University of Alberta

Variable Retention Harvesting: Mortality of Residual Trees and Natural Regeneration of White Spruce

by

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Abstract

In this thesis I examined the impacts of variable retention harvesting on residual tree mortality and natural regeneration of white spruce [*Picea glauca* (Moench (Voss)] in northern Alberta. The VR was done in four overstory canopy compositions (ranging from deciduous dominated to conifer dominated) and at six rates of canopy retention (2%, 10%, 20%, 50%, 75% and 100%). After 10 years there was 32.9 % mortality of aspen (*Populus tremuloides* Michx.) and 16.9 % mortality of spruce in the VR cuts. Mortality of individual trees was greater with low density of trees, in the conifer stands and for trees with short live crowns, which are large and trees near machine corridors. Natural regeneration of spruce was greatest with higher availability of seed trees (>30 ha^{-1}) and on machine corridors, where stocking reached 74%. By contrast, stocking was ≤14% on retention strips, when seed tree density was ≤11 seed trees ha^{-1}.

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Table of Contents

List of Tables

List of Figures

Abbreviations

BA	Basal Area
C	Conifer Dominated Stand
CART	Classification and Regression Tree Analysis
CLAAG	Careful Logging Around Advance Growth
CPRS	Coupe avec protection de la rénération et de sols
CWD	Course Woody Debris
D	Deciduous Dominated Stand
DBH	Diameter at Breast Height
DEM	Digital Elevation Model
DTW	Depth to Water Index
Du	Deciduous Dominated Conifer Understory Stand
EMEND	Ecosystem Management Emulating Natural Disturbance
LiDAR	Light Detection and Ranging
Log	Fresh Log Cover
MRT	Multivariate Regression Tree
Mx	Mixedwood Stand
PLC	Percent Live Crown
RDBH	Relative Diameter at Breast Height
RT	Regression Tree Analysis
TCD	Tree to Corridor Distance
VR	Variable Retention

Chapter 1: General Introduction

1.1 Boreal Forest & Disturbance

The boreal forest ecosystem is often cited as being disturbance driven, with disturbances varying in both type (e.g., fire, insect outbreak, and wind storms) and intensity (i.e., ranging from stand replacing fires to small scale wind storms affecting single trees) (Howard et al. 2004). Boreal disturbances play a significant role in the composition and species diversity of a forest, as they drive the pattern and variability of the landscape (Bergeron 2000). As a result, forest management in recent years has shifted from maximizing timber volumes by clear cutting to emulating natural disturbances (Kohm and Franklin 1997; Lieffers et al. 1996; Thorpe and Thomas 2007).

1.2 Emulating Natural Disturbance & Variable Retention harvesting

Variable retention harvesting (VR) is based upon retaining varying amounts, types and spatial patterns of living and dead trees in an attempt to address a wider array of forest management goals (Franklin et al. 1997; Mitchell and Beese 2002). By maintaining structural elements within the stand, VR harvesting can fulfill: (1) habitat requirements for various organisms (e.g., nesting sites for birds), (2) reduce the negative impacts of harvesting on biodiversity and other essential ecological functions (e.g., biogeochemical cycles) (Attiwill 1994; Bergeron and Harvey 1997; Seymour et al. 2002), and (3) provide the energetic basis to maintain heterotrophic organisms (e.g., course woody debris for saproxylic organisms) (Franklin et al. 1997; Work et al. 2010). Managing stands and forest structures similar to those created following a natural disturbance can prove to be a daunting task. Ecosystem management by emulating natural disturbances requires strategies that encompass both spatial and temporal scales (Thorpe and Thomas 2007). Furthermore, effective management must maintain both the structural and functional processes that occur following natural disturbance (Perera and Buse 2004; Long 2009).

Traditionally, clear-cuts have been thought to emulate fire disturbance; both create homogeneity within the landscape and both kill most of the trees and set the forest back to an earlier phase of succession (McRae et al. 2001). However, differences between clear-cuts and fire do exist; fires tend to leave more live and standing dead trees that can help facilitate regeneration and improve wildlife habitat (Grandhi et al. 1999; McRae et al. 2001; Thorpe and Thomas 2007). Furthermore, clear-cutting can negatively affect biodiversity levels on forested landscape (Niemelä, et al. 1993; Rosenvald and Lõhmus 2008) and is viewed with poor public perception (Hansis 1995). As a result, VR harvesting practices have gained significant recognition as a viable alternative to clear-cutting that better emulate natural disturbance (Franklin et al. 1997; Groot et al. 2005). VR offers more flexibility than clear-cutting and can generate a wider range of structural heterogeneity of both living and dead trees at varying spatial patterns (Mitchell and Beese 2002; Groot et al. 2005). Additionally, through maintenance of mature trees on the landscape VR can help accelerate species and ecological recovery following harvest (Franklin 1997; Bebber et al. 2005).

1.3 Residual Tree Mortality

Mortality of residual trees is one of the major concerns regarding VR harvesting, as early mortality of trees that are left to provide the services as green trees can undermine the entire managerial effort. Tree mortality can play a critical role in stand composition, productivity and structure (Casperson 2006; Chen et al. 2008). While mortality has been considered a stochastic and an irregular event by many (e.g., Eid and Tuhus 2001; Taylor et al. 2007), we also understand that mortality is governed by a wide range of interacting environmental, pathological, physiological and entomological factors (Yang et al. 2003). Mortality remains somewhat unpredictable due to the interaction of these factors, however it has been modeled in terms of various influencing parameters; spatiotemporal information (Taylor and MacLean 2007), species (Yao et al, 2001; Yang et al. 2003) and tree characteristics (Chen et al. 2008). Understanding tree mortality can be further complicated with the application of harvesting treatments. It is often thought that most stand-level mortality following disturbance will be initially high and then taper off once the stand structure is re-established (Volney, 1998). In reality however, since VR harvesting reduces competition between trees, one might expect reduced mortality following harvest. Thus, there is much to learn about the causes of residual tree mortality following harvesting.

Similarly to the experience of a bachelor moving in with their significant other, residual trees will be subjected to new living conditions in a VR relationship. Initially, many residual trees will experience some form of mechanical damage (e.g., crown damage, bark damage exposing the cambium, or root damage) from harvesting equipment that can reduce their survival (e.g., Moore et al. 2002; Seablom and Reed 2005). Furthermore, as a result of mechanical damage, fungal pathogens, such as root rotting fungi (e.g., *Armillaria* *ostoyae* [Romagn.] Hernik or *Armillaria sinapina* Bérubé & Dessureault) may enter a tree's living tissues following logging (Nichols et al 1993; Whitney et al. 2002; Wolken et al. 2009). Harvest will expose residual trees to abrupt changes in wind, temperature, light and humidity and ultimately these can all lead to increased mortality (Thorpe and Thomas 2007). Trees that once were sheltered are now exposed to high wind exposure increasing wind sway that could lead to increased bending possibly cavitation and reduced hydraulic conductivity (Liu et al. 2003).When harvesting plans have predetermined machine corridors/trails (i.e., machine traffic areas), trees near to these openings generally increased frequency of damage and exposure to environmental stressors (Thorpe et al.2008).

Ultimately, it is clear that some trees won't be able to adjust to the new living conditions that are created by VR harvesting, especially with high levels of tree removal. Currently, managers have relatively poor ability to judge when and where to expect high levels of mortality in VR cuts. This is partly so because most studies have only assessed mortality 2-3yrs after operations, while mortality rates are known to remain high for more than a decade (Ruel et al. 2001; Casperson 2006; Thorpe et al. 2008). Such delayed impact can lead to poor inferences about the causes of mortality. Few studies have attempted to model mortality following harvest (e.g., Karlsson et al. 2005; Kiernan et al. 2009), and most studies have been solely focused on windthrown mortality (e.g., Ruel et al. 2001; Scott and Mitchell 2005). Only a handful of studies have examined both standing and fallen dead trees (e.g., Jonsson et al. 2007; Bladon et al. 2008), although including both mortality types can provide better overall assessments of post-harvest residual tree mortality rates.

It should be noted that not all post-harvest mortality is negative, as some mortality might be considered desirable, depending on management goals. Snags (i.e., standing dead) and fallen (i.e., downed logs) have been shown to contribute to the biological legacies in a stand and have high habitat value for forest dwellers and tree regeneration (Harmon et al. 1986; Delong et al. 1997; Jacobs et al. 2007).

1.4 White Spruce Natural Regeneration

Natural regeneration and establishment of white spruce [*Picea glauca* Moench(Voss)] is one of the most pressing issues facing forest managers and silviculturists within the mixedwood boreal forests of western Canada (Peters et al. 2004). White spruce is a widely distributed boreal tree species of particular interest due to high valued end-products such as pulpwood and construction grade lumber (Lapointe et al. 2006). Many spruce seedlings must complete directly with shade intolerant and early successional species such as trembling aspen (*Populus tremuloides* Michx)), and these can inhibit regeneration following harvest (Comeau et al. 2004).

White spruce requires a number of conditions for successful natural regeneration (Lees 1972; Stewart et al. 2001):

First, a seed source must be present within the vicinity. Density of spruce seed tends to decline exponentially away from the seed source (Greene and Johnson 1996). Reliable seed dispersal is likely to be no more than ~200 m from the source tree (Youngblood and Max 1992), with most falling well within 100 m

(Martin-Demoor et al. 2010). Landscape variability can also play a significant role in seed dispersal range. For example, increased harvesting will leave fewer trees within the vicinity, limiting seed dispersal obstructions and providing higher wind speeds for further seed travel. Regeneration is further complicated by inter-annual variation of seed and cone production (Lamontagne and Boutin 2007). Large seed crops normally occur every 2-6 years (Nienstaedt and Zasada 1990; Stewart et al. 2001) but intervals between crops can be as long as 12 years (Wurtz and Zasada 2001). This masting behavior of white spruce is important for explaining some of the apparently stochastic nature of white spruce regeneration following disturbance (Peters et al. 2005; Martin-Demoor et al 2010).

Second, a receptive seedbed is required in order for white spruce seedlings to establish successfully (e.g., Calogeropoulos et al. 2004). A typical seed bed for successful germination and root penetration is one that maintains low porosity where water can rise freely via capillary action and where light availability is moderate to high (Greene et al. 1999). White spruce seedlings often do well on elevated or moisture-retaining exposed mineral soil, and well-decomposed rotten (nurse) logs (Delong et al. 1997; Calogeropoulous et al. 2004). These substrates are common following disturbance, such as fire (Kemball et al. 2006) or harvest where soils are disturbed mechanically (Wurtz and Zasada 2001). Feathermosses (Nienstadt and Zasada 1990) and recently-fallen logs reduce the likelihood of successful regeneration by reducing the availability of ideal substrates. Many obstacles exist when seedbed substrates are considered for white spruce as leaf litter can be fatal if the germinant is not tall enough or stout enough to push through the litter and win exposure to sunlight (Koroleff 1954; Simard et al. 2003).

Third, a suitable microclimate is the next factor needed for successful regeneration of white spruce. Unsuitable microsites may include those with low incoming light (< 8%), high herbaceous competition, extensive deciduous leaf cover and/or are frequently too dry (Groot 1999). Overstory canopy composition can play a significant role in the availability of light, nutrients, pH and litter quality (van Pelt and Franklin 2000; Macdonald and Fenniak 2007) and these factors can negatively impact regeneration rates of white spruce. Conifer dominated canopies provide shade through out the year, creating a much cooler environment (Fenniak 2001) and low light in the understory, while broadleaf canopies dominated by aspen provide warmer environments with higher light transmission during leaf-off periods (Constabel and Lieffers 1996).

Finally, limiting interspecific competition from other boreal forest trees species (e.g., aspen) (e.g., Lieffers et al. 1996) and grass (e.g., Cater and Chapin III 2000) can also increase survival rates of spruce. Removing or reducing the cover of these early-successional competitors can enhance nitrogen uptake, photosynthetic rates and growth in seedlings in terms of height and basal area (Cater and Chapin III 2000). In some circumstances, however, cover of other vegetation is important in reducing frost during the growing season (Groot 1999).

1.5 Studies to Date

Most VR studies to date have primarily focused on the impacts of leaving residual trees on the biodiversity of stands during the period immediately after logging. Studies have focused on mammals (Sullivan and Sullivan 2001; Fisher and Bradbury 2006), beetles (e.g., Jacobs et al. 2007), birds (e.g., Lance and Phinney 2001; Atwell et al. 2008), understory plant communities (e.g., Craig and Macdonald 2009) and mineral nutrition in the soil (e.g., Lapointe et al. 2006). Most of these studies have suggested a positive response to VR systems, however long term persistence of biodiversity remains in question because there have been fewer studies of the long-term influence of trees in these systems. Thus, research to determine which retention intensities will best maintain residual trees or regenerate the next stand of trees is crucial to meet sustainable forest management goals. In terms of the trees, forest managers should have answers to the following questions: at what retention intensity is survival of residual trees optimized? How long do mortality rates of residual trees remain high after VR? Is regeneration of spruce affected by the VR harvesting systems?

1.6 Research Objectives

In this thesis I evaluate the impacts of a VR harvesting system in the boreal mixedwood forest of northern Alberta a decade following logging. In the first study I identify the tree and stand characteristics that influence mortality of aspen (*Populus tremuloides* Michx.) and white spruce trees following variable retention harvesting. These were assessed in relation to: (1) overstory canopy composition, (2) harvesting intensity, (3) tree characteristics, (4) temporal scale: five and ten year post-harvest periods, (5) type of mortality (i.e., standing dead, fallen dead).

In the second study I assessed the natural regeneration of white spruce under a range of overstory retention densities, in different types of overstory canopy compositions and different densities of seed trees. I compared natural regeneration within machine corridors (passive site preparation) to residual interiors, and competition from trees, shrubs and grasses. I also described the efficiency with which residual seed trees contribute to stand stocking through natural recruitment of seedlings.

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Chapter 2: Mortality of residual trees 10 years after variable retention harvest in the boreal forest

2.1 Introduction

In recent decades variable retention (VR) harvesting has gained popularity as an alternative to clear-cutting (Franklin et al.1997; Groot et al. 2005; Thorpe and Thomas 2007). The goal of VR harvesting is to retain a wide range of structural heterogeneity of living and dead trees at varying spatial patterns and retention intensities (Zenner 2000; Mitchell and Beese 2002; Groot et al. 2005). VR harvesting attempts to emulate or recreate the various landscape patterns that occur following a natural disturbance (e.g., fire, wind, insect outbreaks) (Franklin et al. 1997). By maintaining mature trees on the landscape, it is thought that managers can protect biodiversity through provision of legacy elements and accelerate recovery of species and ecological processes following harvest (Franklin 1997; Bebber et al 2005). Furthermore, retaining overstory trees can reduce the stresses of higher wind speeds, increased temperature and increased vapor pressure deficit, factors which are often important issues following harvest (Ruel, 1995; Liu et al. 2003; Heithecker and Halpern, 2007). Nonetheless, these stresses can severely reduce the likelihood of survival of residual trees (Man and Lieffers 1999; Bladon et al. 2006; Kreutzwelser et al. 2008).

Tree mortality plays a critical role in mediating stand composition, productivity and structure (Casperson 2006; Chen et al. 2008). Although mortality is often viewed as a stochastic and an irregular event (Eid and Tuhus 2001; Taylor et al. 2007), it is influenced by a wide range of interacting environmental, pathological, physiological and entomological factors (Yang et al. 2003).

Mortality processes are also affected by harvest prescriptions and their application. For example, residual trees are often mechanically damaged during harvest (e.g., Ostrofsky et al.1986; Moore et al. 2002) and trees located near to areas of machine traffic have been noted to have increased mortality rates (Thorpe and Thomas 2008).

Most post-harvest studies focused on residual tree mortality have been concerned only with fallen mortality (e.g., Ruel et al. 2001; Scott and Mitchell 2005), while few studies have examined both standing and fallen dead trees (e.g., Walter and Maguire 2004; Jonsson et al. 2007; Bladon et al. 2008). Furthermore, most studies have assessed mortality only 2-3yrs after operations; however, mortality rates may remain high for more than a decade (Ruel et al. 2001; Casperson 2006; Thorpe et al. 2008). To our knowledge, no studies have measured residual tree mortality in more than one forest canopy type and there is little published work about multiple retention intensities (Walter and Maguire 2004; Man et al. 2008; Prévost et al. 2010). While a small number of studies have attempted to model tree characteristics that can lead to increases in mortality (e.g., Yao et al. 2001; Yang et al 2003), fewer still have attempted to model mortality following a harvesting practice; e.g., selection harvesting in uneven hardwood stands (Kiernan et al. 2009) and multiple thinning regimes (Karlsson and Norell 2005).

2.1.1 Study Objectives

Our main objective was to identify the stand and tree level characteristics that influence mortality of aspen (*Populus tremuloides* Michx.) and white spruce

[*Picea glauca* (Moench (Voss)] trees following VR harvesting. Potential factors assessed were (1) pre-harvest overstory canopy composition, (2) harvesting intensity, (3) distance to machine corridors, (4) tree characteristics, (5) temporal scale: five and ten year post-harvest periods because these have been commonly supposed to strongly influence postharvest survival (see references above). We also sought to determine how type of mortality (i.e., standing and fallen dead) was affected by these factors.

2.2 Methods

2,2,1 Study Area

Research was conducted at the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment located in the Lower Boreal-Cordilleran ecoregion (Strong and Leggat, 1992) of northern Alberta, Canada (56°44'N-56°51'N and 118°19W-118°27'W). The area is categorized by a continental climate with large differences in mean monthly temperatures (-18°C for January and 16°C for July).Mean annual precipitation is approximately 470mm, with most of the precipitation falling during the growing season (370mm from May to September) (Environment Canada, 2009). Site elevation ranges from 677m to 880 m above sea level, with a predominantly subhygric or mesic soil moisture regime primarily on Luvisolic soils (Kishchuk, 2004).

2.2.2 Experimental Design

The forest used for the EMEND experiment was subdivided into compartments, each approximately 10 ha in size, selected on the basis of overstory species composition. Overstory canopies in relatively homogeneous stands were categorized as: deciduous dominated with >70% of basal area composed of aspen and/or balsam poplar (D), deciduous dominated with a conifer understory with at least 40% stocking of advance growth below the main canopy (Du), mixed conifer and deciduous with ~30-70% of basal area composition of deciduous and conifer (Mx), and conifer dominated >70% of basal area composed of conifer – mostly white spruce (C). Each compartment was randomly assigned to one of 5 variable harvest intensities: 10%, 20%, 50%, 75% and 100% residual (control). There was also a typical clear-cut treatment with 2% retention included in the experiment but mortality rates could not be reliably estimated on clear-cuts for the time frames used in this study because the number of trees was too low. Thus, our study includes 5 variable harvest intensities, 4 overstory canopy compositions and 3 replicates of each combination, so that mortality was assessed over 60 compartments.

