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Factors affecting white spruce and aspen survival after partial harvest

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Summary

1. Variable retention harvest is an increasingly popular management alternative to clear-cutting in boreal forest ecosystems. This harvest system retains a portion of the mature trees to maintain structural elements of the forest and preserve biodiversity. Residual trees must, however, survive in the post-harvest environment to realize these benefits. Here, we investigate which tree and stand characteristics are associated with high survival to aid foresters in designing harvesting prescriptions.

2. We conducted an operational-scale experiment broadly representative of western North American boreal forests. Treatments were four overstorey compositions (ranging from deciduous to conifer dominated) and five rates of canopy retention (10%, 20%, 50%, 75% and a 100% control). Factors affecting mortality were analysed for the leading tree species (aspen *Populus tremuloides* Michx. and white spruce *Picea glauca* (Moench) Voss 5 and 10 years after harvest.

3. Mortality of residual aspen was highest in 10% and 20% retention treatments with *c.*30% mortality after 5 years and *c.* 50% after 10 years. At year 5, most of the dead trees remained upright as snags (87%), but by year 10, *c.*40% of dead trees had fallen. By contrast, mortality was much lower in the 50% and 75% retention treatments, and similar to that of the unharvested control. Results for white spruce mortality were similar, except the shallow-rooted spruce that was more susceptible to be blown down.

4. Regression tree analysis was used to identify individual tree attributes that predict 5- and 10-year survival. Mortality was higher for trees with a low percentage of live crown and high height/diameter ratio, when trees were very tall or were close to machine corridors. Smaller residual spruce trees from deciduous-dominated stands had the lowest mortality rates.

5. *Synthesis and application*. Where live trees are critical elements of wildlife habitat, forest managers should maintain ≥50% in retention harvest systems. At lower levels of retention (≤20%), mortality can be reduced if foresters select retention trees that are stout, possess large live crowns and are small to intermediate in size. These factors can be used to help design partial harvest systems for effective biodiversity conservation strategies.

Key-words: aspen, boreal forest, classification and regression tree analysis, damage, harvest, mortality, MRT, variable retention, white spruce

Introduction

Variable retention (VR) harvesting has gained popularity as a more sustainable alternative to clear-cutting in recent decades (Franklin *et al.*1997; Thorpe, Thomas & Caspersen 2008). This harvesting system aims to retain structural heterogeneity, including both living and dead trees, on post-harvest landscapes (Work *et al.* 2010). By maintaining 'legacy' trees, it is thought that managers can protect biodiversity by accelerating recovery of species and ecological processes following harvest (Franklin *et al.* 1997).

It has become increasingly clear, however, that many of the trees retained after VR logging die shortly after harvesting is completed. Elevated rates of mortality have been recorded

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after VR in the Pacific Northwest (Walter & Maguire 2004) and in the hardwood forests of Ontario, Canada (Caspersen 2006). There have also been similar reports from the boreal forests for black spruce *Picea mariana* (Mill.) B.S.P. (Thorpe, Thomas & Caspersen 2008), aspen *Populus tremuloides* Michx. (Man *et al.* 2008), and for white spruce *Picea glauca* (Moench) Voss, aspen and birch *Betula papyrifera* Marsh. (Bladon *et al.* 2006). Most studies of post-harvest residual tree mortality have been short term (2–3 years), while mortality rates can remain high for a decade or more (Thorpe, Thomas & Caspersen 2008). Furthermore, many studies have focused exclusively on blowdown (e.g. Scott & Mitchell 2005) and have ignored snags, thus severely underestimating mortality. Several studies indicate that the rate of residual tree mortality is greater if only a few residual trees are left (Man *et al.* 2008).

Although tree mortality is often viewed as a stochastic event (Taylor & MacLean 2007), it is also likely to be related to exposure and condition of the tree after VR harvesting (Bladon *et al.* 2008). Some morphological features such as height and height to live crown ratio, are associated with carbohydrate storage (Goodsman *et al.* 2011), a process critical in accommodating environmental change. Damage to trees associated with mortality can be caused by storm events (Valinger & Fridman 1999; Gregow *et al.* 2008) and harvesting machinery (Ostrofsky, Seymour & Lemin 1986). Thorpe, Thomas & Caspersen (2008) noted increased mortality of trees closer to machine corridors.

Although some models use tree characteristics to predict mortality in intact stands (Yao, Titus & MacDonald 2001), few studies have modelled mortality following prescribed harvest, for example selection harvesting in uneven hardwood stands (Kiernan *et al.* 2009), under multiple thinning regimes (Karlsson & Norell 2005) and protection of advance growth in a black spruce forest (Thorpe, Thomas & Caspersen 2008). While these studies have underscored high mortality rates, they provide only limited information on the factors related to mortality.

Our objective was to identify the tree and stand-level characteristics that influence aspen and white spruce mortality in the boreal mixedwood forest 5 and 10 years following VR harvesting. Potential factors assessed were (i) pre-harvest overstorey composition, (ii) retention level, (iii) distance to machine corridors and (iv) tree characteristics.

Materials and methods

STUDY AREA

Research was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment located in the Lower Boreal–Cordilleran ecoregion (Strong & Leggat 1992) of northwestern Alberta, Canada (56°44′N-56°51′N and 118°19′W-118°27′W). The area has a continental climate with mean monthly temperatures of -18 °C for January and 16 °C for July. Mean annual precipitation is 470 mm, with 75% of the precipitation falling from May to September (Environment Canada 2009). Site elevation ranges from 677 to 880 m above sea level, with a predominantly subhygric or mesic soil moisture regime primarily on Luvisolic soils (Kishchuk 2004). Our experimental compartments with treatments related to species composition, and retention level were distributed along this elevation gradient.

