

Seed tree density, variable retention, and stand composition influence recruitment of white spruce in boreal mixedwood forests

Kevin A. Solarik, Victor J. Lieffers, W. Jan A. Volney, Rick Pelletier, and John R. Spence

Abstract: In an operational-scale experiment, we examined natural regeneration of white spruce (*Picea glauca* (Moench) Voss) under various degrees of variable retention harvesting across different overstory canopy compositions. We sampled four types of overstory canopy compositions (ranging from deciduous dominated to conifer dominated) and six rates of retention (2%, 10%, 20%, 50%, 75% and 100%). Spruce seedling densities, maximum height, and stocking rates were assessed in 432 transects and were found to be lowest in the deciduous stands and with 100% canopy retention (control). Regression tree analysis indicated that densities, maximum height, and stocking of spruce seedlings were greatest with higher availability of seed trees ($>30\text{-ha}^{-1}$) and on machine corridors; in these circumstances stocking reached 74%. By contrast, stocking was less than 14% on retention strips with no machine traffic, when seed tree density was less than 11 seed trees $\cdot\text{ha}^{-1}$. However, stocking also declined with higher density of residual trees. Stocking in relation to density of seed trees was highest within clearcuts and lowest within the 75% retention intensity where low light transmission may have limited regeneration success. Passive soil disturbance from skidding appeared to be more important for the establishment of spruce seedlings than was the abundance of competing vegetation.

Résumé : À l'aide d'une expérience à l'échelle opérationnelle, nous avons étudié la régénération naturelle de l'épinette blanche (*Picea glauca* (Moench) Voss) en fonction de différents degrés de coupe à rétention variable et de différentes compositions du couvert dominant. Nous avons échantillonné quatre types de composition du couvert dominant (allant d'un couvert dominé par des feuillus à un couvert dominé par des conifères) et six taux de rétention (2, 10, 20, 50, 75 et 100 %). La densité de semis d'épinette, la hauteur maximale et le coefficient de distribution de la régénération (CDR) ont été estimés le long de 432 transects. La densité de semis d'épinette, la hauteur maximale et le CDR avaient les plus basses valeurs dans les peuplements feuillus et dans le traitement à rétention de 100 % (témoin). Une analyse par arbre de régression a indiqué que la densité, la hauteur maximale et le CDR des semis d'épinette atteignaient les valeurs les plus élevées lorsque la disponibilité des arbres semenciers était élevée ($>30\text{-ha}^{-1}$) et dans les sentiers de débardage. Dans ces circonstances, le CDR atteignait 74 %. Au contraire, le CDR était inférieur à 14 % dans les bandes de rétention où la machinerie ne circulait pas lorsque la densité des arbres semenciers était inférieure à 11 $\cdot\text{ha}^{-1}$. Cependant, le CDR diminuait aussi dans les traitements avec les plus fortes densités d'arbres résiduels. En fonction de la densité des arbres semenciers, le CDR était le plus élevé dans les coupes à blanc et le plus bas dans les coupes à rétention de 75 % où la faible transmission de la lumière peut avoir limité le succès de la régénération. Une perturbation passive du sol due au débardage a semblé plus importante pour l'établissement des semis d'épinette que l'abondance de la végétation concurrente.

[Traduit par la Rédaction]

Introduction

Over the last decade, forest managers and silviculturists have increasingly used variable retention harvesting systems as an approach to sustainable forest management that attempts to emulate natural disturbances (Mitchell and Beese 2002; Bladon et al. 2008). Variable retention leaves living and dead trees in harvested areas to imitate residual trees and forest structure left after natural disturbance (Hunter

1990). However, variable retention 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 are associated with successful regeneration: (i) a seed source, (ii) receptive seedbed, (iii) suitable microclimate, and (iv) limited competition from other vegetation (Lees 1972; Stewart et al. 2001).

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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 every 12 years (Wurtz and Zasada 2001).