The harvesting treatments were carried out in the winter of 1998-99, using a feller buncher, in combination with a grapple skidder. A systematic harvesting pattern was used within compartments: 5 m wide machine corridors were spaced every 20 m (center to center), while 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 the machine corridors and by prescription (e.g., every 4th tree encountered) a randomly selected number of trees (no size bias) within the retention strips to reach desired retention level (note: 75% residual treatments were achieved by removal of trees only within the machine corridors).

Immediately following logging, six permanent tree plots (measuring 2x40 m) were randomly established in the compartment and were laid out perpendicular to the machine corridors. A total of 360 plots were established (Volney *et al.*, 1999).

2.2.3 Data Collection

All aspen and white spruce with a diameter at breast height (1.3 m) (DBH) ≥ 5.0 cm within the permanent plots were located and permanently tagged in the spring of 1999 prior to the growing season. Each tree was assessed for status (living, standing dead or fallen dead), DBH (cm), height (m), height to base of live crown (m), distance of the tree to the nearest machine corridor (tree-to-corridor distance (TCD) (m) (i.e., distance from germination point of the tree to the edge of the closest machine corridor edge), presence (yes/no) of mechanical damage (e.g., crown damage, bark missing-cambium exposed). Trees were re-measured after five and ten years in the late summers of 2003 and 2008. Height and canopy measurements were made with a vertex IV and transponder T3 (Haglof, Sweden©).

2.2.4 Data Analysis

Only trees surviving the harvest of 1998-99 were considered in this analysis. In addition to the variables directly measured in the field, some additional variables were calculated: individual tree basal area (BA), percent live crown ratio (PLC) as crown length/height, slenderness coefficient as height / DBH, relative size of 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, a transect 'wetness' index was assessed. In the spring of 2008 wet areas were mapped within the EMEND landscape using light detection and ranging (LiDAR) information. LiDAR was used to determine flow channels, wet and dry areas, and cartographic depth-to-water index (DTW) derived from the Alberta provincial bare-ground digital elevation models (DEM) [please see Murphy et al. (2009) for detailed methodology].The final wetness map was validated in the field using GPS tracking of wetland boarders and permanent/intermittent streams. Using ArcMap v. 9.3 (Environmental Systems Research Institute., Inc. Redlands, CA, USA) the wet areas map were subdivided into 4 wetness classes: (4) 0-10 cm (hydric), (3) 10-25 cm (sub-hydric), (2) 25-50 cm (mesic), (1) 50-75 cm (sub-mesic), (0) 75+ cm (xeric). The final image was rectified as a grid with a 1 m resolution (i.e., 1 m^2 cells). Each of the permanent transects were then geo-referenced and overlaid on the wet areas map to attribute a single mean wetness value to the entire transect distance.

Data for white spruce and aspen were analyzed separately. The mortality over two time intervals after logging was determined: (1) for the 5 year interval, spring 1999 (prior to growth) to the late summer of 2003, (2) for the 10 year interval, spring of 1999 to late summer of 2008. We also calculated basal area growth over the second period (note: only trees alive at 5 years were used, and the start was based on 2003 tree measurements).

Mortality of individual trees was linked to tree and site variables using classification and regression tree analysis (CART). The technique can be used to analyze causal relationships in ecologically complex, non-parametric data that may involve high-order interactions (Breiman et al., 1984; De'ath and Fabricus 2000; De'ath 2002). Furthermore, the CART analysis makes no assumptions about the form of relationships between species and their environments (e.g., that data are normally distributed), which is often an issue with parametric statistical analyses. In general terms, CART analysis produces dichotomies where similar mortality responses of a species in relation to environmental factors are clustered together and those that are different are split apart. Splitting is done repeatedly in a hierarchical scheme until dissimilarities are minimized. A Euclidian distance measure was used to determine dissimilarity. Classification and regression tree analysis were implemented using the mvpart library (Therneau and Atkinson 2009) for the R programming environment v.2.7.2 (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 useful statistical tools for pruning and cross-validation. 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 (Breiman et al. 1984; De'ath and Fabricuous 2000).

Secondly, contingency tables were used to determine statistical differences in tree mortality as a function of: (1) overstory canopy composition, (2) overstory retention intensity, (3) canopy (≥15 m) and advance growth (<15m in height, non-merchantable) spruce by retention intensity and (4) mechanical damage with TCD. A Pearson's chi-square statistic with a significance level of $\alpha = 0.05$ was used for all contingency analyses. The analysis was implemented using the R statistical base package v.2.7.2 (The R Foundation for Statistical Computing, 2008).

2.3 Results

2.3.1 Aspen

2.3.1.1 Five Year Assessment

Mortality of residual aspen, 5 years post-harvest, was explained in terms of the factors considered by a five-leaf regression tree (i.e., leaf refers to each terminal node within the tree). This tree explained 18% of total variance (Figure 2.1). Mortality was most influenced by overstory retention intensity, where lower intensities (i.e., 10%, 20%) had a pooled mortality rate of 28.3% (n=120) compared to a pooled mortality rate of 9.5% in the 50%, 75% levels of retention (n=189). Mortality at lower retention intensities was further explained by PLC, where trees with ≥24% live crown ratios experienced lower rates of mortality (15.9%, n=63) than those with smaller PLC (<24%) (42.1%, n=57). Mortality in trees with larger PLC was then split by DBH; both trees with ≥50 cm DBH died but among smaller trees (DBH<50cm) mean mortality rate was 13.1% (n=61). Tree height provided the lone split within higher retentions (50% and 75%); both trees ≥31m in height died, but few of the shorter trees died (mean mortality rate = 8.6%, n=187) (Figure 2.1).

Contingency table analyses of mortality by retention intensity after 5 years gave results similar to the MRT (Figure 2.2). Much higher mortality occurred within lower retentions (10%: 28.3% mortality and 20%: 26.8% mortality) compared to the significantly lower mortality within higher levels of retention (50%: 13.9% mortality, 75%: 6.3% mortality and 100% [uncut]: 10.0% mortality) (Figure 2.2). Most aspen trees died as snags (87.2%). There were no differences in mortality among the various canopy compositions for aspen within the first 5 years (Figure 2.3).

2.3.2.2 Ten Year Assessment

A six-leaf tree best described the residual mortality of aspen 10 years after retention harvesting; this explained 21.1% of total variance (Figure 2.4). Retention intensity was the most influential variable, as in analysis of the data after 5 years.

Lower retentions (10% and 20%) experienced more than twice (50%, n=120) the mortality rates observed in the higher retention compartments (22.2%, n=189). Mortality at lower retentions was further split by PLC; trees with <16% live crowns experienced high rates of mortality (92.9%, n=14) and trees with larger crowns had substantially reduced mortality rates (44.3%, n=106) within the lower retention cuts. Within larger PLC (≥16%), TCD provided the final split; trees within 5.85 m of the corridor were more likely to die (53.4%, n=73) than those found further away (24.2%, n=33).

Within the higher retentions (50% and 75%), overstory canopy 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 to trees with greater PLC (28.0%, n=25) (Figure 2.4).

Aspen mortality in the 10 years after logging was highest within the lower retentions (10%: 47.2%; 20%: 52.2%) (Figure 2.2) compared to a mean mortality rate of 21.8% in the higher retentions (50%, 75% and 100%). By year 10, 41.8% of all dead aspen across all retention intensities had fallen. Furthermore, fallen dead aspen were significantly greater over the second re-measurement period (2003-2008: 21 fallen trees) than in the first measurement period (1998-2003: 8 fallen trees) (p=0.008). Aspen mortality was significantly higher within the C-stands (52%) than Du (29%) and D-stands (28%) but not significantly higher than the Mx-stands (36%) (Figure 2.3)

2.3.2 White Spruce

2.3.2.1 Five Year Assessment

White spruce mortality 5 years after retention harvesting was best described by a five leaf tree that explained 25.2% of total variance in spruce mortality (Figure 2.5). Height provided the best indicator of mortality, where trees with a height ≥30 m were more likely to die (39.1%, n=23) than trees <30 m (7.4%, n=405). For the trees ≥30 m in height, retention intensity provided the lone split.

Mortality rates within 10% and 20% (72.7%, n=11) were substantially higher than those within 50% and 75% retentions (8.3%, n=12). For trees with a height <30 m, PLC provided the first split. Trees with a live crown <27% experienced considerably higher mortality rates (50%, n=10) than did those of trees with longer crowns (≥27%) (6.3%, n= 395). Tree slenderness provided the lone split within <27% live crowns. Trees with a slenderness coefficient ≥1.04 (i.e., “slender”) all died (n=5), while trees with slenderness coefficient <1.04 (i.e., stouter) all survived (n=5).

Mortality of white spruce was sensitive to retention intensity. Mortality was 15.5% in the 10% retention and 21.7% in the 20% retention (Figure 2.2) compared to <3% in the higher (75% and 100%) retention compartments (Figure 2.2). In the first 5 years, 47.7% of the dead trees had fallen within lower retentions (10% and 20%: mean of 11.1%) than higher retentions (50%, 75%, and 100%: 0.73%). Spruce mortality did not differ among the C, Mx and D compartments, but mortality differed significantly between C (14.0%) and Du-stands (2.7%) (Figure 2.3).

2.3.2.2 Ten Year Assessment

Mortality of white spruce residuals 10 years after harvesting was explained by a six-leaf tree that explained 31.1% of total variance (Figure 2.6). As in the 5-year analysis for spruce, height was the best indicator of mortality 10 years post harvest. Larger trees (≥30m) were more than 5 times more likely to die (75%, n=20) than shorter trees (<30m) (13.7%, n=408). Mortality of shorter trees was further split by canopy composition. Spruce within D or Du stands had lower rates of mortality (2.8%, n=141) than those found within C and Mx-stands (19.5%, n=267). Within the C and Mx-stands, retention intensity provided the first split, where as there was lower mortality (11.9%, n=194) in the higher retentions (50%, 75%) compared to the lower retention compartments (29.7%, n=73). Within the 10 and 20% retentions, trees closer to the machine corridors (<3.5m), were more than twice as likely to die (63%, n=25) than trees further (≥ 3.5m) from the corridor (27.1%, n=48). Death rates of trees further from the corridor were additionally explained by PLC. Trees with a short live crown (<50%) experienced more mortality (60%, n=15) than did trees with long live crowns (>50%) (12.1%, n=33) (Figure 2.6).

Retention intensity had a large impact on spruce mortality. Mortality was highest within the 10% (27.6%) and 20% (29.4%) treatments, declined moderately in the 50% (16.5%) and was significantly lower in the 75% (6.5%) and control (4.1%) treatments (Figure 2.2). Most dead trees within harvested stands (68.4 %) had fallen by year 10. Astonishingly, spruce experienced no significant increase in fallen mortality 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 that spruce mortality was much higher within the C (26.0%) and Mx-stands (20.3%) than in the Du (2.7%) and D-stands (3.3%) (Figure 2.3). There was little further spruce mortality in the second re-measurement period in either Du or D compartments (Figure 2.3).

2.3.3.3 Canopy & Advance Growth

Mortality of white spruce in the canopy (≥15m tall) in the first 5 years, was 18% higher within the two lower retention cuts (10%: 23.5%; 20%: 30.6%) than in the 50% retention (5.3%) and 75% (0.9%) and controls (0.6%) (Figure 2.7). Results were similar for the 10 year mortality data. Mortality of advance growth ($\leq$15m) white spruce appears to have been higher in the 20% and 50% retention levels (Figure 2.7) but, given these sample sizes, there were no statistically significant differences in mortality across the different residual levels (mean mortality at 5 years: 5.9% and 10 years: 8.4%). When we compared mortality rates of canopy trees with that of advanced growth within the same retention intensity, mortality rates were much higher for canopy trees only in the 10% and 20% retention compartments (Figure 2.7). These were found for both the 5 (10%: $p=0.036$, 20%: $p=0.027$) and 10 year (10%: p=<0.0001), 20%: $p=0.014$) assessments. There were no differences in mortality rate with respect to dominance status in other retention intensities at either the 5 or 10 year assessment.

2.3.4 Residual Growth

2.3.4.1 Aspen Residual Growth

Aspen mortality was assessed over the second re-measurement period with basal area increment included as a possible predictor of mortality during the first five years. A 3-leaf tree explained 8% of total variance (Figure 2.8). Annual basal increment growth provided the root node, where trees that had low growth (<1.374 cm^2/year) were more than 3 times more likely to die (47.2%, n=36) than those that grew more ($\geq$1.374 cm^2/year: 14.9%, n=222). The only other split was determined by canopy composition within the larger basal area growth group. Residual aspen within C and Mx-stands experienced 4 times the mortality rate (35.6%, n=45) of those found within D and Du-stands (8.6%, n=177).

2.3.4.2 White Spruce Residual Growth

Spruce mortality during the second interval, with the incorporation of basal area increment growth during the first five years, was explained by a two-leaf tree that explained 14.6% of total variance (Figure 2.9). The lone split was explained by height where taller trees (≥31m) were 11 times more likely (61.5%, n=13) to die than those that were shorter (<31m) (5.6%, n=373). Thus, growth during the previous 5 years appeared to have no effect on spruce mortality in this experiment.

2.4 Discussion

2.4.1 Stand Level Features

2.4.1.1 Retention Intensity

The strongest predictor of mortality for both species was the level of residual cut. In stands with ≤ 20% retention levels mortality rates were at least double the rates of the 75 and 100% cuts over the 10 years. These results are comparable to those of Bladon et al. (2008) for both species during the period of five years after variable retention harvest in which 10% of trees were retained. Lower retentions were also associated with higher rates of windthrow for spruce, likely due to: (1) a shallower rooting system (Strong and La Roi 1983), (2) higher drag coefficients in conifers, which remain unchanged throughout the year (Rudniki et al. 2004) and (3) the maximum obtainable heights for spruce was greater than the aspen, making the spruce more prone to blowdown (Ruel 1995). In contrast, aspen trees were more likely to remain standing after death and the cause of death was likely related to water stress (Bladon et al. 2007), and increased evaporative demand (Yao et al. 2001) as a result of increased wind speeds (Bladon et al. 2006).

When ≥50% trees were retained, mortality rates at year 10 were significantly reduced in both species. Surprisingly, mortality rates for aspen did not differ between 50, 75 and 100% residual treatments, either 5 or 10 years after harvest, suggesting that aspen can withstand moderate partial harvesting without detectable increases in mortality. The 50% retention treatment 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 threshold for mortality higher than that found in Douglas fir where removal of up to 40% did not increase wind damage (Aubry et al. 2009).

At year 5, the ratios of fallen spruce trees to those dying in place were much higher in the 10% and 20% (16:11) retentions than in the 50%, 75% and 100 % retentions (5:12). This is similar to the findings of Scott and Mitchell (2005) that found the rate of windthrown trees was reduced when retentions are maintained at ≥ 20%. Ultimately, increased harvesting will lead to increased exposure to wind and an increase in susceptibility to being fallen dead (Beese and Bryant 1999; Jonsson et al. 2007). Our study reinforces this claim for the first 10 years following harvest, as some trees can't adjust quickly enough to new environmental conditions that are created and amplified with increasing harvest intensities. This was especially evident at the lowest retention harvests.

2.4.1.2 Mechanical Damage and Trail Distance

In both species trees close to machine corridors had higher rates of mortality, but this effect was only detectable after 10 years. However, we point out that the TCD was a significant predictor of mortality only in the lower retentions (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 which are noted to increase following logging (Nichols et al 1993; Whitney et al. 2002; Wolken et al. 2009). Growth of root rot could be exacerbated by stress related to increased wind speed or high vapor pressure deficit in stands harvested to low retention prescriptions. Interestingly and in contrast to results from other systems (e.g. Gullison & Hardner 1993), even though a fifth of trees in our study had stem damage, this could not be linked to mortality in either of the species. Thorpe et al. (2008) also found that residual mortality rates in black spruce increased with proximity to skid trails (7.35m).

2.4.1.3 Overstory Canopy Composition

Overstory canopy composition had little impact on residual tree mortality within the first 5 years; however, there was some importance of stand composition after 10 years. Residual aspen had higher mortality in the C and Mx stands in the 50 and 75% residuals. In C and Mx-stands this high level of residuals will cast more shade on the shorter aspen (Kobe et al. 1995; Lieffers et al. 1999), therefore increasing carbon stress. Similarly, spruce trees < 30 m tall suffered higher mortality in the C and Mx-stands, presumably because of lower light. The spruce in the D and Du-stands had low mean mortality (3%) with no increases in mortality after 5 years, perhaps reflecting greater light in the leaf-off periods (Constabel and Lieffers 1996). Greater light would support more diameter growth than under a spruce canopy, perhaps also making such trees more wind-firm after partial harvest (Senecal et al. 2004). Another possible reason for increased mortality in the C and Mx-stands was that they tended to be wetter (mean site wetness values: C = 0.76, Mx = 0.96, vs. Du = 0.57 and D = 0.26), thus potentially increasing the susceptibility of the trees to windthrow (Ruel 1995).

2.4.1.4 Advance Growth Protection

In the deciduous-dominated stands with a conifer understory, we found that the white spruce advance growth (height <15m) experienced much lower mortality rates than canopy spruce (≥15 m). In fact, Du-stands had the lowest cumulative mortality rates of all stand types over both periods (2.7%). Similar results for intermediate sized spruce were reported by Prevost et al. (2010). The CLAAG (careful logging around advanced growth) or CPRS (Coupe avec protection de la rénération et de sols) (e.g., Ruel 2000; Greene et al. 2002; Chen and Wang 2006) approaches and understory protection logging (Navratil et al. 1994) have all advocated removing part of the overstory while protecting advance growth. These methods have been moderately successful with survival of advanced regeneration ranging from 32% to 80% (MacDonnell and Groott 1997; Greene et al. 2002).

Although MacIsaac and Krygier (2010) recently 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 trees in our study (discussed below). It has generally been suggested that small trees (<10cm DBH) will experience higher rates of mortality due to their reduced competitive ability (Oliver and Larson 1996; Taylor and MacLean 2007); however, we did not find such a relationship, likely due to increased exposure to light following the removal of overstory canopy trees.