STUDY DESIGN

The forest at EMEND was subdivided into compartments, each *c.*10 ha in size. Overstorey canopies in relatively homogeneous stands were categorized as: deciduous dominated with > 70% of basal area composed of aspen/or balsam poplar *Populus balsamifera* L. (D), deciduous dominated with a conifer understorey with at least 40% stocking of advance growth below the main canopy (Du), 'mixed' with both conifer and deciduous basal area composition ranging from *c.* 30 to 70% (Mx) and conifer dominated > 70% of basal area composed of mostly white spruce (C). Each compartment was randomly assigned to one of five variable harvesting intensities: 10%, 20%, 50%, 75% and 100% (control) residual stem density. Thus, there were 4 overstorey compositions, five harvest intensities and three replicates of each combination, for a total of 60 compartments.

The harvesting was performed in the winter of 1998–99, using a feller-buncher, in combination with a grapple skidder. A systematic harvesting pattern was used: 5-m-wide machine corridors were spaced every 20 m (centre to centre), retaining a 15-m-wide retention strip between machine corridors. All machine corridors ran north–south, perpendicular to the prevailing wind direction, to diminish the threat of wind throw. Harvesting removed all trees within machine corridors and the prescribed proportion of stems within retention strips to reach the desired retention level (75% residual treatments were achieved by removal of all trees within the machine corridors).

Six permanent plots, measuring 2 × 40 m and running perpendicular to the machine corridors, were established in each compartment immediately following logging. These were located at random within the compartment with the start point also located at random with respect to the machine corridor/retention strip pattern. The resulting elongated plots are referred to as 'transects' in this study. The number of trees sampled was not uniform across the various treatments because of different retention prescriptions.

DATA COLLECTION

All trees with diameter at breast height (1·3 m) (DBH) ≥5 cm within transects were permanently tagged in the spring of 1999 prior to the growing season. The status of each tree was assessed as living, standing dead or fallen dead. The following measurements were taken: DBH (cm), height (m), height to base of live crown (m) and distance of the tree to the nearest machine corridor (tree-to-corridor distance (TCD) (m). Presence or absence of mechanical damage (e.g. crown damage, bark missing-cambium exposed) on the tree stem was also recorded.

Trees were re-measured after 5 and 10 years in the late summers of 2003 and 2008. Height and canopy measurements were made with a vertex and transponder.

STATISTICAL ANALYSIS

Only trees surviving the harvest were considered in this analysis. Additional individual tree characteristic variables were calculated. These include: basal area, percentage live crown ratio (PLC) as crown length/total height, slenderness coefficient as height/DBH, relative DBH or standard normal diameter at 1·3 m height (RDBH) $(X_i - X_C)/S_C$, where X_i is the individual tree DBH, X_C is the compartment mean tree DBH and S_C is the compartment standard deviation for DBH.

In addition, transect 'wetness' index was assessed based on LIDAR (light detection and ranging) information collected in spring 2008 to map wet areas within the EMEND landscape. LIDAR data were used to determine flow channels, wet and dry areas, and cartographic depth-to-water index derived from the Alberta provincial bare-ground digital elevation models [see Murphy, Ogilvie & Arp (2009) for methodology]. Using ArcMap v. 9·3 (Environmental Systems Research Institute., Inc. Redlands, CA, USA), the wet areas map were subdivided into four wetness classes: (4) 0–10 cm (hydric), (3) 10–25 cm (subhydric), (2) 25–50 cm (mesic), (1) 50–75 cm (submesic) and (0) 75+ cm (xeric). The final image was rectified as a grid with a 1-m resolution. Each of the permanent transects were then geo-referenced and overlaid on the wet areas map to calculate a single mean wetness value for the entire transect.

Data for white spruce and aspen were analysed separately. Mortality was determined over two time intervals after logging: (i) 5-year interval, spring 1999 (prior to growth) to the late summer of 2003 and (ii) 10-year interval, spring of 1999 to late summer of 2008.

Mortality of individual trees retained at harvest was linked to tree and site variables using classification and regression tree analysis (CART). The technique can be used to identify predictor variables that might explain ecologically complex relationships that may also involve high-order interactions (De'ath & Fabricius 2000). It also handles both metric and categorical data simultaneously in the analyses. Furthermore, CART makes no assumptions about the form of the distribution of the data.

We used CART to produce dichotomies in which groups of trees with similar mortality responses in relation to environmental factors were clustered together to split them from those with different mortality responses. The analysis clusters and splits the data repeatedly in a hierarchical scheme until a Euclidian distance measure of dissimilarity between clusters is minimized. Classification and regression tree analysis were implemented using the mvpart library (Therneau & Atkinson 2009) in R v.2·10·1 (The R Foundation for Statistical Computing, 2008).

Although the mvpart package is designed for multivariate regression tree analysis, it defaults to CART with a single dependent variable and has several statistical options useful for pruning and cross-validating the regression trees (RT). Trees were determined by using 1000 cross-validations and pruned based on the 1-SE (standard error) error rule, whereby selection of the best tree was performed within one standard error of the minimum (De'ath & Fabricius 2000).

We excluded the data from the 100% retention for the CART analyses because we sought to understand only post-harvest mortality. We analysed residual tree mortality both 5 and 10 years after harvest, using three categorical dependant outcomes: living, standing dead and fallen dead. Results of these particular analyses are not presented here, as little variance was explained by the models and only height was a useful predictor of proportional change in the three categories between periods.