A number of specific factors are known to affect regeneration. Seedbed type, for example, can strongly affect whether or not seedlings establish successfully (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 (Nienstaedt and Zasada 1990) recently fallen logs can also reduce the likelihood of successful regeneration by reducing the availability of ideal substrates. Some ideal substrates for survival of white spruce seedlings include elevated or moisture-retaining exposed mineral soil, and well-decomposed rotten (nurse) logs (DeLong et al. 1997; Calogeropoulos et al. 2004).

Overstory canopy composition also affects nutrient availability, pH, and litter quality (Van Pelt and Franklin 2000; Macdonald and Fenniak 2007). Conifer-dominated canopies often provide shade throughout the year, creating a much cooler and darker environment (Fenniak 2001) in the understory, while broadleaf canopies dominated by aspen provide warmer environments with higher light transmissions during leaf-off periods (Constabel and Lieffers 1996). Interspecific competition from other boreal forest trees species (e.g., aspen) (Lieffers et al. 1996) and grass species (Cater and Chapin 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 seedlings (Cater and Chapin 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 Kembal 2005), seed dispersal (Galipeau et al. 1997; Stewart et al. 1998; Lamontagne and Boutin 2007), and understory competition (Cater and Chapin 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).

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) with 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.

Materials and methods

Study area

This study was carried out at the Ecosystem Management Emulating Natural Disturbance (EMEND) site located 90 km northwest 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 677 to 880 m above sea level, with a predominantly subhygric or mesic soil moisture regime on primarily Luvisolic soils (Kishchuk 2004). The EMEND site has a continental climate with mean temperatures of –17.7 °C for January and 15.9 °C for July, and a mean annual precipitation of 431 mm (Environment Canada 2009).

Experimental design

The EMEND landscape was partitioned, prior to harvest, into relatively uniform sections with similar canopy species composition in four categories: (i) deciduous dominated (D) (>70% of basal area composed of aspen and (or) balsam poplar), (ii) deciduous dominated with a conifer understory (Du) (at least 40% stocking of advance growth below the main canopy), (iii) conifer dominated (C) (>70% of basal area composed of conifer — mostly white spruce), and (iv) 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 six variable retention treatments: 2% residual (clearcut), 10%, 20%, 50%, 75%, and 100% residual (control). Thus, in total there were four overstory canopy compositions, six overstory retention levels, and three 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 oriented in a north–south direction, perpendicular to prevailing wind direction (W–E); this was done to help reduce windthrow. The 75% residual treatment was composed 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.

Data collection

Immediately after logging, six permanent transects (2 m × 40 m) 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 to intersect two machine corridors and two retention strips (Volney et al. 1999). In May 2009 (10 years following harvest), eight circular plots of 10 m² were established in two lines running parallel with each transect, 5 m north (four plots) and 5 m south (four plots). Two plots in each transect were centred on the ma-

chine corridors and two plots were centred in the retention strips. Within each plot, we collected the following data: (i) number of white spruce seedlings (minimum of 10 cm in height, ≤ 10 years (based upon whorl counts)); (ii) maximum height of tallest white spruce seedling within each of the eight 10 m² plots; (iii) percentage of grass cover; (iv) percentage of deciduous cover, including juvenile aspen, balsam poplar, and shrub species (mainly *Alnus crispa* (Aiton) (Pursh), *Salix* spp., *Viburnum edule* (Michx.) Raf., *Rosa acicularis* Lindl., *Shepherdia canadensis* (L.) Nutt., and *Rhododendron tomentosum* (Stokes)); (v) cover of decayed logs (decay classes: 4–7, Mills and Macdonald 2004); and (vi) cover of fresh logs (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.

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 height (cm), root collar diameter (mm), and 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 to determine the time of recruitment of white spruce seedlings after harvest.