2.4.1 Tree Level Features

2.4.2.1 Percent Live Crown (PLC)

Percent live crown (PLC) was one of two variables that modeled as a predictor for all models. For both aspen and spruce, we showed that trees with high PLC had lower mortality rates (Figures 3.1, 3.4, 3.5, 3.6). PLC is a good indicator of overall tree vigor often linked to growth release following harvest (Smith et al. 1997; Ruel et al. 2000), and for this reason it is included in growth and forest health models (Monserud and Sterba, 1999). Our data suggest that trees with larger PLC are vigorous enough to endure wind and water stresses following harvest. Thus, trees possessing larger crowns should be strongly considered for buffer zones to help minimize wind exposure and potentially reduce post-harvest residual mortality rates.

2.4.2.2 Tree Size

Tall trees (≥30 m), especially spruce, were prone to higher mortality over both 5 and 10 year periods, a relationship generally found in other studies (e.g., Coates 1997; Ruel et al. 2003). Conifers experience limitations in hydraulic conductivity (e.g., Domec et al.2009) after attaining a certain height, and this can result in reduction of vigor (Yao et al 2001) after harvest. Furthermore, risk of windthrow generally increases once trees reach 10 to 12 m in height (Ruel et al. 2003; MacIsaac and Krygier 2010). Our study reinforces these findings as windthrown mortality rates were found to increase with increasing height (mean windthrown height = 22.2 m).

Residual aspen with large DBH (≥50cm) were found to be more prone to mortality, although this was only a weak relationship (n =2). Large aspen are vulnerable to similar risk factors as tall trees (see discussion above). In addition, spruce residual mortality was linked with tree slenderness at 5 years. Rudniki et al. (2007) suggested that stouter trees limit stem oscillations that can damage xylem and this tendency may help to reduce sway during wind events that can lead to windthrow following harvest (Bladon et al 2008).

2.4.2.3 Growth

Basal area increment during 1998-2003 weakly predicted aspen mortality during 2003-2008. Residual aspen with basal area increment ≥1.374cm^2/year had a pooled mortality rate 1/3 that of trees that had grown more slowly. This is consistent with suggestions that shade intolerant species are likely to die if their growth rate falls below some minimum level (Kobe et al. 1995, Senecal et al. 2004). Growth was, however, not a useful predictor for mortality of the shade tolerant spruce at EMEND. This may likely be due to the delay in growth exhibited by spruce in response following partial harvest. For example, Youngblood (1991) showed spruce growth lagged for 2 years but then increased up to 164% eight years after a shelterwood cut. This presumed delay in growth for conifers could contribute to a weak relationship between growth and mortality, especially within the first 5 years.

2.4.2.4 Unexplained Mortality

The best model for residual tree mortality within this study explained only 31.1% of the variability in tree mortality (Figure 2.6), while the poorest model explained a mere 18% (Figure 2.1). This poses the question, what is causing the 68.9-82.0% of unexplained mortality within the residual tree mortality models? There are likely a number of contributing factors (e.g., soil-tree interactions, weather and metrological) that may provide further explanation of the unexplained mortality in these systems. Potentially it could be attributed to the following: (1) in all models (Figures 2.1, 2.4-2.6) ‘leaves’ with the lowest mortality rates possessed the highest number of residual trees (e.g., Figure 2.5, where 395 trees [92.2% of total trees] had a mortality rate of 6.3%, which amounts to 25 trees). These tended to be the higher retention intensities and thus, we find most of the unexplained mortality occurring within these ‘leaves’. (2) No disease and/or pest agents were included in the mortality models. Including disease and or pest parameters may provide an increase in the amount of mortality occurring within these trees.

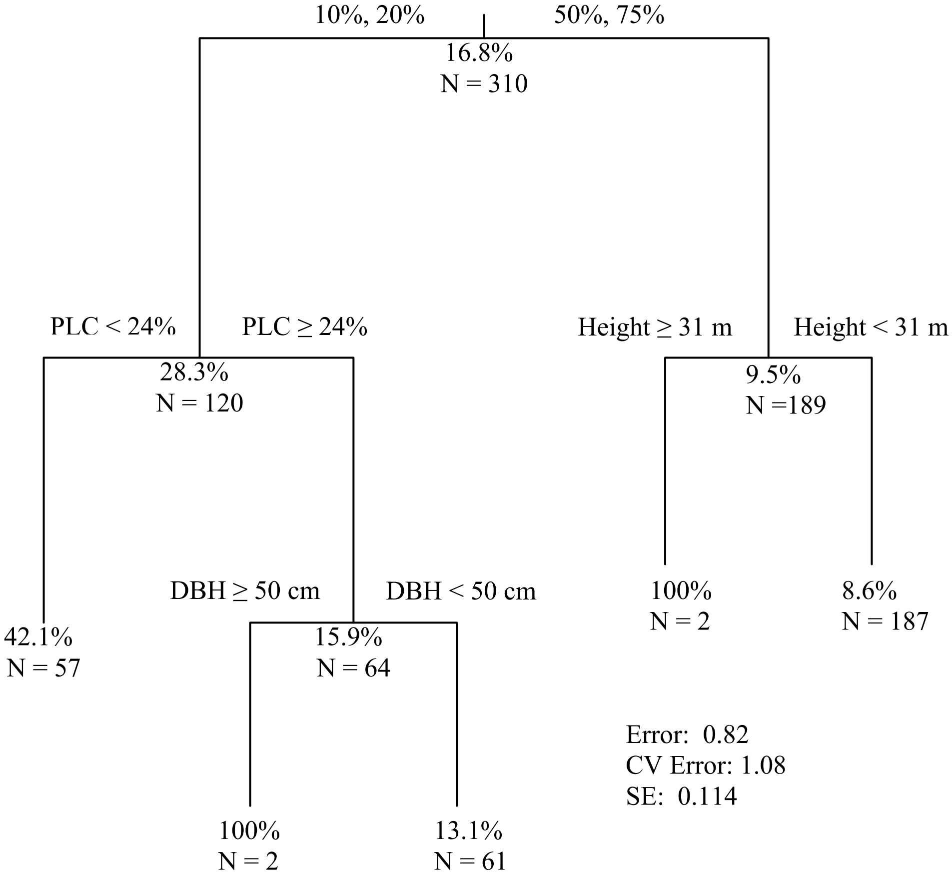

Figure 2.1 Regression tree analysis of % mortality of residual aspen trees 5 year after variable retention harvest. The explanatory variables considered were residual intensity, percent live crown (PLC), height and DBH. This tree explained 18% of the total variance and the vertical depth of each split is proportional to the variation explained.

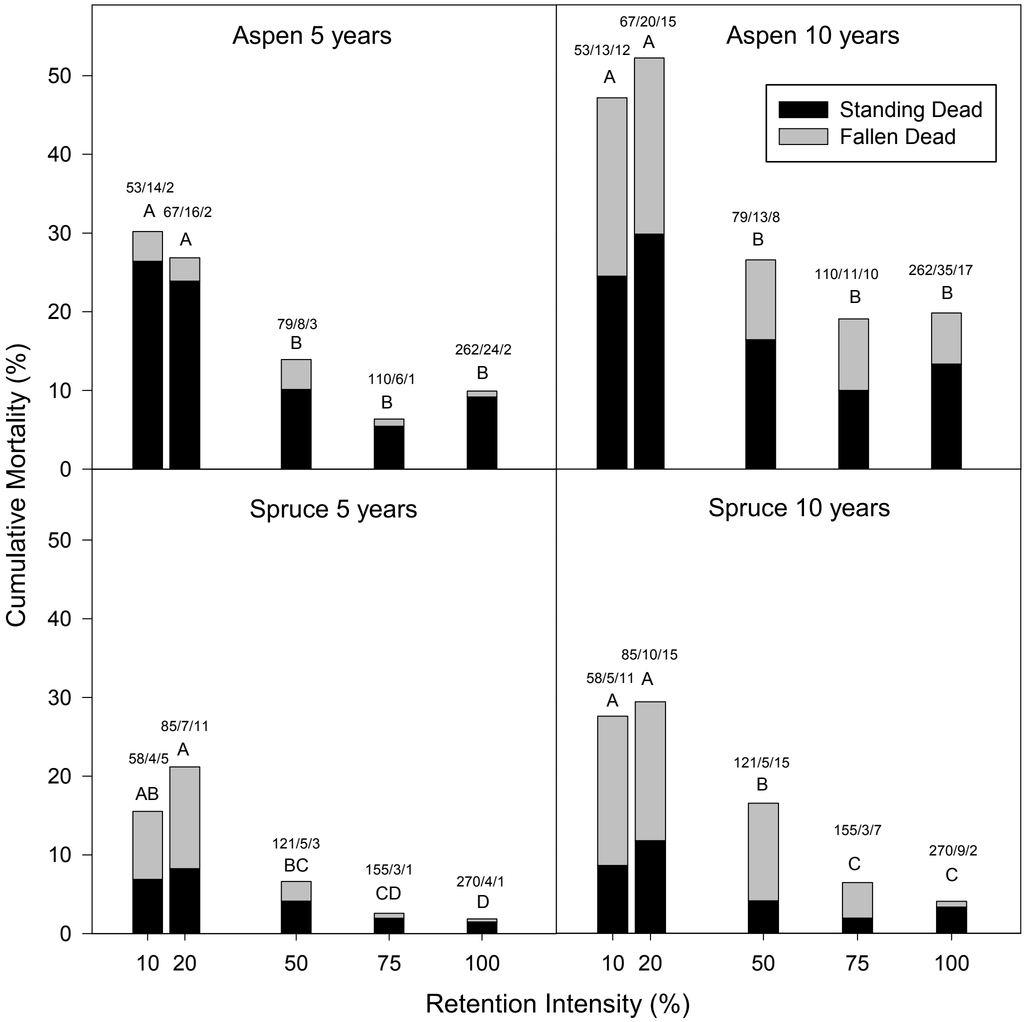

Figure 2.2 Aspen and white spruce residual tree cumulative mortality by retention intensity, for 5 and 10 years post-harvest and type of dead (fallen and standing). Cumulative mortality bars with different letter are significantly different at α =0.05, Pearson's chi square paired comparisons. Numbers refer to the frequency of total trees/standing dead/fallen dead per treatment.

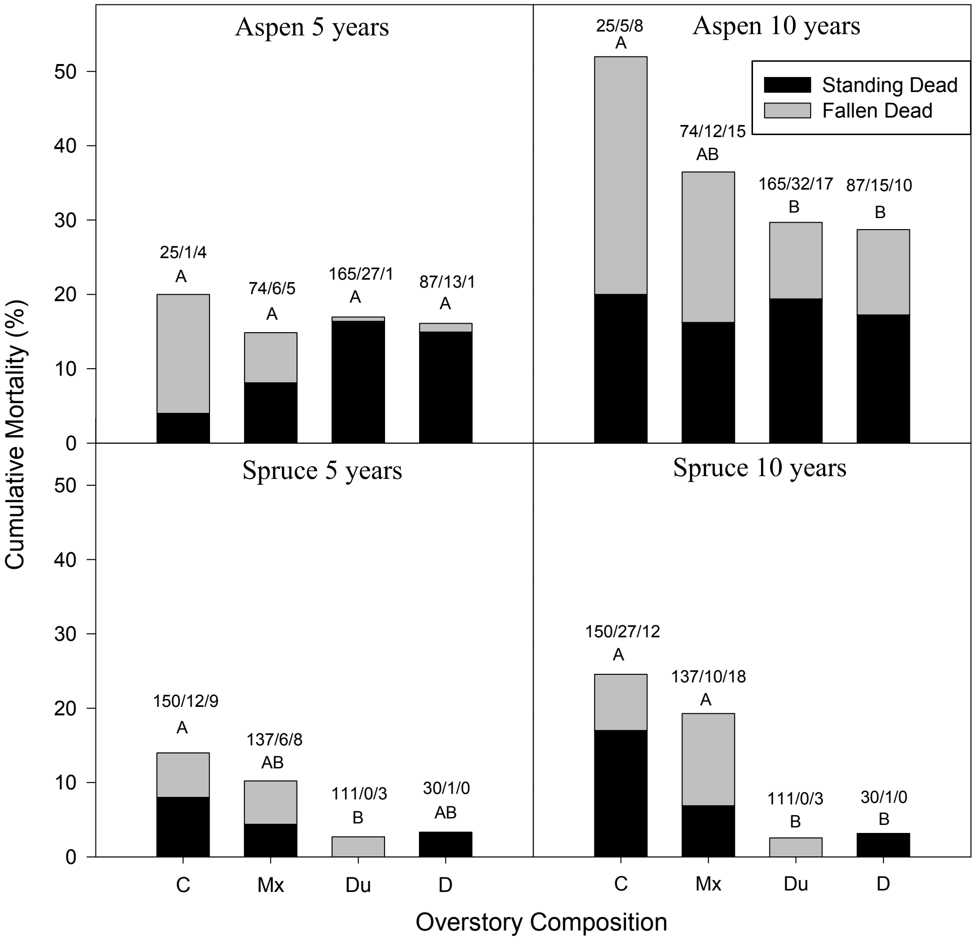

Figure 2.3 Aspen and white spruce residual tree cumulative % mortality by overstory composition for 5 and 10 years post-harvest and type of dead (fallen and standing). Cumulative mortality bars with different letter are significantly different at α =0.05, Pearson's chi square paired comparisons. Numbers refer to the frequency of total trees/standing dead/fallen dead per canopy composition.

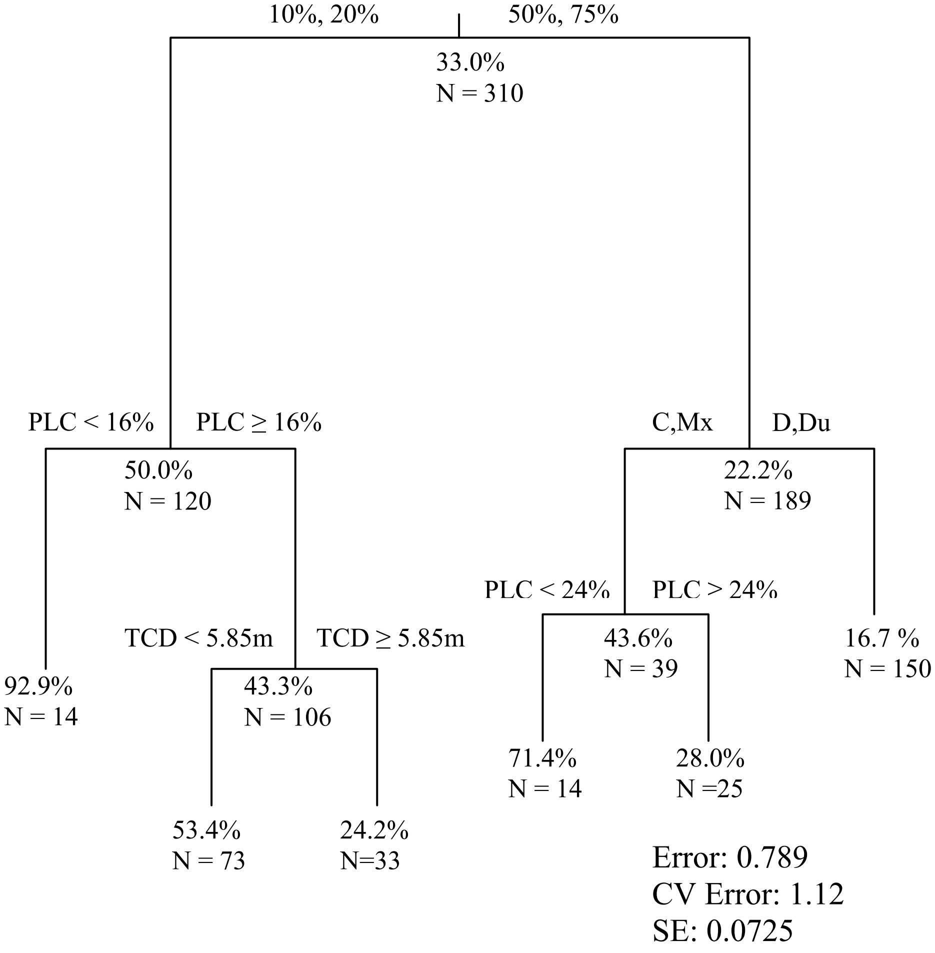

Figure 2.4 Regression tree analysis of % mortality of residual aspen trees 10 year after variable retention harvest. The explanatory variables considered were residual intensity, percent live crown (PLC), overstory canopy composition and tree to corridor distance (TCD). This tree explained 21.1% of the total variance and the vertical depth of each split is proportional to the variation explained.

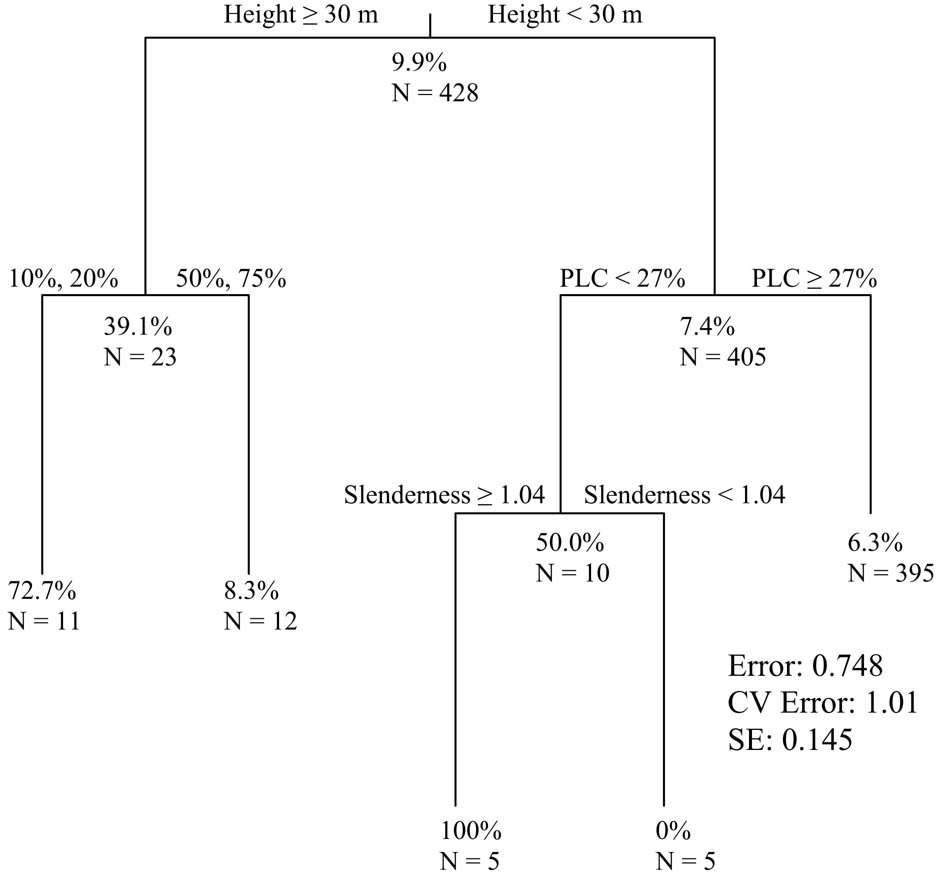

Figure 2.5 Regression tree analysis of % mortality of residual white spruce trees 5 year after variable retention harvest. Regression tree analysis of 5 year residual status (% mortality) of spruce from the 10, 20, 50 and 75% residual intensities. The explanatory variables considered were height, residual intensity, percent live crown (PLC) and bole slenderness. This tree explained 25.2% of the total variance and the vertical depth of each split is proportional to the variation explained.