Contingency tables were used to assess tree mortality as a function of: (i) overstorey composition, (ii) retention level, (iii) two categories of living spruce (canopy trees ≥15 m and non-merchantable advance growth <15 m in height (trees larger than this were usually harvested) by retention level, and (iv) downed and standing dead trees of aspen vs. spruce. A Pearson's chi-square statistic with a significance level of $\alpha = 0.05$ was used for all contingency table analyses. We included data from the unharvested control (100%) compartments in these analyses. This allowed us to compare mortality rates between retention compartments and untreated controls. These analyses were implemented using the R statistical program.

Results

ASPEN MORTALITY 5 YEARS POST-HARVEST

Mortality of residual aspen 5 years post-harvest was explained in relation to predictor variables by a five-leaf RT (i.e. leaf refers to each terminal node) accounting for 18% of the total variance (Fig. 1). Tree mortality was higher at lower (10% and 20%) overstorey retention levels, 28·3% ($n = 120$), than the pooled mortality rate (9·5%, $n = 189$) in the 50% and 75% retention compartments. Trees with larger ≥ 24% live crown ratios experienced lower rates of mortality (15·9%, $n = 63$) than those with smaller PLC (42·1%, $n = 57$). Mortality in trees with larger PLC was next split by DBH; both trees with ≥ 50 cm DBH died, but among smaller trees (DBH < 50 cm), mean mortality rate was only 13·1% ($n = 61$). Tree height provided the lone split within higher retention compartments (50% and 75%); both trees ≥ 31 m in height died, but few of the shorter trees died (mean mortality rate = 8·6%, $n = 187$) (Fig. 1). Slenderness coefficient was as good as tree height at explaining this last split, where slenderness ≥ 0·50 indicated lower mortality (Table S1). Furthermore, TCD was a second- or third-ranked alternative predictor of mortality for each of the four splits, where trees further away from the corridor's edge had a reduced mortality rate (Table S1).

Contingency table analysis of mortality by retention levels after 5 years corroborated some results from the RT analysis (Fig. 2). Much higher mortality occurred within lower retentions (10%: 29·6% mortality and 20%: 26·8% mortality) than

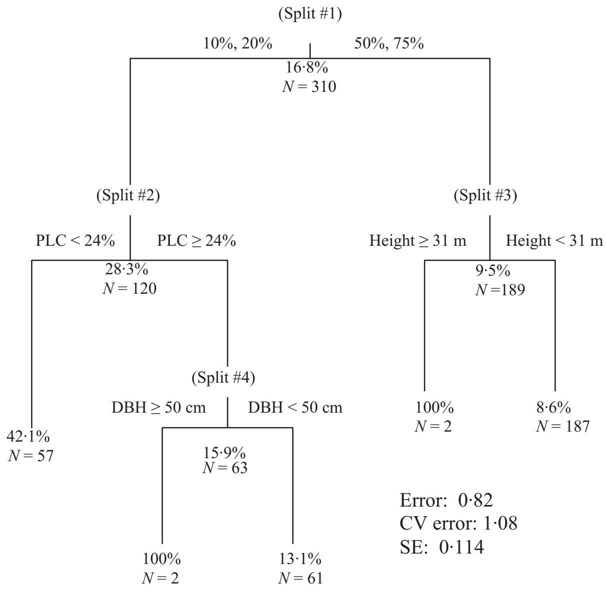

Fig. 1. Regression trees analysis of % mortality of residual aspen trees 5 year after variable retention harvest. This tree explained 18% of the total variance, and the vertical depth of each split is proportional to the variation explained.

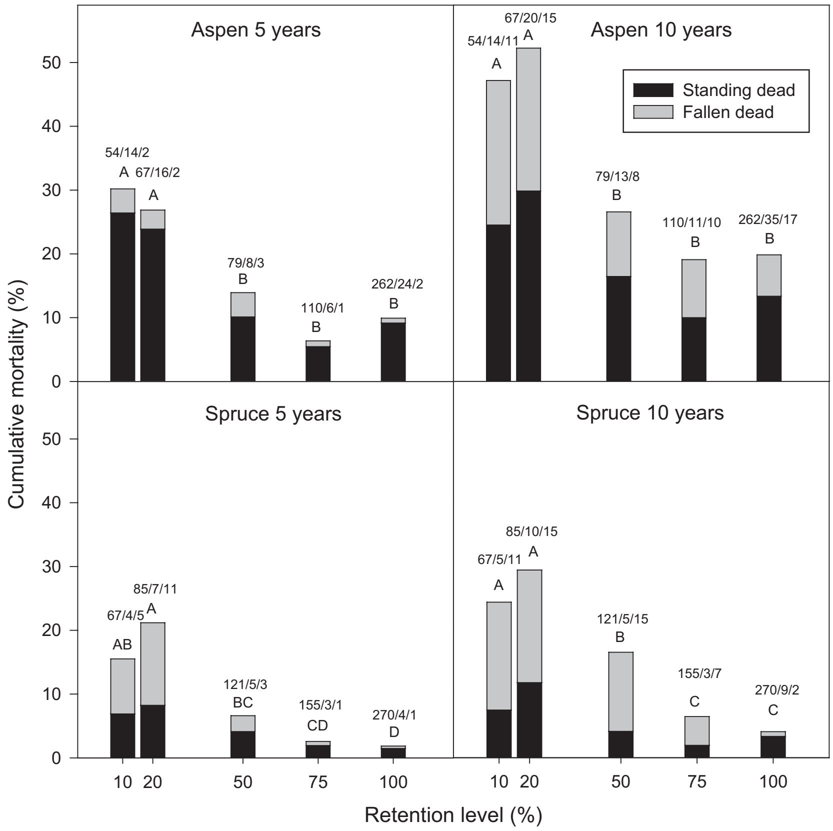

Fig. 2. Aspen and white spruce residual tree mortality by retention level, for 5 and 10 years post-harvest and type of death (fallen and standing). Bars with different letters are significantly different at $\alpha = 0.05$, Pearson's chi-square paired comparisons. Numbers refer to the frequency of total trees/standing dead/fallen dead per treatment.

