tree survival (alive = 1; dead = 0) and status (standing = 1; fallen = 0) of dead trees. Bold text indicates significance ( $P < .10$ ).

Source	Growth			Survival			Status of dead trees		
	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P
DBH	<b>181.01</b>	1	< 0.01	<b>16.48</b>	1	< 0.01	2.14	1	0.14
DTW	1.55	1	0.21	0.00	1	0.98	0.28	1	0.60
PLC	<b>123.45</b>	1	< 0.01	<b>72.35</b>	1	< 0.01	<b>4.07</b>	1	<b>0.04</b>
Time	0.01	1	0.94	1.60	1	0.21	–	–	–
Species	<b>6.35</b>	2	<b>0.04</b>	<b>14.21</b>	2	< 0.01	–	–	–
TRT	<b>13.43</b>	1	< 0.01	<b>38.86</b>	1	< 0.01	–	–	–
Time × Species	1.11	2	0.57	2.15	2	0.34	–	–	–
Time × TRT	<b>25.95</b>	1	< 0.01	1.93	1	0.16	–	–	–
Species × TRT	<b>24.73</b>	2	< 0.01	<b>16.09</b>	2	< 0.01	–	–	–
Time × Species × TRT	<b>26.00</b>	2	< 0.01	1.76	2	0.41	–	–	–
DBH × TRT	–	–	–	<b>15.94</b>	1	< 0.01	–	–	–
DBH × Time × TRT	–	–	–	0.22	1	0.64	–	–	–
DBH × Species × TRT	–	–	–	3.99	2	0.14	–	–	–
DBH × Time × Species × TRT	–	–	–	2.28	2	0.32	–	–	–

Notes: DBH = log-transformed diameter at breast height. DTW = log-transformed LiDAR-derived depth to water. PLC = percent live crown. TRT = retention level.

natural mixedwood forests (Stadt et al., 2007), i.e., growth of *Populus* species is more suppressed in these highly competitive environments. However, *Populus* trees, especially those that are smaller, have higher potential short-term growth rates than white spruce (Bragg, 2001; Man and Lieffers, 1999), and for this reason likely have inherently greater potential for growth release shortly after partial harvest when resource availability increases and competition is reduced (Wilson and MacLean, 2015).

Previous studies have shown that the effects of partial harvest on both mortality and growth of residual trees can vary through time (e.g., Bose et al., 2014a); however, how long demographic rates would be affected and whether this varied among species has been unclear. At EMEND tree mortality associated with harvest treatments decreased over time (lower in the second five-year than in the first five-year period post-harvest) for both white spruce and trembling aspen (Fig. 1B). Interestingly, the effects of harvest on tree growth showed opposite trends for white spruce and *Populus* species, increasing for white spruce but decreasing for balsam poplar, similar to the patterns found in eastern Canada (Prévost and Dumais, 2014). Thus, *Populus* trees appear to manifest a quicker, but less sustained, growth response

to partial harvest in comparison to that of white spruce. One likely reason for the declining growth response observed in balsam poplar is that the hardwood species suffered from transpiration stress in the second five-year period as the climate records show two consecutive dry growing seasons in the study area (i.e., 2005–2006; Environment Canada 2013).

#### 4.2. Effects of tree characteristics

Both DBH and percent live crown strongly affected mortality and growth responses of residual trees in partial harvests. Larger trees and trees with higher PLC generally had greater survival and growth, consistent with findings of previous studies (D’Amato et al., 2011; Ruel et al., 2000; Wilson and MacLean, 2015). Significant interactions between DBH and retention level on tree mortality (i.e., the higher mortality rates observed for larger trees at lower retention levels; Figs. 1B and 2B) contrast with results from an eastern Canadian study which reported higher mortality of small aspen trees at low retention level (Bose et al., 2014b). Our results may be explained by the susceptibility of large trees to blowdown. For instance, 21 of the 36 spruce trees that

**Table 3**

Analysis of variance table for growth and survival models summarizing type-III tests for significance in analysis 2. A linear mixed-effects model, with random effects of species crossed with plot within compartment within cover type, was fit for annual diameter growth rate. Generalized linear mixed-effects models, with the same random effects, were fit for tree survival (alive = 1; dead = 0) and status (standing = 1; fallen = 0) of dead trees. Bold text indicates significance ( $P < .10$ ). CType = cover type. See Table 2 for other abbreviations.