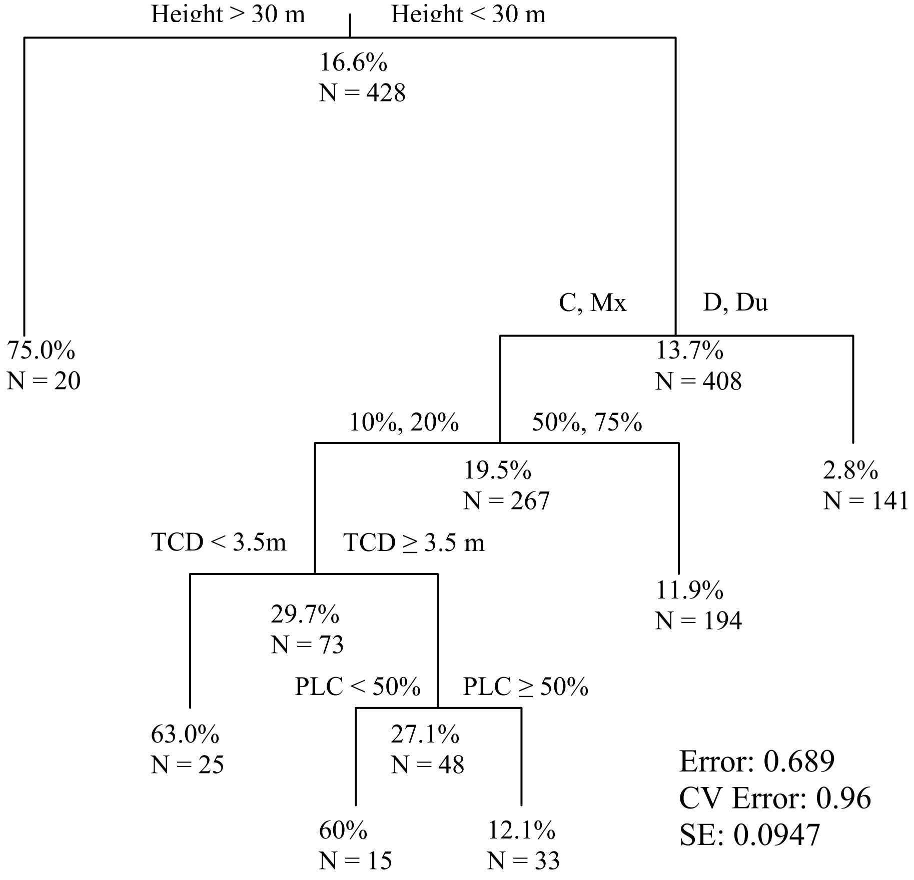

Figure 2.6 Regression tree analysis of % mortality of residual white spruce trees 10 year after variable retention harvest. The explanatory variables considered were height, overstory canopy composition, residual intensity, tree to corridor distance (TCD) and percent live crown (PLC). This tree explained 31.1% of the total variance and the vertical depth of each split is proportional to the variation explained.

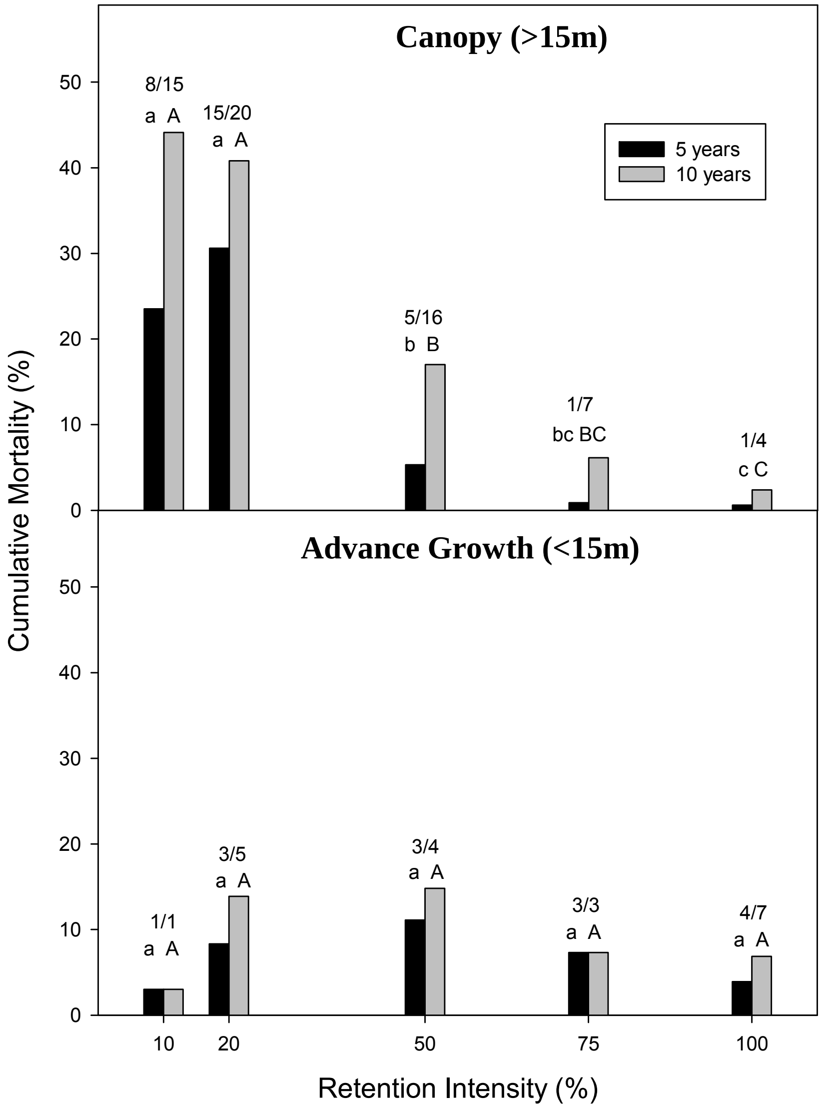

Figure 2.7 Mortality by retention intensity for canopy (≥15m) and advance growth (<15m) white spruce at 5 and 10 year post-harvest measurements within Du-stands. Letters indicated differences at α =0.05 of Pearson's chi square paired comparisons. Cumulative mortality bars with different letter are significantly different at α =0.05, Pearson's chi square paired comparisons. (Note: lower case letters compare the 5 year mortality rates, while capital letters compare rates 10 years after harvest. Numbers refer to the frequency of dead trees per treatment.

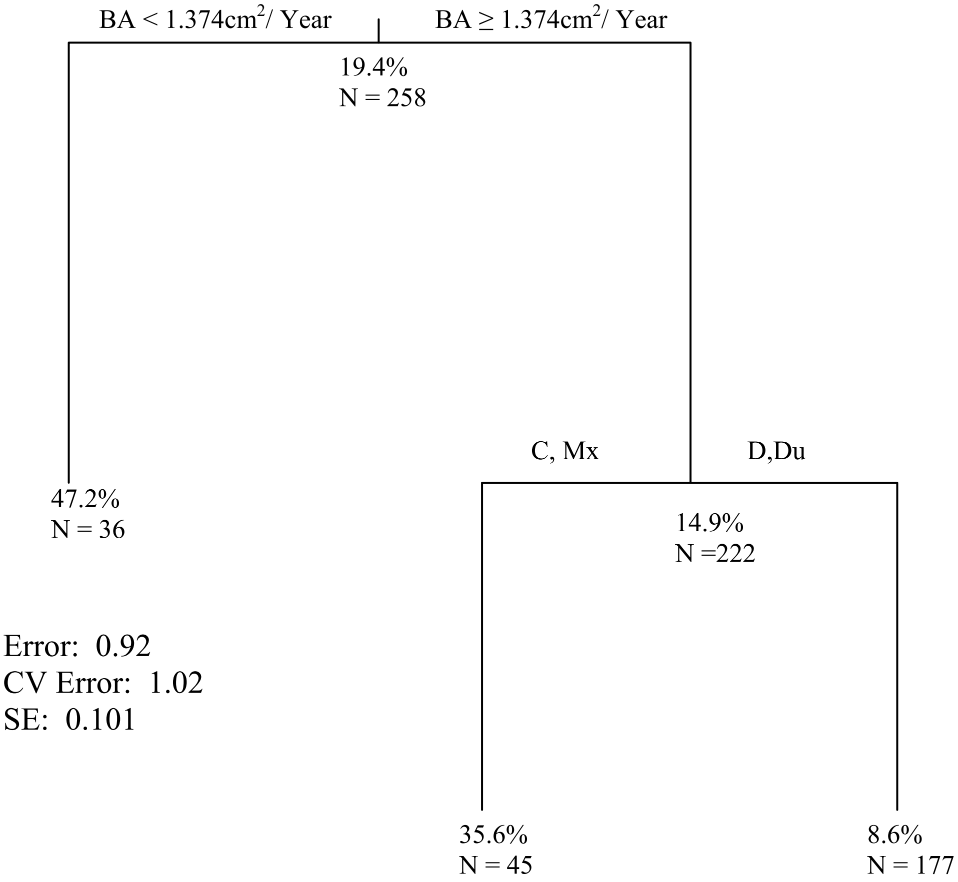

Figure 2.8 Regression tree analysis of % aspen mortality over the second re-measurement period with basal area increment included after variable retention harvesting. The explanatory variables considered annual basal area increment growth and overstory canopy composition. This tree explained 8% of the total variance and the vertical depth of each split is proportional to the variation explained.

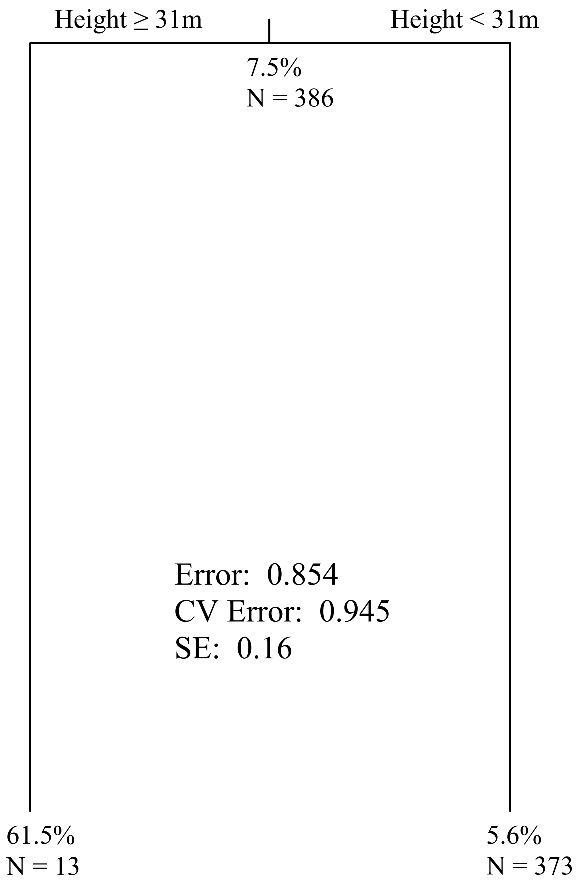

Figure 2.9 Regression tree analysis of % white spruce mortality over the second re-measurement period with basal area increment included after variable retention harvesting. The lone explanatory variable considered of height. This tree explained 14.6% of the total variance and the vertical depth of each split is proportional to the variation explained.

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Chapter 3: Seed tree density, variable retention and stand composition influence recruitment of white spruce in boreal mixedwood forests[1]

3.1 Introduction

Over the last decade, Canadian forest managers and silviculturists have increasingly used variable retention (VR) harvesting systems as an approach to sustainable forest management that attempts to emulate natural disturbances (Mitchell and Beese 2002; Bladon et al. 2008). VR leaves living and dead trees in harvested areas to imitate residual trees and forest structure left after natural disturbance (Hunter 1990). However, VR has not been well studied in terms of its ability to produce conditions suitable for natural regeneration of white spruce [*Picea glauca* (Moench (Voss)] on an operational scale in the boreal forest.

Natural regeneration of white spruce is extremely variable and a number of conditions must be met for successful regeneration: (1) a seed source, (2) receptive seedbed, (3) suitable microclimate and (4) limited competition from other vegetation (Lees 1972; Stewart et al. 2001). Even when a seed source is present, the extent of regeneration is difficult to predict. Optimal seed crops normally occur every 2-6 years (Nienstaedt and Zasada 1990; Stewart et al. 2001) but intervals between crops can be as infrequent as 12 years (Wurtz and Zasada 2001).

Several specific factors are known to affect regeneration. Seedbed type, for example, can strongly affect whether or not seedlings establish successfully

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(e.g., Delong et al. 1997; Stewart et al. 2001; Calogeropoulos et al. 2004). Leaf litter can be an important obstruction to white spruce regeneration, proving fatal if the germinant is not tall enough or stout enough to push through the litter and win exposure to sunlight (Koroleff 1954; Simard et al. 2003). Feathermosses and (Nienstadt and Zasada 1990) recently-fallen logs can also reduce the likelihood of successful regeneration by reducing the availability of ideal substrates. However, at the same time elevated or moisture-retaining exposed mineral soil and well-decomposed rotten (nurse) logs prove to be ideal substrates for survival of white spruce seedlings (Delong et al. 1997; Calogeropoulous et al. 2004).

Overstory canopy composition also affects availability of nutrients, pH and litter quality (van Pelt and Franklin 2000; Macdonald and Fenniak 2007). Conifer dominated canopies often provide shade through out the year, creating a much cooler environment (Fenniak 2001) and low light in the understory, while broadleaf canopies dominated by aspen provide warmer environments with higher light transmissions during leaf-off periods (Constabel and Lieffers 1996). Inter-specific competition from other boreal forest trees species (e.g., aspen) (Lieffers et al. 1996) and grass (Cater and Chapin III 2000) can also reduce survival rates of spruce. Removal or reduction in coverage of these early-successional competitors can enhance nitrogen uptake, photosynthetic rates and height and basal area growth in white spruce seedlings (Cater and Chapin III 2000).

Most studies of white spruce regeneration have been at a relatively small scale, focusing on receptive seedbeds (Delong et al. 1997; Simard et al. 2003; Wang and Kemball 2005), seed dispersal (Galipeau et al. 1997; Stewart et al.

1998; Lamontagne and Boutin 2007) and understory competition (Cater and Chapin III 2000). While there have been studies that considered the effects of harvest intensity by shelterwood (Man and Lieffers 1999; Wurtz and Zasada 2001; Prévost and Pothier 2003; Lapointe et al. 2006) and variable retention (Calogeropoulos et al. 2004; Martin-Demoor et al. 2010), most have been limited to one forest stand type. Few studies have looked at the impact of stand composition on natural regeneration (e.g., Groot 1999; Legaré et al. 2002), and to our knowledge, the present study is the first investigation of white spruce natural regeneration to be performed at an operational scale (~750 ha).

3.1.1 Study Objectives

We evaluated natural regeneration of white spruce under a range of overstory retention densities, in different types of overstory canopy compositions and different densities of seed trees. We compared natural regeneration within machine corridors (passive site preparation) to residual interiors, and competition from trees, shrubs and grasses. We also described the efficiency with which residual seed trees contribute to stand stocking through natural recruitment of seedlings.

3.2 Methods

3.2.1 Study Area

This study was carried out at the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment located 90 km north-west of Peace River in Alberta, Canada (56°44’N-56°51’N and 118°19’W-118°27’W). The site is part of the Clear Hills Upland Ecoregion within the Boreal Plains Ecozone

(Wiken 1986) and ranges from 677m to 880 m above sea level, with a predominantly subhygric or mesic soil moisture regime on primarly Luvisolic soils (Kishchuk 2004). The EMEND site has a continental climate with mean temperatures of -18°C for January and 16°C for July, and a mean annual precipitation of 470mm (Environment Canada 2009).

3.2.2 Experimental Design

The EMEND landscape was partitioned, prior to harvest, into relatively uniform sections with similar canopy species composition in four categories: (1) deciduous dominated (D) (>70% of basal area composed of aspen and/or balsam poplar), (2) deciduous dominated with a conifer understory (Du) (at least 40% stocking of advance growth below the main canopy), (3) conifer dominated (C) (>70% of basal area composed of conifer – mostly white spruce), (4) mixed C and D (Mx) (~30-70% of basal area composition of deciduous and conifer). In total there were 18 compartments allocated to harvest or as controls for each overstory composition, each approximately 10 ha in size. Each compartment was randomly assigned to one of the 6 variable retention treatments: 2% residual (clear-cut), 10%, 20%, 50%, 75% and 100% residual (control). Thus, in total there were 4 overstory canopy compositions, 6 overstory retention levels and 3 replicates for a total of 72 compartments.

Harvesting was done in the winter of 1998/1999, using a feller buncher and grapple skidder combination. The partial harvests were done using a systematic pattern, i.e., 5 m wide machine corridors (skid-trails) spaced every 20 m (center to center), while retaining a 15 m wide retention strip between machine corridors. All machine corridors and retention strips were orientated in a north-south direction, perpendicular to prevailing wind direction; this was done to help reduce wind-throw. The 75% residual treatment was comprised of machine corridors only, while in the other harvesting treatments, trees were removed in the retention strip to achieve desired levels of stem retention, with no bias for size or species. There were no well-defined machine corridors in the clear-cut treatments.