in the higher retentions (50%: 13·9% mortality, 75%: 6·3% mortality and 100%: 9·9% mortality) (Fig. 2). In addition, these analyses showed that most aspen trees died standing as snags (87·2%) and that mortality rates of aspen did not differ among the various canopy composition classes within the first 5 years (Fig. 3).

ASPEN MORTALITY 10 YEARS POST-HARVEST

A six-leaf RT best described mortality of residual aspen 10 years after retention harvest, explaining 21·1% of total variance (Fig. 4). As in analysis of the data 5 years post-harvest, retention level was the most influential variable. Lower retention levels (10% and 20%) experienced more than twice (50%, $n = 120$) the mortality rates observed in the higher retentions (22·2%, $n = 189$). Mortality at lower retention levels was further split by PLC; trees with $< 16\%$ live crowns experienced higher rates of mortality (92·9%, $n = 14$) than trees with larger crowns (43·3%, $n = 106$). Within the larger PLC ($\geq 16\%$) class of trees, TCD provided the final split; trees within 5·85 m of a machine corridor were more likely to die (53·4%, $n = 73$) than those found further away (24·2%, $n = 33$). Within the higher retention compartments (50% and 75%), overstorey composition provided the first split. Aspen had much lower mortality rates within D- and Du-stands (16·7%, $n = 150$) than within C and Mx-stands (43·6%, $n = 39$). The final split occurred within the C- and Mx-stands, where trees with lower PLC ($< 24\%$) were more likely to die (71·4%, $n = 14$) compared with trees with greater PLC (28·0%, $n = 25$) (Fig. 4). Alternative predictor variables offered little additional insight (Table S2).

Cumulative aspen mortality 10 years after logging was higher within the lower retention compartments (10%: 46·3%; 20%: 52·2%) (Fig. 2) than in the compartments with higher (50%, 75% and 100%) retention levels (mean mortality rate = 20·8%). By year 10, 39·6% of dead aspen had fallen across all retention levels. Furthermore, significantly more dead aspen (21 snags) fell during the second re-measurement period than over the first measurement period (eight, $P = 0{\cdot}008$). Aspen mortality was significantly higher within C-stands (52%) than in Du-stands (29%) and D-stands (28%), but not significantly higher than in Mx-stands (36%) (Fig. 3).

WHITE SPRUCE MORTALITY 5 YEARS POST-HARVEST

White spruce mortality 5 years post-harvest was best described by a five-leaf RT that explained 25·2% of total variance (Fig. 5). Taller trees (height ≥ 30 m) were more likely to die (39·1%, $n = 23$) than were shorter trees < 30 m (7·4%, $n = 405$). For trees ≥ 30 m in height, retention level provided the lone split. Mortality rates within 10% and 20% retentions

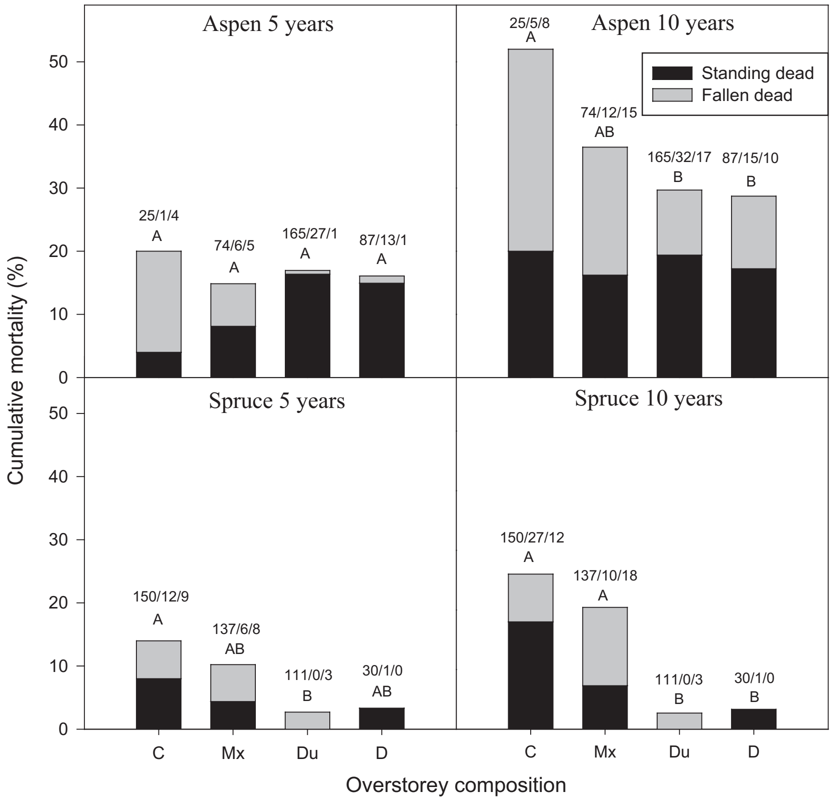

Fig. 3. Aspen and white spruce residual tree mortality by overstorey composition for 5 and 10 years post-harvest and type of death (fallen and standing). Bars with different letters are significantly different at $\alpha = 0.05$, Pearson's chi-square paired comparisons. Numbers refer to the frequency of total trees/standing dead/fallen dead per canopy composition.