Source	Growth			Survival			Status of dead trees		
	$\chi^2$	df	P	$\chi^2$	df	P	$\chi^2$	df	P
DBH	<b>183.84</b>	1	< 0.01	<b>14.07</b>	1	< 0.01	0.13	1	0.72
DTW	1.44	1	0.23	0.02	1	0.89	2.78	1	0.10
PLC	<b>125.35</b>	1	< 0.01	<b>89.44</b>	1	< 0.01	0.71	1	0.40
Time	1.51	1	0.22	3.10	1	<b>0.08</b>	<b>6.51</b>	1	<b>0.01</b>
CType	<b>14.35</b>	3	< 0.01	2.04	3	0.56	<b>12.63</b>	3	<b>0.01</b>
TRT	<b>45.53</b>	1	< 0.01	<b>26.05</b>	1	< 0.01	<b>8.62</b>	1	< 0.01
Time × CType	2.34	3	0.50	<b>7.82</b>	3	<b>0.05</b>	0.81	3	0.85
Time × TRT	<b>4.10</b>	1	0.04	2.78	1	0.10	0.00	1	0.97
CType × TRT	6.11	3	0.11	5.36	3	0.15	2.63	3	0.45
Time × CType × TRT	<b>9.51</b>	3	<b>0.02</b>	0.06	3	0.99	0.99	3	0.80
DBH × TRT	–	–	–	<b>10.17</b>	1	< 0.01	–	–	–
PLC × TRT	–	–	–	<b>6.32</b>	1	<b>0.01</b>	<b>10.08</b>	1	< 0.01
DBH × Time × TRT	–	–	–	0.29	1	0.59	–	–	–
PLC × Time × TRT	–	–	–	1.50	1	0.22	0.11	1	0.74
DBH × CType × TRT	–	–	–	1.28	3	0.73	–	–	–
PLC × CType × TRT	–	–	–	<b>7.48</b>	3	<b>0.06</b>	<b>7.99</b>	3	<b>0.05</b>
DBH × Time × CType × TRT	–	–	–	1.47	3	0.69	–	–	–
PLC × Time × CType × TRT	–	–	–	2.43	3	0.49	1.11	3	0.77

died in treated stands during the second five years were blown down and had much larger DBH than average. This suggests that trees growing vigorously prior to removal of adjacent trees will face higher probability of windthrow after the treatment because of their pre-treatment biomass allocation choice.

We found that interaction between PLC and retention level influenced tree survival, something that has been controversial in the literature. Based on the assumption that PLC is a good indicator of wind firmness (Temesgen et al., 2005) and understanding that windthrow decreases with increasing PLC (Scott and Mitchell, 2005), we expected post-harvest mortality rates to increase less for trees with larger PLC. However, we found the opposite, especially in the mixedwood stands (Fig. 2C); furthermore, dead trees that had larger PLC when alive were more likely to be blown down at low retention levels (Table S9; Fig. S3). Thus, we suggest that increases in crown area and wind drag associated with larger PLC counteract positive effects of higher PLC on tree stability (Ruel, 1995).

#### 4.3. Effects of site wetness

Water stress could play a critical role in affecting tree mortality and growth in boreal forests of western Canada (Hogg et al., 2005; Michaelian et al., 2011). However, no such effects were revealed at EMEND. This might be explained by the lack of variation of the DTW index among plots in the current study. Particularly, most trees studied here were located in the dry end of the wetness gradient. Only 23% of residual trees located in areas with DTW < 1 m, which can be defined as wet areas (White et al., 2012). Additional study at the wet end of the gradient may reveal effects of site wetness on post-harvest stand dynamics.

#### 4.4. Limitations

Our interpretations come with qualifications. First, although the timeline is unusually long for this sort of work, it is not long enough to determine how long the effects of retention level on tree survival and growth will last. Second, we did not examine recruitment here, although it is vital to on-site tree demographics and, together with patterns of survival and growth, determines overall forest dynamics. Third, tree demography could be influenced by factors other than those considered in this study, e.g., nutrient availability, pathogen and insect attacks and extreme weather conditions, etc. However, EMEND is a long-term project designed to run for one stand rotation, or approximately 80–100 years. Milestone analyses such as this, at various times after harvest are essential for developing an understanding of the recovery trajectory of forest stands post-harvest and for identifying key factors that determine such recovery.

In summary, our study showed that unharvested trees in higher retention levels were more likely to survive but grew more slowly. In contrast, at lower retention more trees died, especially over the first five years' post-harvest, but the survivors grew faster. Thus, short-term objectives for stand structural legacy and wildlife habitat objectives will be poorly met by low levels of retention forestry in the long run. However, if maintaining an uninterrupted supply of large diameter deadwood, especially trees entering the decay cycle as logs, is a significant objective, the dynamics revealed by our study are encouraging. Such dynamics emulate significant aspects of stand responses following wildfires. Most importantly, our study provides a basis for weighing the fiber consequences of specific harvest retention prescriptions against other considerations at the stand level, while managing landscapes through a VR approach.

Short-term growth release of *Populus* species could provide opportunities for a second entry of retention harvest to recoup some volume and move stands more quickly along a successional sequence toward more spruce-dominated stands (Bergeron et al., 2014). Especially if blocks of aggregated retention are also left on harvested landscapes, VR

harvest could effectively hasten structural development of landscapes similar to 'old growth' with low densities of larger trees and some residual trees entering the decay cycle as standing dead snags. Species- and site-specific analyses demonstrated that increased growth following retention harvests was more short-term for shade-intolerant *Populus* species than for white spruce. Thus, depending on the original retention prescription, second harvests directed mainly at hardwoods might be economically rewarding and ecologically justified if other desired outcomes of retention are not overridden. Interactions between retention level and tree covariates indicate that larger trees are more vulnerable in dispersed VR harvest, suggesting such trees will be better protected by aggregated retention on harvested landscapes. Finally, we also note that the residual forest structure left by the first entry of the VR system is similar to other partial harvest systems (Bose et al., 2014c) and thus, most of the above conclusions should hold for other silvicultural prescriptions leaving green-tree retention at harvest.

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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.01.026>.

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