3.2.3 Data collection

Immediately after logging, 6 permanent transects (2m x 40m) were randomly established within each of the 72 compartments, for a total of 432 transects. These transects were established in an east-west orientation, perpendicular to the machine corridors in order to intersect 2 machine corridors and 2 retention strips (Volney et al. 1999). In May 2009 (10 years following harvest), 8 circular plots of 10 m^2 were established in two lines running parallel with each transect, 5 m north (4 plots) and 5 m south (4 plots). Two plots in each transect were centered on the machine corridors and two plots were centered in the retention strips. Within each plot we collected the following data: (1) number of white spruce seedlings (minimum of 10 cm in height, ≤ 10 years (based upon whorl counts), (2) maximum height of tallest white spruce seedling within each of the eight, 10 m^2 plots, (3) grass cover (%), (4) deciduous cover (%), including juvenile aspen and balsam poplar and shrub species [mainly *Alnus crispa* (Ait.) (Pursh), *Salix* spp., *Viburnum edule* (Michx.) Raf., *Rosa acicularis* Lindl., *Shepherdia canadensis* (L.) Nutt. and *Rhododenron tomentosum* (Stokes)], (5) cover of decayed logs (CWD) (decay classes: 4-7, Mills and Macdonald 2004), and (6) cover of fresh logs (Log) (decay classes: 1-3, Mills and Macdonald 2004). The overstory basal area of the individual transect was used as a way of specifically assessing retention in the vicinity of the transect (Volney, pers, comm).

The first seedling (minimum height of 10 cm and ≤ 10 whorls) found at the transect was collected. Although there was a potential to collect 432 seedlings, some transects had no regeneration thus only 342 seedlings were sampled. Seedlings were measured for: (1) height (cm), (2) root collar diameter (mm) and (3) age. Seedlings were aged by taking thin sections of the stem at the estimated root collar and at 1 cm above and below. Sections were mounted on microscope slides and rings were counted using a compound microscope. Data were used to estimate the error in estimation of age in the field, and secondly, to determine the time of recruitment of white spruce seedlings after harvest.

Aerial photographs were taken of the study area in late June 1999, during the first summer following harvest; a total of 158 photos at a 1:5000 scale were taken. Photographs were printed on AMKTOP 30, Topar A3, 304.977mm film using a KL clear, AGFA color H100 filter. Photos were then scanned individually using a Scanmaker 1000XL Microtek 6400x3200 DPI 48Bit color scanner at 1200DPI and tagged in image file format. Using ArcMap v. 9.3 (Environmental Systems Research Institute., Inc. Redlands, CA, USA) these images were geo-referenced by linking image features to spatially referenced transport, utility, hydrology and forest pattern vector layers. The image was then rectified as a grid.

Polygons were then created for each image and extraneous information was clipped from each photograph.

Mosaics were then created from the clipped grids. GPS coordinates of permanent tree plots were established on the photos. A 60 m buffer zone was overlayed on the mosaic around each transect; within this oval plot (1.5 ha^{-1}) all white spruce trees with potential to supply seed for regeneration of the eight subplots were counted. The basis for selecting seed trees were: (1) tree color (conifers being darker), (2) shape (conifers have a conical shape both in terms of vertical view and shadows), (3) canopy dominance: trees were selected if they displayed a clear crown visually and if they appeared to be in a dominant position in comparison to their neighbors (edge trees often allowed for a clear view of crown length allowing for inferences about canopy tree height). It was difficult to distinguish white spruce from other conifers, however, balsam fir (*Abies balsamea* (L.) Mill) and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) together comprise <1% of total tree species in the EMEND compartments, based upon permanent sample plots. The black spruces of adjacent peatlands were easily distinguishable from upland spruce in photographs based upon their narrow crowns. Final seed tree selections were verified and cross referenced by field data about trees (and their sizes) located on and near the permanent sample plots.

3.2.4 Data Analysis

3.2.4.1 Compartment Level Analysis

Compartment level analyses provided a ‘macro-scale’ assessment of regeneration at the scale of the ~10 ha cutting compartment, as is relevant to forest managers. Data from the six transects, each with eight plots, were averaged for each compartment prior to analysis (n=3). A fully randomized, 4x6 factorial design with four overstory canopy composition treatments (D, Du, Mx, C) and six overstory retention treatments (2%, 10%, 20%, 50%, 75% and 100%) was used to analyze seedling density, seedling maximum height and stocking rate (i.e., percentage of 10 m^2 plots within each compartment with at least one spruce seedling). In order to accurately represent seedling density and stocking over the entire compartment, densities and stocking were weighted based on area represented (i.e., corridor x 0.25, interior x 0.75 were added together to estimate the average for the compartment). Since data for seedling density and stocking rates did not meet the assumptions of normality and homogeneity of variance, an inverse transformation ($1/(x+1)$) was applied. In addition, the response surface between density or stocking and level of retention intensity were tested against first, second and third degree polynomials.

A split plot analysis (Appendix B) was performed to incorporate environmental variables (i.e., those reflecting inter-specific competition) with regards to the corridor and residual interiors. The Tukey-Kramer test at a significance level of $\alpha = 0.05$ was used for all post-hoc comparisons among treatment means. At the compartment level all data were analyzed using the mixed procedure (proc mixed) in SAS v.9.2 (SAS Institute Inc., Cary, NC, USA).

3.2.4.2 Transect Level Analysis

Transect level *analysis* provides a 'micro-scale' assessment of regeneration and incorporates the site parameters of corridor and interior in partially harvested compartments (i.e., 10%, 20%, 50%, 75% retention). This subset of data contained the average of 4 regeneration plots for corridors and the 4 for interiors from each transect, giving a total of 576 data points [i.e., 6 transects x 48 compartments x 2 site parameters (corridor and interior)].

Heterogeneity of variance simply precluded use of parametric statistics for assessment of seedlings at the transect level. Regression trees (RT) are well-suited for data exploration when there is severe heterogeneity of variance (De'ath 2002), such as characterized our compartment-level data. In short, RT analysis produces dichotomies in a hierarchical manner, where environmental variables that produce similar predictions of the dependant variable are clustered together and those that are different are split apart. Analyses were performed for each of the dependent variables: seedling density, maximum height and stocking rate. A Euclidian distance measure was used to determine dissimilarity. All data were analyzed using R v.2.10.1 (The R Foundation for Statistical Computing) and the mvpart library (Therneau and Atkinson 2009). Tree selection was determined by 1000 cross-validations interactively using the 'pick' option. Appropriate and final tree selection was further reassured by using the 1-SE (standard error) error rule, whereby selection of the best tree is performed within one standard error of the minimum (De'ath and Fabricius 2000).

The ability of seed trees (within 60 m of the regeneration transects) to produce regeneration in various overstory residual intensities was assessed by using the Chapman-Richard's function (Sit and Poulin-Costello 1994). The stocking % (S) was described in relation to the number of seed trees (T):

$$S = a\,(1 - e^{-bT})^{c} \qquad \text{Eq. 1}$$

Parameters a, b and c were estimated using non-linear regression (proc NLIN) in SAS. A constant of 0.001 was added to both stocking % and seed trees for all measurements in order to include zero values in fitting the Chapman-Richard's function. The estimated parameters were then used to calculate the stocking % per number of residual seed trees by overstory retention intensity for (1) the average stocking (weighted by corridor and interior - see methods above) and (2) stocking within corridors only.

3.3 Results

3.3.1 Seedling Age

In terms of age structure, there were two clear peaks in recruitment: at ages 9 (year 2000: 1 year post harvest, n=97) and 7 (2002: 3 years post-harvest, n=125) (Figure 3.1). A total of 10 of the 342 seedlings were older than 10 years old, indicating that ~3% of seedlings that were considered to be 10 years old or less, based upon whorl counts, were actually older. Astonishingly half of the misclassified seedlings were from the unharvested compartments.

3.3.2 Compartment Level Analysis

Seedling densities showed a significant quadratic decline with retention intensity (p=0.0006) (Figure 3.2); however, only the control had significantly lower densities than all other retention intensities. In terms of maximum height, seedlings found in C-stands (34.2cm tall) and Mx stands (30.7cm) were significantly (p = 0.0002, Table 3.1) taller than those in D-stands (22.8cm), but these were not significantly (p = 0.0772) taller than those found in Du-stands (26.9cm) (Figure 3.3). Surprisingly, average seedling height was not significantly affected by the retention intensity (p = 0.1591, Table 3.1).

Stocking rates were lowest in D-stands (20.8%) compared to the cutting units from the other overstory compositions: C-stands (43.0%), Du-stands (38.5%), and Mx-stands (30.5%) (Figure 3.3). Similarly to seedling densities, stocking rates gradually declined (following a quadratic form) with retention intensity. The highest stocking rates occurred in the clear-cuts (53.7%) and the lowest rates within control compartments (7.8%) (p = <0.0001) (Figure 3.2).

No environmental variables (e.g., grass or deciduous competition) provided significant explanation of seedling densities, height or stocking, nor were there significant interactions among effects of any of these variables. Corridors had (1) twice the mean grass coverage (corridor: 24.9%, interior: 11.7%; p= <0.0001, Tables B1) and (2) somewhat higher deciduous cover (corridor: 67.9%, interior: 64.3%; p= 0.0177, Table B2), while the interiors had

(1) higher cover of CWD (corridor: 4.3%, interior 6.5%; p=<0.0001) and (2) cover of Logs (corridor: 6.3%, interior 9.5 %; p=<0.0001). C-stands had the highest mean grass coverage (25.6%), nearly twice that found within D-stands (13.6%) (p=0.0202). Deciduous cover was influenced by overstory retention intensity (p=0.0210) and compartments with lower retention (i.e., 2%, 10%, 20%) had higher mean cover than those with higher retention (50%, 75%, 100%) (Respective averages: 73.2% vs 54.9%). Overstory canopy composition significantly impacted cover of both CWD (p=0.0075) and Logs (p=0.0168). C and Mx-stands had at least three times more CWD (7.0%) than D-stands (2.0%). Log cover was highest within the Mx-stands (10.6%) and lowest within Du-stands (5.0%).

3.3.3 Transect Level Analyses

The RT analysis for seedling density produced a six-leaf tree (i.e., leaf refers to each terminal point within the tree) that explained 50.5% of total variance within transects across all overstory retention compartments (Figure 3.4). Seedling density was most influenced by the corridor/interior dichotomy, as it provided the root node (6.42 seedlings per 10 m^2 in corridor plots, n=288 and vs. 0.93 seedling per 10 m^2 interior plot, n=288) (Figure 3.4). The second split was within the corridor group and related to overstory canopy composition where there were 14.4 seedlings per plot in C-stands (n=72) compared to 3.77 (n=216) in the group of D, Du and Mx-stands. The third split occurred within the D, Du, Mx group and was determined by the number of seed trees; if there were fewer than 32 seed trees ha^{-1}, seedling density was low (1.07, n=104) and increased 6-fold

(6.28, n=112) in the group with seed tree density greater than 32 ha^{-1}. The fourth split was within C-stands concerning seed tree densities, where transects with <70 seed trees ha^{-1} had low seedlings per plot (4.79, n=30) and if transects had >70 seed trees ha^{-1}, density went up nearly 5-fold (21.2, n=42) (Figure 3.4). The final split occurred within transects with >70 seed trees, where the highest overall seedling densities (28.1 seedlings per 10 m^2, n=26) occurred within plots with lower levels of basal area retained (<32.5 m^2 ha^{-1}).

The regression tree for seedling height explained 18.6% of the variance with a three-leaf tree (Figure 3.5). The first split was determined by overstory canopy composition where seedlings were shorter in the D and Du-stands (25.2 cm, n=190) compared to those in C and Mx-stands (34.1 cm, n=212). Data from the C and Mx-stands were further split into interior and corridor; maximum height of seedlings in the interior were 25.9 cm (n=87) compared to 39.8 cm in the corridor (n=125).

For stocking rates a six-leaf regression tree explained 43.2% of total variance (Figure 3.6). Stocking was low (22.7%, n=226) when there were <30 seed trees ha^{-1} but was 2.5-fold higher (54.6%, n=350) with ≥30 seed trees ha^{-1}. The group with <30 seed trees ha^{-1} was further split by seed tree numbers per ha^{-1}, above and below 11; stocking was low (14.1%, n=110) when seed trees ha^{-1} were <11 and double (30.8%, n=116) when there were ≥11 seed trees ha^{-1}. Stands with ≥30 seed trees ha^{-1} were further split by interior or corridor position. The interiors had lower stocking (35.4%, n=175) compared to the corridors (73.7%, n=175). The final split of the interior group was based on residual density. Stocking was low (13.8%, n=49) within the 75% residuals and nearly 3-fold higher in the 10%, 20% and 50% residuals (43.8%, n=126). Stocking rates were similarly affected by overstory residual intensities within the corridors; stocking in the 75% residuals was low (56.1%, n= 49) compared to the stocking in the 10%, 20% and 50% retention corridors (80.6%, n=126) (Figure 3.6).

3.3.4 Efficiency of seed trees

The increased stocking observed with increase in seed tree density was steepest in the clear-cuts (Figure 3.7). Retention of only 5 seed trees ha^{-1} produced an average of 59% stocking within the clear-cuts, which was substantially higher than in any of the partial harvest compartments (Table 3.2). Thus, stocking tended to reach higher levels in the clear-cuts, 10% and 20% retentions, while the average stocking peaked at less than 40% in the 75% retention. There was, however, substantial variation in the data (Figure 3.7). When considering only the corridors of the partial cut treatments, stocking level increased substantially at a given seed tree density relative to the average stocking of both corridors and interiors (Table 3.2). Nonetheless, these stocking rates in corridors of partially harvested compartments, at a given density of seed trees, still tended to be lower than in clear-cuts.

3.4 Discussion

3.4.1 General Findings

This study is the first to simultaneously assess a range of factors [e.g., overstory canopy composition, variable retention level, competing vegetation (grass and shrub cover) and concentration of seed trees] that might affect success of white spruce regeneration on an operational scale. It showed that regeneration ten years after harvest: (1) was greater with high numbers of seed trees within 60 m, (2) was greater on machine corridors when the local site had been disturbed at harvest, and (3) was reduced when canopies were dominated by deciduous species (apparently because these sites had few seed trees). Furthermore, stocking was quite high within clear-cuts, even with low numbers of seed trees.

3.4.2 Compartment Level

Surprisingly, there was little benefit to spruce regeneration density or stocking from any of the different levels of partial harvest (Figure 3.2). In fact, clear-cuts had higher levels of stocking at low levels of seed trees compared to compartments with higher retention levels (Figures 3.2 and 3.7; Table 3.2). This is in contrast to the common belief that it is difficult for spruce to establish in clear-cuts (Steill 1976; Greene et al.1999; Wurtz and Zasada 2001; Prévost and Pothier 2003) because of inadequate microclimatic conditions (Man and Lieffers 1999).

White spruce is considered to be intermediate or moderate in shade tolerance (Nienstadt and Zasada 1990). In a controlled experiment on the EMEND site growth of planted white spruce was actually best under 50% retention in the D-stands and showed a decline in growth both in the clear-cuts or conditions with more shading (Gradowski et al. 2008), findings consistent with the idea of moderate shade tolerance for white spruce. We speculate that white spruce was able to establish well in the clear-cuts in our operational scale study for two reasons. First, the increased area of forest floor scuffed by the passive site preparation from skidding increased the area of receptive seedbeds compared to the defined machine trails. Machine scuffing of the forest floor appears to have been sufficient to remove the top layer of feathermoss or leaf litter that can inhibit regenerative success and expose a suitable seedbed of mineral soil (e.g., Delong et al. 1997; Calogeropoulos et al. 2004). Second, given that most of the seed was cast 1 or 3 years after harvest (Figure 3.1), there was sufficient time for some grass and deciduous cover to develop; this cover might have provided protection from extreme temperatures and high vapour pressure deficit (Groot 1999) on completely exposed sites. Thus, in this operational-scale experiment, increased receptivity of seedbeds seemed to the most important variable for establishment; the importance of micro-environmental conditions could not be assessed directly.

Seedling densities were lowest in the D-stands (Figure 3.3); likely because these had the fewest seed trees (average of 37 seed trees ha^{-1} over all the retention intensities). We saw no evidence; however, that seedling recruitment differed between conifer seedbeds (with feathermosses) and deciduous seedbeds (with leaf litter) if seed tree density was similar. Thus, exposure of mineral soil or decomposed organic layers may be more important to successful regeneration than the nature of the ground-layer vegetation.

Among seedlings that did establish within D-stands, maximum height within a 10 m^2 plot was 10 cm shorter than those seedlings within the C-stands. This contrasts with results of Gradowski et al. (2008) showing that planted spruce grew best in the D-stands at EMEND. D-stands are likely less shaded (Constabel and Lieffers 1996; Messier et al. 1998) and had warmer soils (Macdonald and Fenniak 2007) than C-stands, and thus higher temperatures should have increased growth of seedlings in D-stands. The most likely reason for the lower maximum height in D-stands observed in our study, however, may relate to the low number of seedlings found in a 10 m^2 plot. Thus, maximum seedling height may have been confounded with seedling density.

3.4.3 Transect Level

Our transect level analyses corroborated many features of the compartment-level analysis but also contributed new insights. First, there was a 6-fold increase in seedling density in machine corridors relative to interior positions (Figures 3.4, B2). As all overstory trees had been removed on corridors, the resulting higher light availability could have positively influenced seedling survival and height growth (Figures 3.5, B2). As in clear-cuts, skidding will have exposed mineral soil in corridors. Surprisingly, variation in seedling densities within the retention strips (Figure 3.4) was not further explained by number of seed trees, overstory canopy composition, or level overstory retention, further underscoring the overwhelming importance of a receptive seedbed, in natural regeneration of spruce after harvest (Nienstadt and Zasada 1990; Prévost and Pothier 2003). Second, the importance of seed trees in producing seedlings (Figure 3.4) and increasing stocking (Figure 3.6) was also evident in our data, supporting other findings (Greene et al. 1999, 2002; Martin-DeMoor et al. 2010). Third, maintaining very high levels of overstory cover reduced regeneration success, measured in terms of either density (Figure 3.4) or stocking (Figure 3.6), even if residual cover was composed of potential seed trees (Figure 3.7). It is likely that long-distance dispersal of seed was better in clear-cuts (Greene et al.

1999) because of greater ground-level wind speeds than in partial cuts. Fourth, dense canopies will result in low light illumination and low temperatures in these stands that may reduce survival of white spruce (Constable and Lieffers, 1996; Macdonald and Fenniak 2007).