(72·7%, $n = 11$) were substantially higher than those within 50% and 75% retentions (8·3%, $n = 12$). For trees < 30 m in height, PLC provided the first split. Trees with a PLC < 27% experienced considerably higher mortality rates (50%, $n = 10$) than did trees with longer crowns (≥27%) (6·3%, $n = 395$). Tree slenderness provided the lone split within trees with smaller live crowns. Slender trees (slenderness coefficient ≥ 1·04) all died ($n = 5$), while stouter trees (slenderness coefficient < 1·04) all survived ($n = 5$). Wetness index was a weak alternative predictor variable for the second split, where the group with lower mortality tended to occur on wetter transects; however, surprisingly, this trend for wetness was reversed for the final split (Table S3).

Mortality of white spruce was sensitive to retention level with higher mortality observed in the 10% (13·4%) and 20% (21·2%) retention compartments, moderately declined in the 50% (6·6%) retention compartments and lowest in the 75% and 100% retention compartments (< 2%) (Fig. 2). In the first 5 years, 59·2% of dead white spruce had fallen over within lower retentions (10% and 20%: total mortality: 17·8%), and this was much higher than seen at higher retention levels (50%, 75%, and 100%: 3·1%). Spruce mortality did not differ among the C-, Mx- and D-compartments, but mortality was significantly higher in C- (14·0%) than in Du-stands (2·7%) (Fig. 3). Five years after harvest, a much higher proportion (51%) of dead spruce had fallen over in retention compartments, compared with fallen aspen (15·4%) (Fig. 2, Chi-square test $P < 0·01$).

WHITE SPRUCE MORTALITY 10 YEARS POST-HARVEST

Mortality of white spruce residual trees 10 years after harvest was depicted by a six-leaf RT that explained 31·1% of the total variance (Fig. 6). As in the 5-year analysis for spruce, height was the best indicator of mortality 10 years post-harvest. Taller trees (≥30 m) were more than five times more likely to die (75%, $n = 20$) than shorter trees (< 30 m) (13·7%, $n = 408$). Mortality of shorter trees was further split by overstorey composition. Spruce within D- and Du-stands had lower rates of mortality (2·8%, $n = 141$) than those within C- and Mx-stands (19·5%, $n = 267$). Within the C- and Mx-stands, retention level provided the first split, where there was lower mortality (11·9%, $n = 194$) in the higher retentions (50% and 75%) compared with the lower retention (10% and 20%) compartments (29·7%, $n = 73$). Within the 10% and 20% retentions, trees closer (< 3·5 m) to the machine corridors were more than twice as likely to die (63%, $n = 25$) than trees further (≥3·5 m) from a corridor (27·1%, $n = 48$). Mortality rates of trees further from the corridor were additionally explained by PLC. Trees with a smaller PLC (< 50%) experienced higher mortality rates (60%, $n = 15$) than did trees with a larger PLC (≥50%) (12·1%, $n = 33$) (Fig. 6). PLC was also an alternative

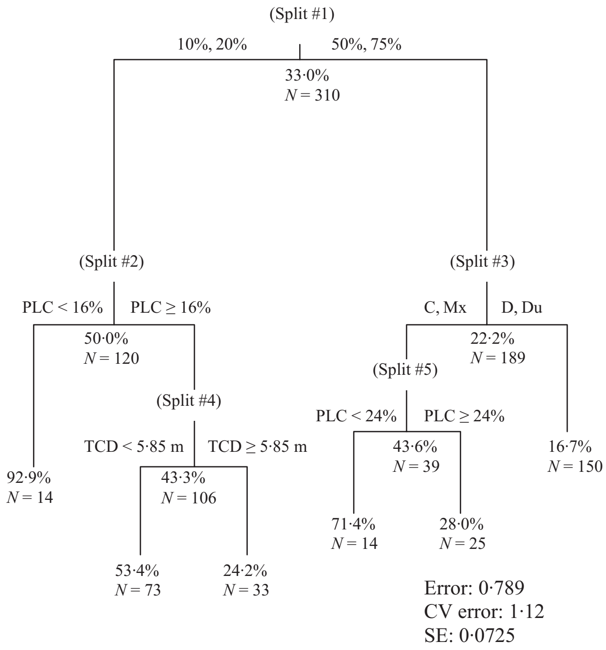

Fig. 4. Regression trees analysis of % mortality of residual aspen trees 10 year after variable retention harvest. This tree explained 21.1% of the total variance, and the vertical depth of each split is proportional to the variation explained.

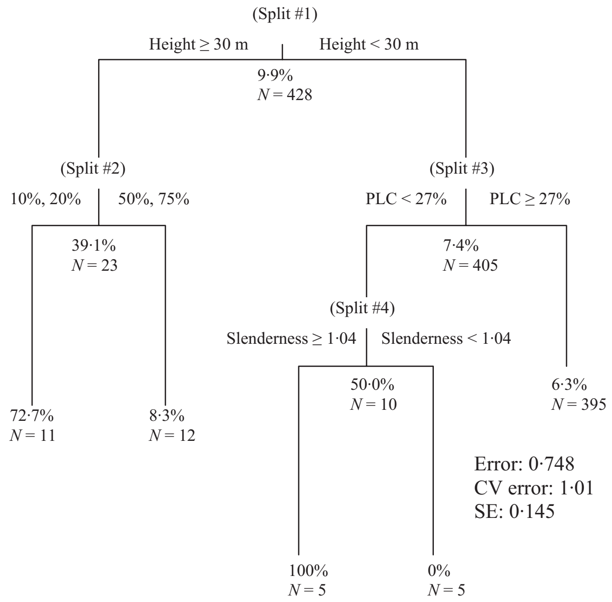

Fig. 5. Regression trees analysis of % mortality of residual white spruce trees 5 year after Variable retention harvest. This tree explained 25.2% of the total variance, and the vertical depth of each split is proportional to the variation explained.