Aerial photographs of the study area were taken in late June 1999, during the first summer following harvest; a total of 158 photos at a 1:5000 scale were taken. Photographs were taken with an RMK TOP30 camera equipped with a Topar A3 lens (focal length of 304.977 mm) using a KL clear, AGFA color H100 filter. Photos were then scanned individually at 1200 dpi using a Microtek ScanMaker 1000XL 48-bit color scanner (with an optical resolution of 6400 \times 3200 dpi) and were tagged in image file format. Using ArcMap version 9.3 (Environmental Systems Research Institute, Inc. 2008), these images were georeferenced 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. Global positioning system coordinates of permanent tree plots were established on the photos. A 60 m buffer zone was overlaid on the mosaic around each transect; within this oval plot (1.5-ha⁻¹) all white spruce trees with the potential to supply seed for regeneration of the eight subplots were counted. The bases for selecting seed trees were (i) tree color (with conifers being darker), (ii) shape (conifers have a conical shape both in terms of vertical view and shadows), and (iii) 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 neighbours (edge trees often allowed for a clear view of crown length, allowing for inferences into 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 (W.J.A Volney, unpublished data). The black spruce trees 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.

Data analysis

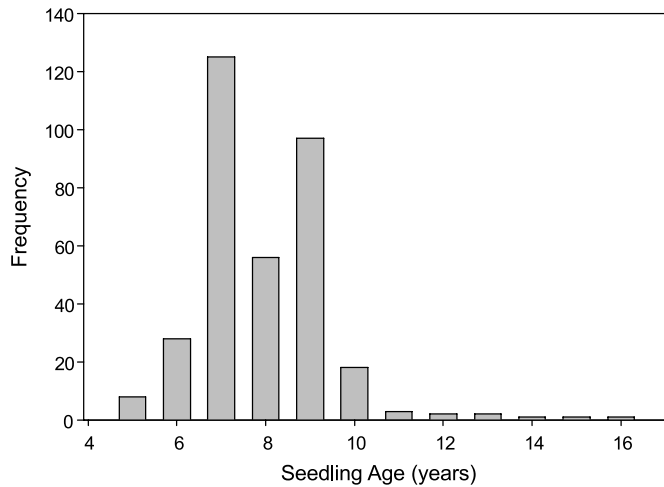
Compartment-level analyses provided a macroscale assessment of regeneration at the scale of the ~ 10 ha cutting compartment, as is relevant to forest managers. Data from the six transects, each with eight plots, were averaged for each compartment prior to analysis ($n = 3$). A fully randomized 4 \times 6 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 m² plots within each compartment with at least one spruce seedling). To accurately represent seedling density and stocking over the entire compartment, densities and stocking were weighted based on area represented (i.e., corridor \times 0.25 and interior \times 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. The Tukey–Kramer’s test ($\alpha = 0.05$) was used for all post-hoc comparisons of means. In addition, the response surface between density or stocking and level of retention intensity was tested against first-, second-, and third-degree polynomials.

A split-plot analysis was performed to incorporate environmental variables (i.e., those reflecting interspecific competition) with regards to the corridor and residual interiors. The Tukey–Kramer’s 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 version 9.2 (SAS Institute Inc. 2009).

Transect-level analysis provides a microscale 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 four regeneration plots for corridors and the four for interiors from each transect, giving a total of 576 data points (i.e., 6 transects \times 48 compartments \times 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

Fig. 1. Age distribution of randomly selected seedlings. Note that the cutting was done between years 10 and 11.



were analyzed using R version 2.10.1 (R Development Core Team 2008) and the *mypart* 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):

$$[1] \quad S = a(1 - e^{-bT})^c$$

Parameters a , b , and c were estimated using nonlinear regression (proc NLIN) in SAS. A constant of 0.001 was added to both S and T for all measurements to include zero values in fitting the Chapman–Richard’s function. The estimated parameters were then used to calculate the S per number of residual seed trees by overstory retention intensity for (i) the average stocking (weighted by corridor and interior — see Methods above) and (ii) stocking within corridors only.