We did not detect impacts of interspecific competition (from grass or deciduous species) on seedling density, seedling maximum height nor stocking rates in RT analysis when corridor/interiors location were considered; it must also be remembered seedlings located within corridors had better growth and stocking, but corridors also had higher rates of grass and deciduous cover (Tables B2, C1-C4) . This is unexpected given the literature describing reduced growth in relation to competition from aspen regeneration (Groot 1999) or grass competition (Lieffers et al. 1994; Cater and Chapin III 2000). The best microsites (corridors) simply had higher cover of grass and deciduous plants, and thus any grass and deciduous competition may have been overwhelmed by other factors with stronger overall effects. These findings make it clear that microsite is a more important variable than interspecific competition, at least at the scale of competition observed in this study. Finally, it should also be mentioned that two apparently strong mast years (2000 and 2002, see Figure 3.1) may have provided ample recruitment of seedlings to replace mortality caused by the competitive effect of the deciduous and grass cover in our study.

We also failed to detect any impact of either rotten or solid logs (Table B2, C1-C4). It has long been recognized that rotten logs can provide improved local micro-habitats by elevating seedlings above interspecific competition, as well as increasing moisture and mineral uptake (Day 1972; Lieffers et al. 1996; Delong et al. 1997; Simard et al. 2003). Machine traffic on corridors probably removed, crushed or shattered many of the logs at EMEND. Thus, scuffing associated with skidding traffic likely produced more adequate seedbeds than were lost due to destruction of rotten logs. Also, while removal of solid logs on corridors likely created more seedbeds immediately after logging, the presence of solid logs (inappropriate as seedling microsites) in the interior may have removed seedbeds.

3.4.4 Advance Regeneration (Du-stands)

Our study clearly indicates that harvesting with variable overstory retention and protection of advanced regeneration in the understory with prescribed machine corridors can produce multi-cohort stands of white spruce and aspen. The CLAAG (careful logging around advance growth), CPRS (Coupe avec protection de la rénération et de sols) (e.g. Ruel 2000; Greene et al. 2002; Chen and Wang 2006) or understory protection logging (Navratil et al. 1994) have advocated similar techniques to remove part of the overstory while protecting advanced growth. Most foresters believe that this produces a two-cohort stand, but the present study strongly suggests that a three cohort stand (i.e, original overstory, protected understory and regeneration) will be in existence a decade after logging, if white spruce seed trees are retained in the stand.

Table 3.1 Analysis of variance of white spruce seedling density, maximum seedling height and stocking rates ten years following variable retention harvesting. Effects of overstory composition prior to logging, level of canopy retention, and their interaction are represented. Significant probability values at α < 0.05 are in bold.

Sources of Variation	DF	Seedling Density ($N/10m^2$ plot)*	Maximum Seedling Height (cm)	Stocking (%)*
Overstory composition	3	**0.0015**	**0.0002**	**0.0322**
Overstory Retention	5	**<0.0001**	0.1591	**<0.0001**
Composition x Retention	15	0.7897	0.8688	0.8030
Error	48			
Total	71			

* Represents data that were inverse transformed (1/(x +1)).

**Note: Stocking is the percentage of 10 m^2 plots with at least one seedling.

Table 3.2 Summary of non-linear regression for stocking in relation to seed tree density for the different levels of retention (see Eq. 1). Parameter estimates, mean square error (MSE), Pseudo-R^2 and % stocking by seed tree density in the different overstory retention levels. Data were analyzed for the average for the transects (weighted for the interiors and corridors) and in the second part of the table, for the corridors only.

Overstory Retention	Parameter Estimates			MSE	Pseudo-R^2	% Stocking			
	a	b	c			5 Seed Trees ha^{-1}	10 Seed Trees ha^{-1}	25 Seed Trees ha^{-1}	50 Seed Trees ha^{-1}
Clear Cut (2%)	69.4895	0.1308	0.2129	808.0	0.3452	59.44	64.98	68.92	69.47
10%	97.6764	0.0225	1.2920	312.1	0.7379	5.40	12.33	32.85	58.82
20%	76.1839	0.0098	0.3715	512.9	0.3900	24.65	31.60	43.25	53.61
50%	57.4529	0.0610	0.8236	638.4	0.2792	19.17	30.17	46.94	55.20
75%	36.6993	0.1342	0.7643	480.6	0.1197	21.24	29.11	35.72	36.67
Corridors Only									
10%	95.9790	0.0543	2.9700	521.3	0.6834	1.36	7.25	39.67	78.31
20%	90.5900	0.0142	0.4261	837.3	0.3891	28.91	38.27	54.14	67.90
50%	91.3743	0.0191	0.5122	881.6	0.3991	26.78	37.29	55.64	71.24
75%	57.8290	0.1137	0.5394	1085.4	0.1231	36.85	46.94	55.99	57.72

* Pseudo-R^2 calculated by: 1- (SS$_{\text{residual}}$/ SS$_{\text{total corrected}}$) (Schabenberger et al. 1999)

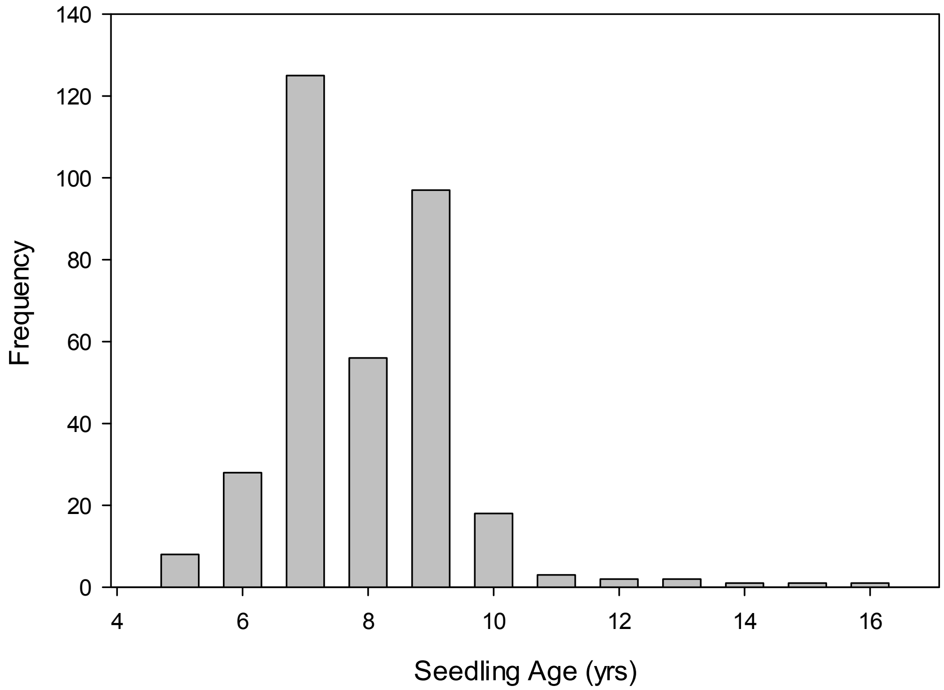

Figure 3.1 Age distribution of randomly-selected seedlings. Note that the cutting was done between years 10 and 11.

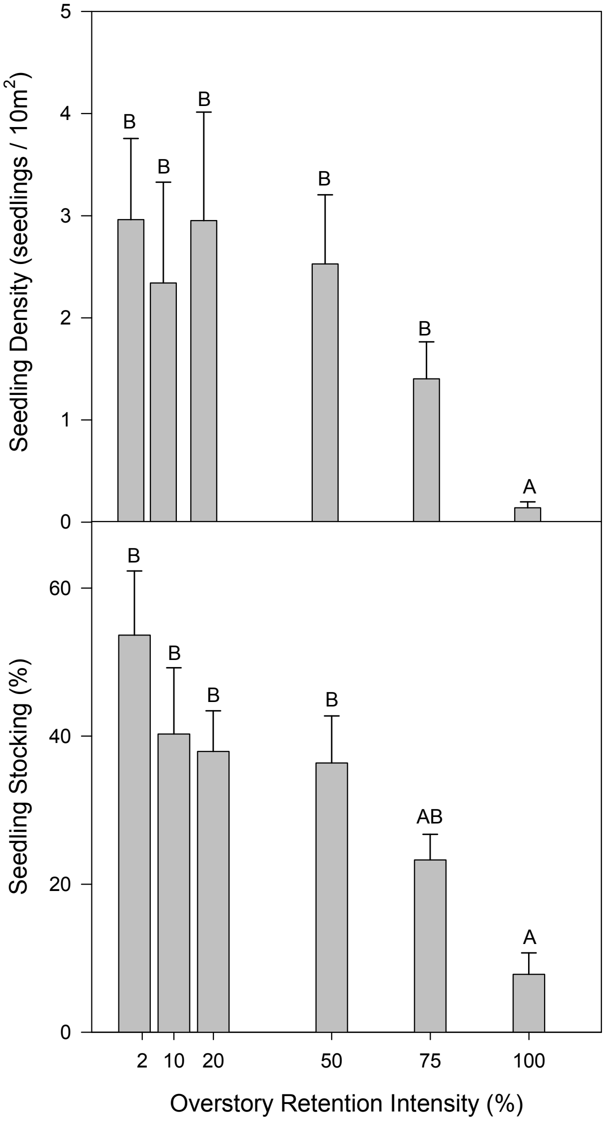

Figure 3.2 The effect of overstory retention intensity (0 – clearcut, 100-control) on seedling density and seedling stocking rates. Bars with the same letter were not significantly different (Tukey’s test, $\alpha = 0.05$).

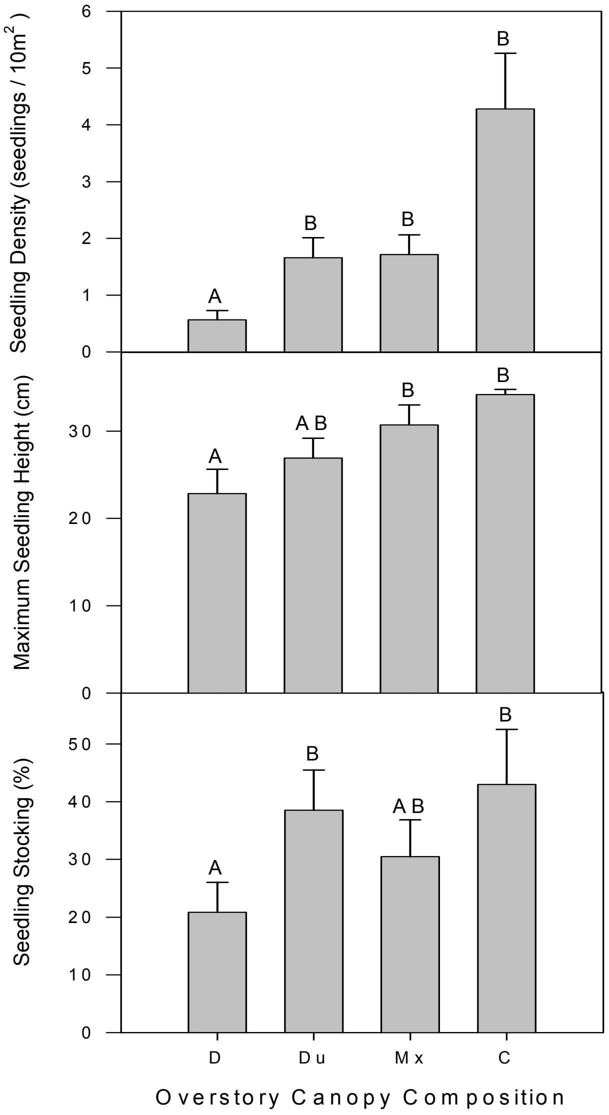

Figure 3.3 The effect of overstory composition on seedling density, seedling maximum height (cm) and stocking rates for EMEND experiment. Bars with the same letter were not significantly different (Tukey's test, $\alpha = 0.05$).

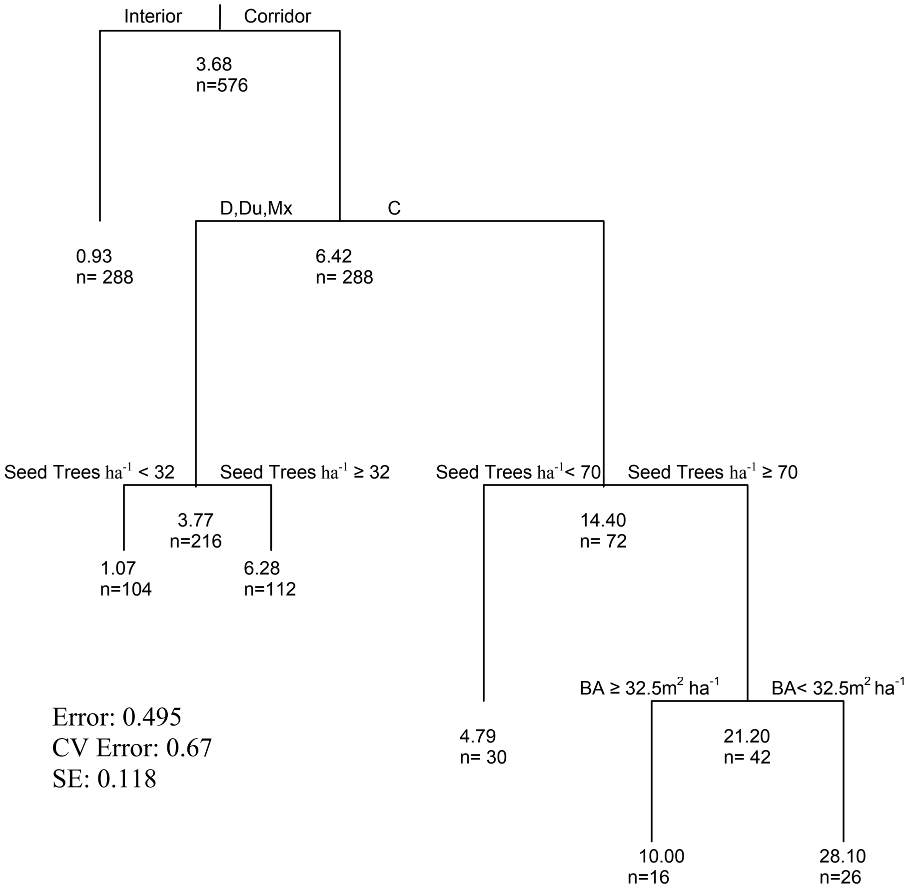

Figure 3.4 Regression tree analysis of white spruce seedling density per 10 m^2, for the individual transects from the 10, 20, 50 and 75% retention of mature trees. The explanatory variables considered were corridor/interior location, overstory canopy composition, density of seed trees surrounding the transect, total basal area of residual trees on the transect, rotten and solid wood, deciduous cover of saplings and shrubs and grass cover. This tree explained 50.5% of the total variance and the vertical depth of each split is proportional to the variation explained.

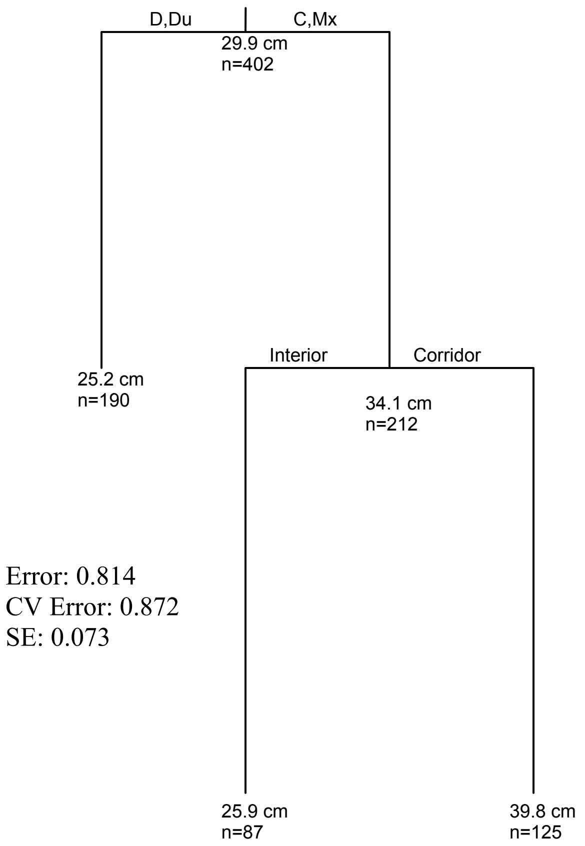

Figure 3.5 Regression tree analysis of white spruce seedling maximum height (cm) per 10 m^2 plot, for the individual transects from the 10, 20, 50 and 75% retention of mature trees. The explanatory variables considered in the model tested were corridor/interior location, overstory canopy composition, number of seed trees surrounding the transect, total residual basal area, decomposed and solid wood, deciduous cover of saplings and shrubs and grass cover. This tree explained 18.6% of the total variance. Note, as there were some transects without any seedlings, total sample size was reduced compared to other regression tree analyses.

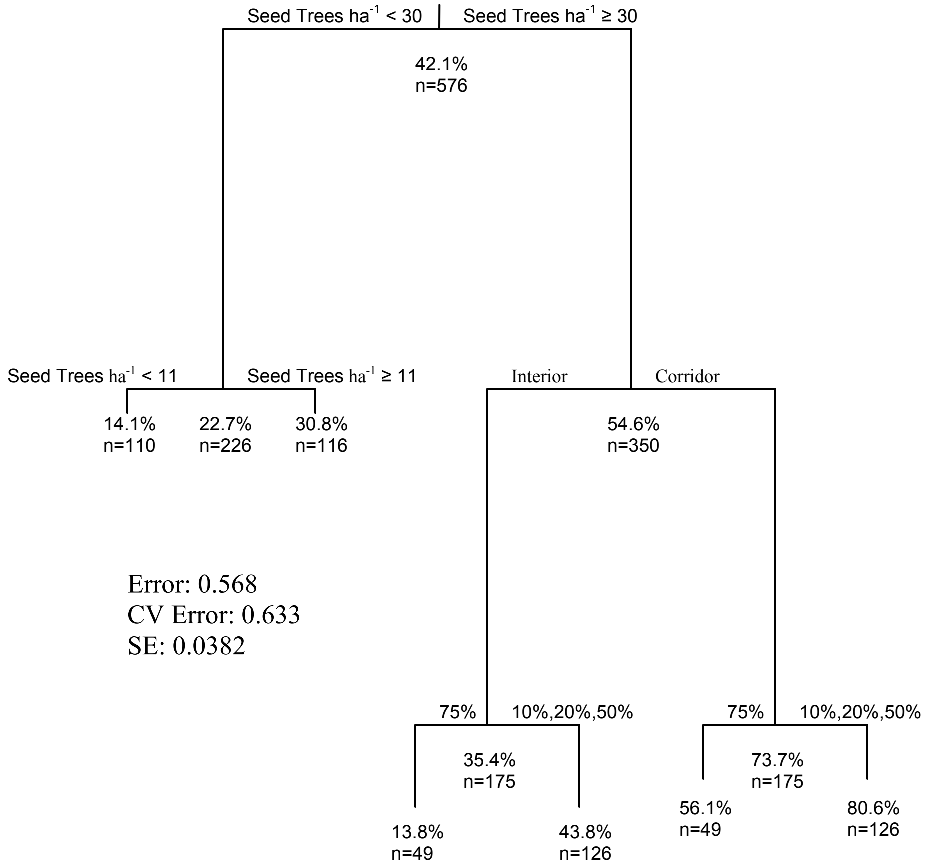

Figure 3.6 Regression tree analysis of seedling stocking (% of 10 m^2 plots with a spruce tree) for the individual transects from the 10, 20, 50 and 75% retention of mature trees. The explanatory variables considered were corridor/interior location, overstory canopy composition, number of seed trees surrounding the transect, total basal area, rotten and solid wood, deciduous cover of saplings and shrubs and grass cover. This tree explained 43.2% of the total variance.