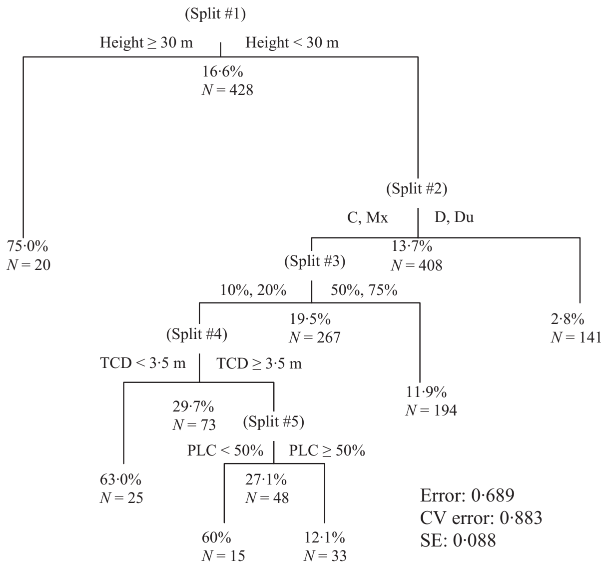

Fig. 6. Regression trees analysis of % mortality of residual white spruce trees 10 year after variable retention harvest. This tree explained 31.1% of the total variance, and the vertical depth of each split is proportional to the variation explained.

variable for splits 2, 3 and 4 (Table S4), where trees with high PLC had lower mortality.

Retention level had a large impact on spruce mortality. Mortality was highest within the 10% (24·0%) and 20% (29·4%) retentions, declined moderately in the 50% (16·5%) and was significantly lower in the 75% (6·5%) and control (4·1%) treatments (Fig. 2). Two-thirds of dead trees within harvested stands (67·6%) had fallen over by year 10. We found no increase in the rate of spruce fall over the second re-measurement period (2003–2008: 22 fallen trees) as compared to the first measurement period (1998–2003: 20 fallen trees) (P = 0·6564). Paired comparisons revealed higher spruce mortality within the C- (26·0%) and Mx-stands (20·3%) than in the Du- (2·7%) and D-stands (3·3%) (Fig. 3). Also interesting is the lack of elevated spruce mortality during the second re-measurement period in either Du- or D-compartments (Fig. 3) in comparison to those observed in the first 5 years.

CANOPY SPRUCE VS. ADVANCE GROWTH

Mortality of white spruce in the canopy (≥15 m tall) in the first 5 years was 18% higher within the lower retentions (10%: 23·5% mortality; 20%: 30·6%) than in the 50% (5·3%) and 75% retention (0·9%) and control (0·6%) compartments (Fig. 7). Analysis of the 10-year mortality data gave similar results. There was little difference in mortality of advance growth (≤15 m) white spruce among different levels of retention during both the 5- and 10-year periods (Fig. 7), but mortality increased from 5·9% at year 5 to 8·4% at year 10. Comparing mortality rates of canopy trees with that of advance growth within the same retention category, we found much higher mortality rates for canopy trees in the 10% and 20% retention compartments. This trend characterized the data from both the 5- (10%: P = 0·036, 20%: P = 0·027) and 10-year assessments (10%: P < 0·0001), 20%: P = 0·014). Mortality rates did not differ with respect to dominance status in other retention levels for either assessment.

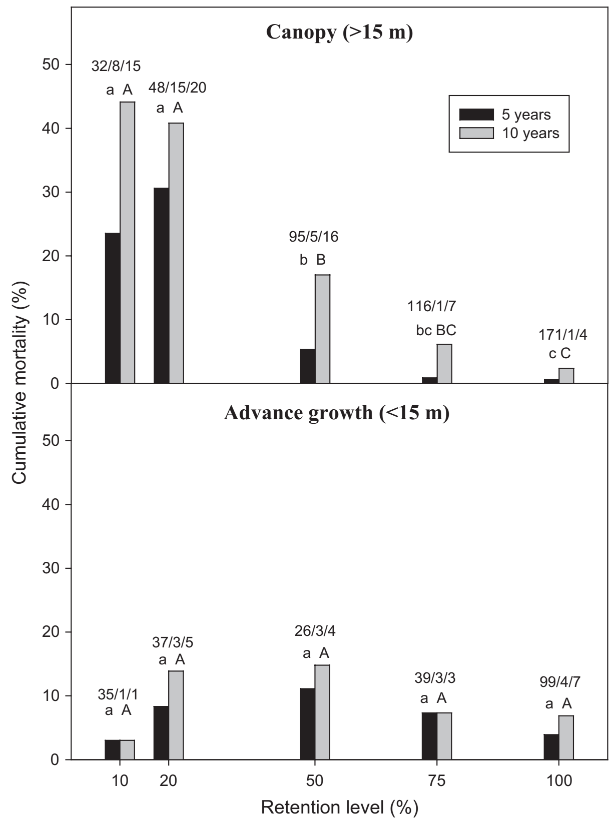

Fig. 7. Mortality by retention level for canopy (≥15 m) and advance growth (< 15 m) white spruce at 5 and 10 year post-harvest measurements within Du-stands. Letters indicated differences at $\alpha = 0.05$ of Pearson's chi-square paired comparisons. Numbers refer to total trees/frequency of dead trees per treatment at 5 years/frequency of dead trees per treatment at 10 years.