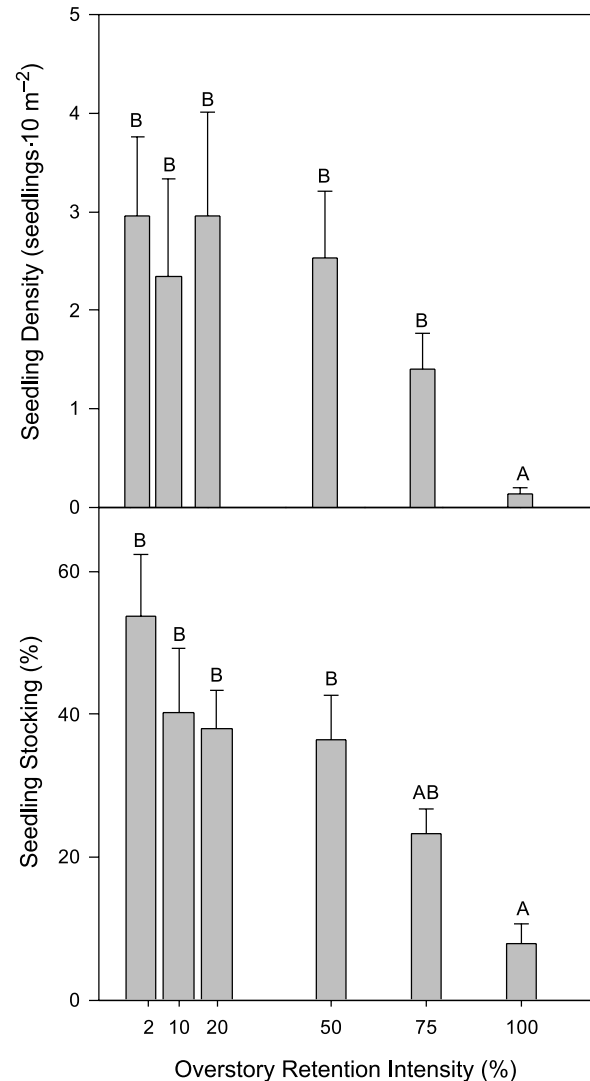
Results

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

Compartment level analysis

Seedling densities showed a significant quadratic decline with retention intensity ($p = 0.0006$) (Fig. 2); however, only the control (100% retention) had significantly lower densities than all other retention intensities. In terms of maxi-

Fig. 2. The effect of overstory retention intensity on seedling density and seedling stocking rates. Bars with the same letter were not significantly different (Tukey’s test, $\alpha = 0.05$).