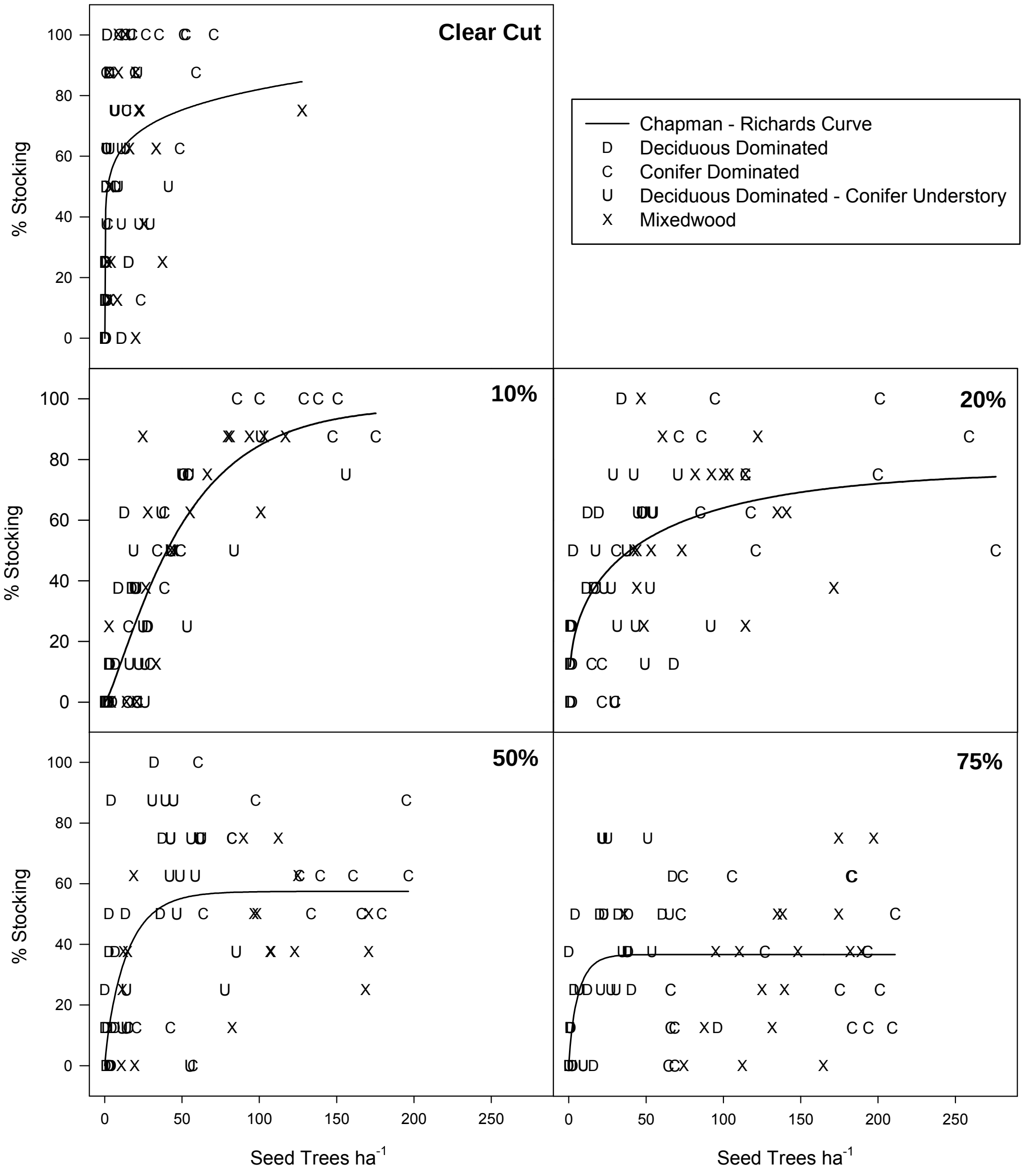

Figure 3.7 Percent stocking in relation to density of seed trees, for clear-cuts, 10, 20, 50 and 75% residuals. Data were fit with the Chapman-Richard's function using data from the corridors and interior positions combined, weighted by their area. Data from the uncut control were excluded from the analysis. N =72, parameters are in Table 3.2.

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Chapter 4: General Conclusions

4.1 Overview

This thesis aimed to evaluate the impacts of VR harvesting on residual tree mortality and natural regeneration of white spruce in the boreal mixedwood forests of northern Alberta a decade following harvest.

4.1.1 Residual Tree Mortality

In chapter 2, I assessed mortality of residual aspen and spruce in relation to stand (i.e., retention intensity canopy composition, mechanical damage and distance from machine trails) and tree level characteristics (percent live crown, height, DBH, relative size and slenderness). When retention intensities were low (10%, 20%), mortality rates for both aspen and spruce were at least double that observed in compartments of higher retentions (50%, 75% and 100%) 10 years after harvest. Additionally, dead spruce was much more likely to be fallen than standing as snags; however, in aspen there were more standing dead trees. I found that distance to machine corridor was an important predictor of residual tree mortality, but only after 10 years, and speculate this may be due to the gradual build up of root decay fungi (Whitney et al. 2002; Wolken et al. 2009) following the damage associated with logging. Overstory canopy composition had little effect on mortality rates during the first 5 years; however, after 10 years, mortality was highest for both aspen and white spruce in stands that had been conifer dominated before harvest. In contrast, spruce in both the originally deciduous dominated and deciduous dominated-conifer understory compartments had low mean mortality (3%) with no increases in mortality after 5 years.

A number of important tree level characteristics significantly influenced residual tree mortality rates for both aspen and spruce. Trees of both species with low percent live crown were more likely to die and, percent live crown was included in all models that explained mortality over both post harvest periods. Residual tree height was a useful predictor, as I found trees with a height ≥ 30 m were prone to much higher mortality rates in both species; this has also been reported for other species (e.g., Coates 1997; Ruel et al. 2003). DBH and slenderness coefficient were found to have a weak influence on mortality at only the 5 year post-harvest period. Surprisingly, damage to the bole from logging equipment was not a good predictor of mortality. It should

4.1.2 White Spruce Regeneration

I measured natural regeneration of white spruce 10 years after VR (chapter 3). My research objectives were to evaluate influences of seedling density, height and stocking rates under a range of overstory retention densities, different types of overstory canopy compositions and different densities of seed trees. I compared natural regeneration within machine corridors (passive site preparation) to that within residual interiors, and assessed competition from trees, shrubs and grasses at the compartment (~10 ha) and transect (80 m^2) level. I also described the efficiency with which residual seed trees contribute to stand stocking through natural recruitment of seedlings.

At the compartment level, regeneration densities and stocking of spruce was unaffected by retention intensity – the unharvested control treatment, however, did have lower regeneration compared to all other retention intensities.

Surprisingly, clear-cuts had the highest stocking rates at the lowest level of seed trees within 60 m proximity. Good regeneration in clear-cuts is thought to be related to passive preparation of seedbeds as a result of random skidding patterns. Seedling densities and heights were found to be impacted by overstory canopy compositions, where they were the lowest within the deciduous dominated stands. This was presumably due to the lack of viable seed trees within close proximity, thus reducing the quantity of seedlings within the deciduous forest type.

A transect level analysis revealed a 6-fold increase in seedling density in the machine corridors in comparison to the retention interiors. As in the clear-cuts, skidding can expose mineral soil and improve regeneration success. Furthermore, height of the tallest seedlings within the mil-hectare plots was greater in the corridors. Maximum height in the corridors was 39.8 cm compared to 25.9 cm in the retention interior. Poor regenerative success and growth within the interiors is likely due to the lack of a receptive seedbed and reduced light availability.

Effects of interspecific competition from grass and deciduous competition on spruce regeneration were not evident within the study. The highest rates of grass and deciduous competition occurred within the corridors, masking any ability to detect an influence of the negative effects of competition compared to the positive features of the corridor. I suggest that microsite quality within this study provides a stronger overall effect on regeneration than competition in the context of this study and that overall it deserves more attention in VR studies.

Finally, work in the deciduous stands with a spruce understory clearly indicates that VR harvesting with prescribed machine corridors can produce multi-cohort stands. Seedling densities, height and stocking, however, were comparable to that found within the other stand types.

4.2 Management Implications

4.2.1 Residual Tree Mortality

Ten years after logging more than 50% of residual aspen and 30% of residual spruce were dead in the 10 and 20% retention compartments. This would be considered an 'operational failure' based upon the 10% designation of critical windthrow mortality used by Coates (1997). The high values that I report, however, may be quite acceptable if a large number of snags and downed wood are the management goals. Both snags and downed logs have high habitat value (Harmon et al. 1986) and in the mixed wood system both are significant legacy elements following retention harvest. Aspen mortality leads more frequently to snags while spruce more frequently found to be fallen to become downed logs. If the primary objective of the management strategy is to retain live trees for habitat elements and ecosystem functions (Franklin et al 2002), maintaining ≥50% residuals will result in most of the trees surviving over a 10 year interval, relative to unharvested stands. If managers choose lower levels of retentions, trees with higher PLC ratios, that are stout, and that are small to intermediate in size (in the case of spruce) will have a higher likelihood of survival of the first 10 years. These relationships could provide important information for planning retention harvests to optimize habitat legacies.

Other work at these sites suggests that achieving the highest initial rates of aspen regeneration through suckering will require high harvest intensity (Gradowski et al. 2008). For spruce regeneration, however, it is most important to retain an adequate number of seed source trees within the vicinity (~60 m) to secure adequate natural regeneration (Solarik et al. 2010). Managers should be aware of the trade-off provided by the machine corridors; although mortality of residual elements will be higher in closer proximity to corridors (Thorpe and Thomas 2008), corridors also provided the best regeneration sites for both spruce and aspen at EMEND (Solarik et al. 2010).

In order to use this information effectively managers must be clear about the exact goals of harvest prescriptions (e.g., increasing course woody debris, increasing gap availability for regeneration, reducing residual mortality). In the boreal mixed wood system, variable retention harvesting appears to provide a means to speeding up recovery of some biodiversity elements following a disturbance (Work et al. 2010). However, our results suggest other goals (e.g., minimizing mortality of legacy elements, growth of residual trees subsequent to harvest) deserve consideration in implementing a variable retention harvesting system that will be deemed an ‘operational success’.

4.2.2 White Spruce Natural Regeneration

This study illustrates that on average, leaving 30 or more seed trees ha^{-1} can produce 55% stocking and stocking is further increased on the systematic machine corridors employed in partial retention harvests. In clear-cuts, the same average level of stocking might be achieved with as few as 5 seed trees ha^{-1}, but there would be considerable spatial variation in success. Secondly, the biodiversity values sought through use of partial retention would not be met on clearcut blocks. Nonetheless, in this region, clear-cutting and passive site preparation is an acceptable means of producing natural white spruce regeneration, provided that seed trees are retained within 60 m. Clear-cutting should therefore be considered as an acceptable harvesting approach for some blocks in a landscape-oriented harvesting plan. In partial-cut sites with a systematic network of machine corridors, regeneration will be patchy, with 6x as much regeneration on the corridors as in the wider area of undisturbed substrates between the corridors. Intentionally disturbing the forest floor of these interior positions could potentially increase the overall stocking levels in these stands. My study also showed that natural regeneration in an understory protection cut is possible, suggesting that multi-cohort stands can be produced by understory protection system using defined machine corridors.

4.2.3 Tree Mortality and Regeneration: A link

For seedlings to have enough space, nutrients and light some overstory trees must be removed or be in declining health. As overstory trees are removed either through harvesting or natural mortality (i.e., senescence), it will become easier for seedlings to obtain resources. VR harvesting is associated with two kinds of mortality: (1) harvested trees are removed from the system (2) residual trees that can’t adapt to the new environmental conditions created by the harvest will die soon after harvest. In both cases, removal of overstory canopy trees increases resources (i.e., light, water) to the understory (Kneeshaw and Bergeron

1998). The residual trees that do die will eventually become rotten logs that serve as habitat elements for many creatures (i.e., insects, small mammals and birds) or important substrates for plant and fungal growth, including that of white spruce seedlings. In terms of natural spruce regeneration, retaining an adequate number of seed source trees within the vicinity (~60 m) can secure adequate natural regeneration. In contrast, retaining too many seed trees will limit space for regeneration. Implementing a systematic machine corridor system will provide a form of passive site-preparation that increases the area of receptive seedbeds. However, managers must be aware of the trade-offs of associated with machine corridors. Although regeneration will be highest within these disturbed sites, residual mortality will be higher for trees in close proximity (Thorpe and Thomas 2008).

4.3 Future Research

4.3.1 Residual Tree Mortality

Only a handful of studies have assessed residual tree mortality following VR harvesting at operational scales within the boreal forest. Therefore, several areas require additional research. (1) Long term studies remain rare. Presently most studies have only focused on mortality within the first 2-3 years following harvest (Thorpe and Thomas 2007). My study shows that mortality rates are high for at least a decade. (2) More frequent re-measurement will permit better understanding of the mechanisms of mortality over time. The ability to follow the time course of residual tree mortality is essential to effective emulation of natural disturbance. (3) More assessments of VR harvesting systems under various overstory canopy compositions and different forest ecosystems should be conducted. Most tree mortality studies have been focused within the Pacific Northwest and Ontario (Thorpe and Thomas 2007). The ability to make inferences about the factors contributing to mortality of various tree species can support better implementation of these harvesting systems. (4) Re-examining the impact of mechanical damage and trail proximity could prove useful as trees close to machine corridors eventually developed higher rates of mortality, but the mechanisms for this were not clear in my study.

4.3.2 White Spruce Natural Regeneration

There have been numerous studies to date on natural regeneration of white spruce at the stand level; however no studies have considered the landscape level. (1) An increase in the number of landscape level regenerative studies is required. This should be done in order to properly assess natural regeneration of white spruce within a forest management unit or whole forest. (2) The natural regeneration of the spruce at the EMEND site should be re-measured at year 20, so that we understand seedling mortality rates within these VR cuts. If stocking remains high this will convince managers that natural regeneration of spruce can be successful in VR. (3) Competition from grasses and deciduous species may not be as important to natural regeneration at the landscape level as would be suggested from all of the individual small-scale studies of effects of competition on tree growth. Because there are many microsites tested from the large seed rain there may be many sites found where competition is not an issue. (4) I'd further recommend the examination of a potential correlation between harvest and seed crop: To my knowledge there have yet to be any studies that have examined the possibility of a ‘stress crop’ (i.e., seed trees releasing a final crop prior to death, due to post-harvest conditions). The idea of a stress crop on the residuals trees is supported by the mast year in 2000 which would have been induced in the first season after logging.

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Appendix A: Summary of Residual Tree Data

Table A1: Summary statistics about compartment composition by tree species across retention intensities (10%, 20%, 50% and 75%).

Status	N	Variable	Mean	SD	Minimum	Maximum
White Spruce	428	Height (m)	18.52	7.01	3.2	38.80
		DBH (cm)	20.67	10.44	5.00	59.60
		Live Crown (%)	63.92	16.14	3.80	95.50
		Slenderness	0.96	0.20	0.45	1.89
		Basal Area5(m^2 ha^{-1})	0.041	0.041	2.96x10^{-3}	0.29
Aspen	309	Height (m)	21.01	4.44	6.60	36.10
		DBH (cm)	22.82	8.15	5.60	54.80
		Live Crown (%)	27.64	9.49	2.30	79.20
		Slenderness	0.98	0.21	0.44	1.92
		Basal Area (m^2 ha^{-1})	0.05	0.03	2.46 x10^{-3}	0.24

Table A2: Summary of residual tree counts by species and retention intensity. L: Living trees, SD: Standing Dead, FD: Fallen Dead.

Species	Retention Intensity	Total Trees (n)	Status 2003			Status 2008		
			L	SD	FD	L	SD	FD
White Spruce	10	58	49	4	5	42	5	11
	20	85	67	7	11	60	10	15
	50	121	113	5	3	101	5	15
	75	155	151	3	1	145	3	7
	100	270	265	4	1	251	9	2
Aspen	10	54	38	14	2	29	13	12
	20	67	49	16	2	32	20	15
	50	79	68	8	3	58	13	8
	75	110	103	6	1	89	11	10
	100	262	236	24	2	210	35	17
Canopy White Spruce (≥15m)	10	34	26	3	5	19	5	10
	20	49	34	6	9	29	8	12
	50	94	89	4	1	78	5	11
	75	114	113	0	1	107	1	6
	100	168	167	1	0	164	4	0
Advance Growth White Spruce (<15m)	10	33	32	1	0	32	0	1
	20	36	33	1	2	31	2	3
	50	27	24	1	2	23	0	4
	75	41	38	3	0	38	2	1
	100	102	98	3	1	95	5	2

Appendix B: White Spruce Regeneration - Split Plot Analysis

1.1 Methods

A split plot analysis was undertaken to breakout effects of the machine corridor and residual interiors as an additional analysis to the compartment level ANOVA. Since seedling density again failed to meet the assumptions of homogeneity of variance, variance was modeled among overstory canopy composition and a Sidak-Holm adjustment was used and tested at a significance level of $\alpha = 0.05$. Seedling maximum height, stocking, grass, deciduous, decomposed logs (CWD) and solid logs (Log) rates were analyzed using a Tukey-Kramer test at a significance level of $\alpha = 0.05$ for all post-hoc comparisons among treatment means. Data was analyzed using the general linear model (GLM) and mixed procedure (proc mixed) in SAS v.9.3 (SAS Institute Inc., Cary, NC, USA).