Discussion

STAND-LEVEL FEATURES: RETENTION LEVEL

Retention level was the strongest predictor of mortality for residual aspen and was also an important predictor for white spruce. In compartments with ≤20% retention levels, mortality rates over 10 years were at least double those for the 75% and 100% retentions. The high rates of mortality in the 10% retention compartments are comparable to those reported by Bladon *et al.* (2008) for both species during the period of 5 years after harvest. The highest rates of windthrow for spruce occurred within the lower retention compartments (10%, 20%), particularly in the first 5 years. These were probably due to: (i) shallower root systems (Strong & LaRoi 1983), (ii) higher drag coefficients in conifers, which remain unchanged throughout the year (Rudnicki, Silins & Lieffers 2004), and (iii) greater maximum heights for spruce compared with aspen [there were 86 (20·1%) spruce and 47 (15·2%) aspen trees ≥25 m in the harvested stands], making the spruce more prone to blowdown (Ruel 1995). In contrast, aspen were more likely to die first and remain standing as snags, especially at year 5. Increases in aspen mortality following VR harvesting may reasonably be attributed to increased susceptibility to atmospheric water stress (Bladon *et al.* 2007) and increased evaporative demand (Yao, Titus & MacDonald 2001) associated with increased wind exposure (Bladon *et al.* 2006) and/or sunscald (Shepperd 2001).

When ≥50% trees were retained, mortality observed in year 10 was significantly reduced in both species. Surprisingly, mortality rates for aspen did not differ among 50%, 75% and 100% residual treatments, either 5 or 10 years after harvest, suggesting that aspen can withstand moderate partial harvest without detectable increases in mortality. The 50% retention treatments tended to show intermediate levels of mortality for both species; however, the difference observed between this treatment and the uncut control was significant only for spruce. Thus, we observed a lower threshold for mortality than in Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco, where removal of up to 60% did not increase susceptibility to wind damage (Aubry, Halpern & Peterson 2009).

At year 5, ratios of fallen spruce trees to those dying in place were much higher in 10% and 20% (16:11) retentions than in 50%, 75% and 100% retentions (5:12). Scott & Mitchell (2005) similarly found increased rates of windthrow in harvest retentions ≤ 20%. Ultimately, any harvesting was shown to increase the proportion of blowdown in spruce at year 5 and 10 compared with numbers of trees dying as snags, as reported for other conifers (Jönsson *et al.* 2007). Our study reinforces this claim for the first 10 years following harvest, as many of the larger trees in the low residual treatments could not quickly adjust to new environmental conditions and thus died in association with windthrow. The rate of this kind of mortality remained high in the 5–10-year period after logging, which contrasts with observations of reduced mortality after 5 years (MacIsaac & Krygier 2010).

MECHANICAL DAMAGE AND TRAIL DISTANCE

Higher rates of mortality in both species occurred for trees close to machine corridors, but this effect was detectable only after 10 years and in the lower retention compartments (10% and 20%). We speculate that this delay in mortality in relation to TCD is attributable to the gradual build-up of root decay fungi such as *Armillaria ostoyae* [Romagn.] Hernik or *Armillaria sinapina* Bérubé & Dessureault; both of these species increase in spruce and aspen following logging (Whitney *et al.* 2002). Thorpe, Thomas & Caspersen (2008) also found that residual mortality rates in black spruce increased with proximity to skid trails. Interestingly, and in contrast to results from other systems (Gullison & Hardner 1993), even though a fifth of trees in our study had suffered stem damage during harvest operations, this could not be linked to mortality in either of the species. Thus, the main effect of harvesting must flow from either soil compactions, root damage or wind directly from blowdown or indirectly from greater evaporative demand.

OVERSTOREY COMPOSITION

Overstorey composition had little impact on residual tree mortality within the first 5 years. However, stand composition was important after 10 years, suggesting that impacts have more to do with post-harvest conditions than with the physical effect of harvests themselves. Residual aspen trees experienced higher mortality in the C-stands, especially in the 50% and 75% retention compartments. In C-stands, high levels of residual spruce will cast more shade on the shorter aspen (Kobe *et al.* 1995), therefore increasing carbon stress. Similarly, spruce trees < 30 m tall suffered higher mortality in the C- and Mx-stands, presumably because these smaller trees could have been already weakened through competition from taller neighbours prior to retention harvest.

The spruce in the D- and Du-stands had low mean mortality (3%) with no increases in mortality after 5 years, perhaps because these trees were in better condition prior to logging because of better light conditions under a deciduous canopy (Constabel & Lieffers 1996). Greater light would support more growth in diameter than under a spruce canopy, perhaps also making such trees more wind-firm after partial harvest (Senecal, Kneeshaw & Messier 2004).

CANOPY SPRUCE VS. ADVANCE GROWTH

In Du-stands, we found that white spruce with advanced growth (height < 15 m) experienced much lower mortality rates than did canopy spruce (≥15 m) in the 10% and 20% retention levels. In fact, Du-stands had the lowest cumulative understorey mortality rates among all stand types over both periods (2·7%). Similar results for intermediate-sized spruce were reported by Prévost, Dumais & Pothier (2010). Greene *et al.* (2002) and MacIsaac & Krygier (2010) advocate removing part of the overstorey while protecting advance growth, and the results of this study underscore the benefits of this approach.