1.2 Results

Overall, seedling density within machine corridors was 3.7 times greater than positions in the residual interior (p=0.0001, Table B1, Figure B1). A decline in seedling density from the C-stands (14.37 seedlings/10 m^2), to the Mx-stands (5.95 seedlings) and Du stands (4.18 seedlings), to the D-stands (1.18 seedlings) was found in corridors (Figure B1). Furthermore, within some plots, densities were as high as 179 seedlings; however, these high levels were masked by collapsing the information to compartment averages. Interior seedling densities did not differ significantly different over the overstory canopy compositions (Figure B1).

Seedlings in the corridors were significantly taller than those in interiors (p=0.0002, Table B2); in particularly, within the C-corridors, where heights were 10 cm taller; this was a much larger difference than all other canopy x corridor/interior interactions, particularly the D stands (p= 0.0172) (Figure B2). Mean seedling heights within the corridor were 31.7 cm tall, while those within the residual interior were 24.3 cm tall. There was, however a corridor by composition interaction (p=0.0172) which can be explained by the large beneficial effect of corridor on seedling height in the C stands, compared to virtually no difference between corridor and interiors in the D stands.

As seen with seedling densities (Figure B1, Table B2), retention intensity had no impact on height (p=0.5401, Table B2). There was a marginal difference in stocking in relation to overstory composition (p=0.0953) with the C stands having the highest stocking. Stocking rates were 2 times higher on the corridor than in the interior (p= <0.0001, Table B2). A strong interaction between canopy composition and corridor/interior (p=0.0049) was related to strong difference in stocking between corridor and interior for the Mx and Du stands but relatively little difference in the D stand (Table B2, Figure B3). A retention intensity and corridor/interior interaction (p = 0.0208) was driven by sharp declines in stocking rates within 75% retention compared with only minor declines in 10% retention (Table B1, Figure B4).

Grass coverage was higher within C-stands (25.6% coverage) and Mx-stands (19.2%) than Du (14.8%) and D-stands (13.6%) (p = 0.0202, Table B1). The only other influence on grass cover was explained by the machine corridor/

residual interior. Corridors had much higher (24.9%) cover than the interior plots (11.7%) (p = <0.0001). Deciduous cover was found significantly higher within lower retention intensities (10%: 75.8% cover, 20%: 70.4% cover) than the higher retentions (50%: 63.9% cover, 75%: 54.5% cover) (p = 0.0210, Table B1). Deciduous cover was significantly higher within the machine corridor (64.9%) than the residual interior (64.4%) (p = 0.0177). CWD was influenced by canopy composition, where Mx (7.8%), C (7.1%) and Du-stands (4.7%) had significantly higher cover than D-stands (2.1%) (p = 0.0075). The residual interiors had higher rates of CWD (6.5%) than found within the machine corridors (4.4%) (p = <0.0001). Coverage of Log were found to be significantly higher within Mx (10.6%) than Du (5.0%) and D-stands (6.6%) but not significantly different from C-stands (9.3%) (p = 0.0168). Finally, Log cover was found to be significantly higher within interior (9.5%) than corridor plots (6.3%) (p = <0.0001).

Table B1: Analysis of variance of % coverage of grass, deciduous, course woody debris (CWD) and solid logs (Log) following ten years variable retention harvesting. Effects of overstory canopy composition, overstory retention intensity and corridor/interior location. Note that the 0% and 100% retention intensity were excluded from these analyses. Probability values in bold are significant (Tukey's α = 0.05).

Sources of Variation	DF	Grass (%)	Deciduous (%)	CWD (%)	Log (%)
Overstory composition	3	**0.0202**	0.9069	**0.0075**	**0.0168**
Overstory Retention	3	0.1108	**0.0210**	0.7314	0.1719
Composition x Retention	9	0.8843	0.9902	0.9354	0.1762
Main Plot Error	33				
Main Plot Total	47				
Corridor/Interior	1	**<0.0001**	**0.0177**	**<0.0001**	**<0.0001**
Composition x Corridor/Interior	3	0.2448	0.0830	0.4330	0.1187
Retention x Corridor/Interior	3	0.6127	0.5722	0.0543	0.2086
Composition x Retention x Corridor/ Interior	9	0.8991	0.7834	0.8525	0.3454
Subplot Error	32				
Subplot Total	48				
Total	95				

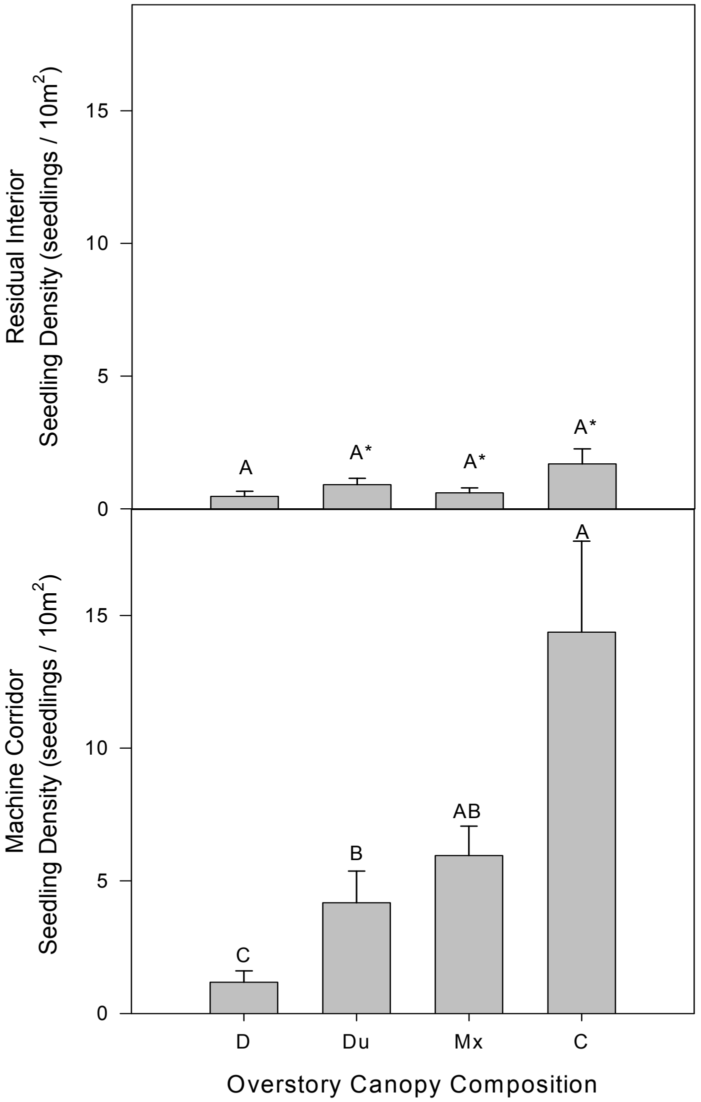

Figure B1: Overstory canopy effect on seedling density by location within the residual interior (above) and machine corridor (below). Bars with the same letter were not significantly different (Sidak $\alpha = 0.05$). (*) Indicates differences among the machine corridor and residual interior within same overstory canopy composition.

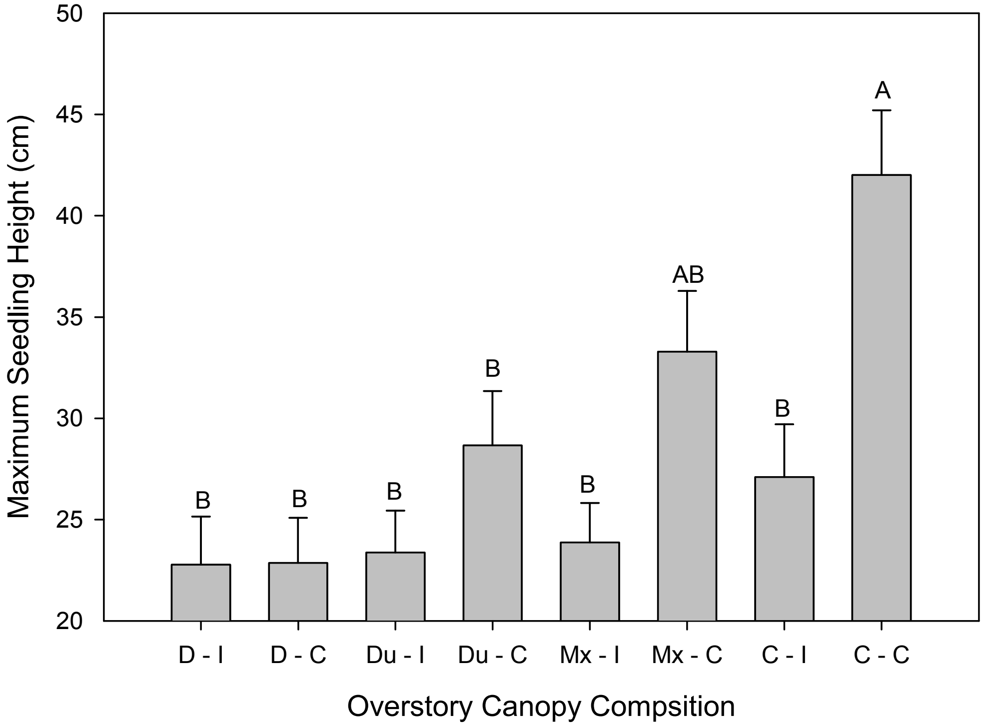

Figure B2: Overstory canopy composition and machine corridor (C) and residual interior (I) interaction effect on maximum seedling height (cm). Bars with the same letter were not significantly different (Tukey's $\alpha = 0.05$).

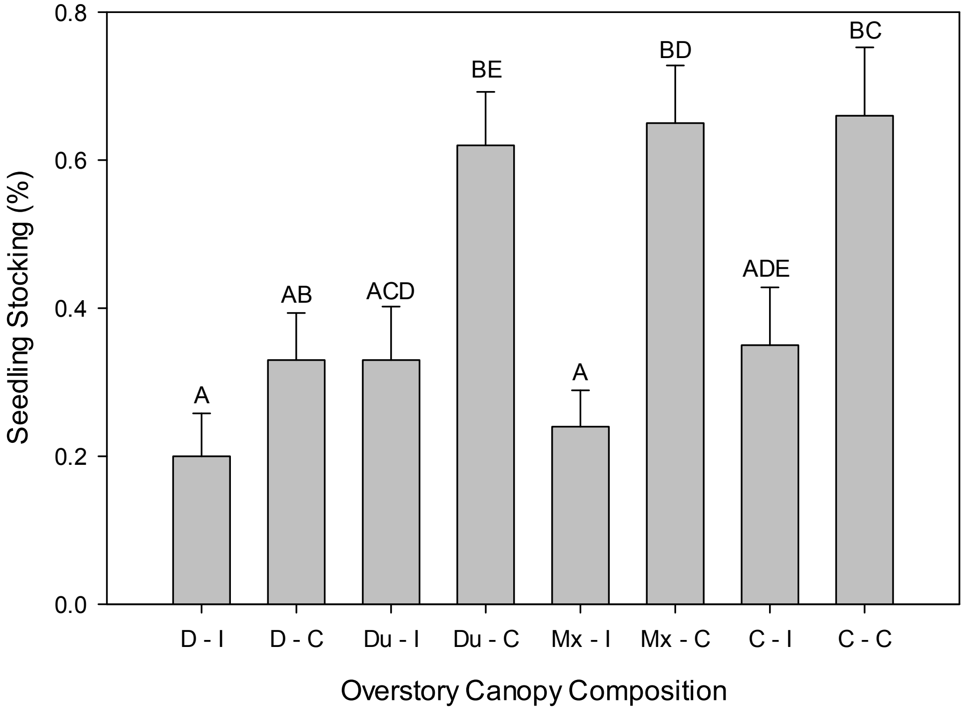

Figure B3: Overstory canopy composition and machine corridor (C) / residual interior (I) interaction effect on seedling stocking rates. Bars with the same letter were not significantly different (Tukey's $\alpha = 0.05$).

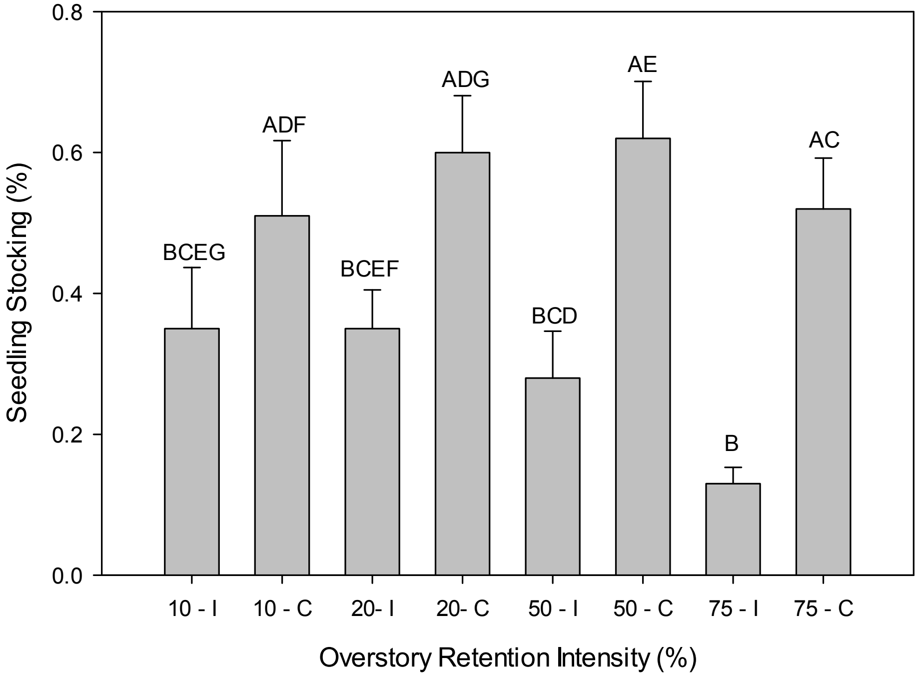

Figure B4: Overstory retention intensity and machine corridor (C) / retention interior (I) interaction effect on seedling stocking rates. Bars with the same letter were not significantly different (Tukey's $\alpha = 0.05$).

Table B2: Analysis of variance of seedling density, maximum seedling height and stocking rates ten years following variable retention harvesting. Effects of overstory canopy composition, overstory retention intensity and corridor/interior location. Note that the 0% and 100% retention intensity were excluded from these analyses. Probability values in bold are significant at $\alpha = 0.05$.*Modeled by overstory canopy composition

Sources of Variation	DF	Seedling Density (N/10m^2 plot)*	Maximum Seedling Height (cm)	Stocking (%)*
Overstory composition	3	**0.0002**	**0.0064**	0.0953
Overstory Retention	3	0.5919	0.3035	0.4556
Composition x Retention	9	0.5643	0.8251	0.9154
Main Plot Error	33			
Main Plot Total	47			
Corridor/Interior	1	**<0.0001**	**0.0002**	**<0.0001**
Composition x Corridor/Interior	3	**0.0002**	**0.0172**	**0.0049**
Retention x Corridor/Interior	3	0.8648	0.5401	**0.0208**
Composition x Retention x Corridor/ Interior	9	0.6280	0.9528	0.5921
Subplot Error	32			
Subplot Total	48			
Total	95			

Appendix C: Independent site variables means by overstory residual intensity classified by overstory canopy composition

Table C1: C-stand independent variable transect means by overstory residual intensity and corridor/interior location

Overstory Residual Intensity	# Seed Trees (60m)	% Grass Cover		% Deciduous Cover		% CWD Cover		% Log Cover	
		C	**I**	**C**	**I**	**C**	**I**	**C**	**I**
Clear-cut	37.94	30.83		70.94		6.34		6.42	
10%	108.06	33.90	19.43	79.10	83.26	4.31	9.17	7.67	9.56
20%	151.17	40.67	18.92	64.96	69.60	6.18	8.79	7.88	15.74
50%	157.33	34.43	14.07	64.58	61.54	7.89	8.61	7.42	10.78
75%	204.50	27.58	15.53	53.21	52.51	6.08	5.43	7.65	8.31
Control	276.61	4.44		38.03		8.26		8.73	

Table C2: Mx-stand: Independent variables for transect means by overstory residual intensity and corridor/interior location.

Overstory Residual Intensity	# Seed Trees (60m)	% Grass Cover		% Deciduous Cover		% CWD Cover		% Log Cover	
		C	**I**	**C**	**I**	**C**	**I**	**C**	**I**
Clear-cut	31.39	38.18		72.72		6.78		3.65	
10%	70.61	37.81	18.76	77.03	80.76	3.10	9.03	3.53	8.32
20%	132.72	22.71	11.71	70.35	64.46	8.44	12.46	6.67	14.00
50%	128.61	23.01	14.13	75.08	57.04	4.88	6.31	6.36	7.50
75%	202.00	17.39	8.03	62.22	53.86	9.19	9.28	15.99	22.22
Control	257.39	4.17		51.76		8.89		7.06	

Table C3: Du-stand: Independent variables for transect means by overstory residual intensity and corridor/interiorlocation.

Overstory Residual Intensity	**# Seed Trees (60m)**	**% Grass Cover**		**% Deciduous Cover**		**% CWD Cover**		**% Log Cover**	
		C	**I**	**C**	**I**	**C**	**I**	**C**	**I**
Clear-cut	17.94	24.36		71.70		2.27		4.42	
10%	78.39	28.00	9.71	69.17	64.44	1.94	4.60	3.43	6.94
20%	66.06	24.32	10.35	73.54	63.99	2.03	6.60	3.24	6.32
50%	69.50	18.04	6.01	66.94	59.79	5.25	7.86	3.68	5.40
75%	36.78	18.40	3.76	56.18	52.94	3.97	5.67	3.38	7.85
Control	69.33	2.26		33.10		9.57		6.53	

Table C4: D-Stand: Independent variables for transect means by overstory residual intensity and corridor/ interior location.

Overstory Residual Intensity	**# Seed Trees (60m)**	**% Grass Cover**		**% Deciduous Cover**		**% CWD Cover**		**% Log Cover**	
		C	**I**	**C**	**I**	**C**	**I**	**C**	**I**
Clear-cut	2.78	25.20		78.16		1.35		4.39	
10%	11.94	21.92	11.96	80.76	76.60	1.22	1.71	5.26	7.71
20%	14.67	15.24	7.78	78.19	77.92	1.93	3.74	7.26	8.67
50%	13.50	27.32	13.33	62.64	63.61	1.44	2.94	4.42	5.83
75%	38.11	9.02	2.49	53.75	51.50	0.77	2.65	7.32	6.81
Control	9.83	2.26		62.71		4.99		7.38	