Although MacIsaac & Krygier (2010) showed increased susceptibility of advance growth to windthrow following harvest when regeneration heights were ≥7·5 m, we found no link between height (mean height: 14·5 m) and mortality in Du-compartments. This is perhaps due to the relatively robust tree-level characteristics (67·5% PLC; slenderness coefficient: 0·9) that characterized spruce trees in the Du-stands of our study.

TREE-LEVEL FEATURES: PERCENTAGE LIVE CROWN

PLC was one of two variables included as a predictor for all models and both species; trees with high PLC had lower mortality rates (Figs 1, 4, 5 and 6). PLC is a good indicator of overall tree vigour and is often linked to growth release following harvest (Smith, Jarvis & Odongo 1997). Our data suggest that trees with larger PLC are more vigorous and able to endure wind and water stresses following harvest. The threshold at which PLC was useful for prediction of mortality, however, differed between tree species. After 5 years, mortality of aspen increased if green tree residuals had a PLC crown < 16% and < 27% PLC for spruce; after 10 years, mortality of aspen increased if PLC was < 24% and < 50% for spruce. Thus, trees with larger crowns should be favoured when legacy trees are expected to live. When selecting trees for retention, however, spruce should have longer crowns than aspen. It is noteworthy that the shade-intolerant aspen has shorter live crowns than the intolerant spruce.

TREE SIZE AND SLENDERNESS COEFFICIENT

Tall trees (≥30 m), especially spruce, were prone to higher mortality over both 5- and 10-year periods after harvest, a relationship linked to blowdown in this and other studies (e.g. Coates 1997; MacIsaac & Krygier 2010); however, there were also many large trees that died as snags. Conifers (Domec *et al.* 2009) and deciduous trees (Bladon *et al.* 2006) experience limitations in hydraulic conductivity (after attaining a certain height, and this can result in a reduction of vigour) (Yao, Titus & MacDonald 2001) after harvest.

Slenderness coefficient was not a particularly strong predictor of mortality, which is in contrast to other studies (e.g. Navratil 1996), where it is commonly used as good predictor of post-harvest survival. Only at the 5-year evaluation in the last split was there an increase in mortality in the slender trees.

OVERALL PREDICTION OF MORTALITY

Cumulatively, mortality rates across all retention levels between 10% and 75% were 16·5% for spruce and 32·9% for aspen by year 10, suggesting that these legacy elements will move rapidly into the coarse woody material pool following retention harvests. The CART analyses in the study explained 18–31% of variation in mortality. While these values may seem low, it must be remembered that accurately predicting mortality, especially in harvested stands, is a most difficult aspect of modelling stand dynamics (Kobe *et al.* 1995). The unexplained variance in these analyses could probably be attributed to some combination(s) of several broad issues. First, for each species, the CART analyses with the poorer explanatory ability had the lower overall mortality rate. Our technique only differentiates dead trees from living trees, and thus does not reflect a gradient in health that might be seen in stressed conditions (i.e. no disease or pest agents were included in these analyses). Secondly, the meteorological and physiological factors influencing tree health after partial harvest, discussed previously, are complex and need further study. Finally, susceptibility to wind throw is influenced by root diseases, soil type, landscape position and tree size, and their interactions (Ruel 1995) result in a complexity that renders prediction difficult.

Management Implications

Where live trees are needed for wildlife habitat and biodiversity goals (Work *et al.* 2010), for a decade or more after logging, residual densities ≥50% support survival of most trees over a 10-year interval and hold mortality rates at levels comparable to mortality in mature unharvested stands. In situations of lower levels of retention, longevity of residual trees may be extended by leaving 'healthier' trees at harvest. Trees with high PLC had higher rates of survival. Small- to intermediate-sized spruce had higher survival and quickly adapted to the new conditions. Also, the trees retained from deciduous-dominated stands were more likely to survive.

Our study underscores the fact that aspen dies as snags, while white spruce are more frequently blown down as green trees, contributing to ecological function as decaying logs. In our sites, mortality of residual aspen (49·6%) and residual spruce (27·0%) in the 10% and 20% retention compartments might be considered an 'operational failure' (Coates 1997) if retained trees are counted in expectation of future harvest, or if living trees are required to support stand development aims. However, such high rates of mortality may be desirable when habitat to support saproxylic biota and continued nutrient recycling is desirable.

Finally, managers may wish to consider the mortality rates in the VR harvesting systems in design of practices to protect biodiversity within forest lands. In some circumstances, it may be better to allocate the 10–20% loss in forest volume typical of VR, to a larger network of reserves or to longer rotations. Work is being performed on the EMEND landscape to evaluate the benefits to biodiversity from VR harvesting compared with these and other strategies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Tree and stand predictor variables that could alternatively be used as criteria in the RT analysis for the categorization of the 5 year post harvest residual mortality of aspen shown in Fig. 1.

Table S2. Tree and stand predictor variables that could alternatively be used as criteria in the RT analysis for the categorization of the 10 year post harvest residual mortality of aspen shown in Fig. 4.

Table S3. Tree and stand predictor variables that could alternatively be used as criteria in the RT analysis for the categorization of the 5 year post harvest residual mortality of spruce shown in Fig. 5.

Table S4. Tree and stand predictor variables that could alternatively be used as criteria in the regression trees analysis for the categorization of the 10 year post harvest residual mortality of spruce shown in Fig. 6.

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