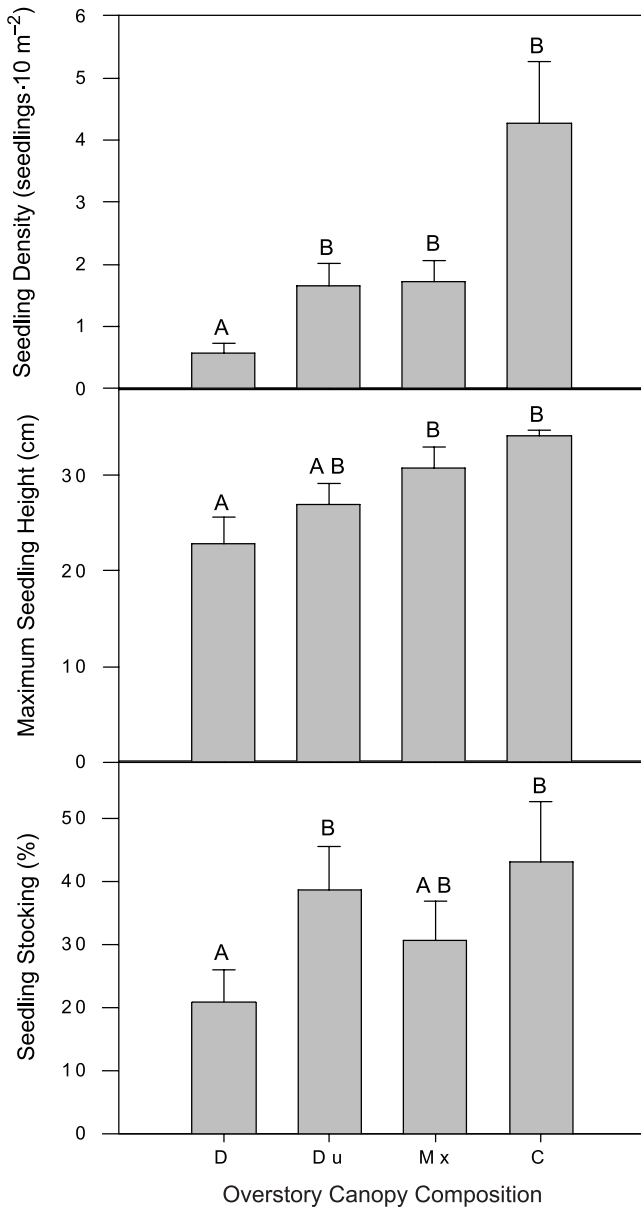


imum height, seedlings found in C stands (34.2 cm tall) and Mx stands (30.7 cm) were significantly ($p = 0.0002$) taller than those in D stands (22.8 cm), but these were not significantly ($p = 0.0772$) taller than those found in Du stands (26.9 cm) (Fig. 3). Surprisingly, average seedling height was not significantly affected by the retention intensity ($p = 0.1591$, Table 1).

Stocking rates were lowest in D stands (20.8%) compared with the cutting units from the other overstory compositions: C stands (43.0%), Du stands (38.5%), and Mx stands (30.5%) (Fig. 3). Similar to seedling densities, stocking rates gradually declined (following a quadratic form) with retention intensity. The highest stocking rates occurred in the clearcuts (53.7%) and the lowest rates within control compartments (7.8%) ($p < 0.0001$) (Fig. 2).

No environmental variables (e.g., grass or deciduous competition) provided significant explanation of seedling densities, height, or stocking (data not shown) nor were there any significant interactions among effects of these variables. Corridors had twice the mean grass cover (corridor: 24.9%,

Fig. 3. The effect of overstory composition on seedling density, seedling maximum height (cm), and stocking rates for the EMEND experiment. Bars with the same letter were not significantly different (Tukey's test, $\alpha = 0.05$).



interior: 11.7%; $p = <0.0001$) and somewhat higher deciduous cover (corridor: 67.9%, interior: 64.3%; $p = 0.0177$), while the interiors had higher cover of decayed logs (corridor: 4.3%, interior: 6.5%; $p = <0.0001$) and higher cover of fresh logs (corridor: 6.3%, interior 9.5%; $p = <0.0001$). C stands had the highest mean grass cover (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 decayed logs ($p = 0.0075$) and fresh logs ($p = 0.0168$). C and Mx stands had at least

three times more decayed log cover (7.0%) than D stands (2.0%). Decayed log cover was highest within the Mx stands (10.6%) and lowest within Du stands (5.0%).

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. Seedling density was most influenced by the corridor–interior dichotomy, as it provided the root node (6.42 seedlings·10 m⁻² in corridor plots, $n = 288$, vs. 0.93 seedlings·10 m⁻² in interior plots, $n = 288$) (Fig. 4). The second split was within the corridor group and was related to overstory canopy composition, where there were 14.4 seedlings per plot in C stands ($n = 72$) compared with 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 sixfold (6.28, $n = 112$) in the group with seed tree density greater than 32·ha⁻¹. The fourth split was within C stands and concerned seed tree densities, where transects with <70 seed trees·ha⁻¹ had low seedling densities per plot (4.79, $n = 30$), and if transects had >70 seed trees·ha⁻¹, density went up nearly fivefold (21.2, $n = 42$) (Fig. 4). The final split occurred within transects with >70 seed trees, where the highest overall seedling densities (28.1 seedlings·10 m⁻², $n = 26$) occurred within plots with lower levels of basal area retained (<32.5 m²·ha⁻¹).

The regression tree for seedling height explained 18.6% of the variance with a three-leaf tree (Fig. 5). The first split was determined by overstory canopy composition, where seedling height was lower in the D and Du stands (25.2 cm, $n = 190$) compared with the 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 was 25.9 cm ($n = 87$) compared with 39.8 cm in the corridor ($n = 125$).

For stocking rates, a six-leaf regression tree explained 43.2% of total variance (Fig. 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 hectare, above and below 11 — stocking was low (14.1%, $n = 110$) when seed trees·ha⁻¹ were <11 and double that (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%, $n = 175$) than 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 threefold 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 with the stocking in the 10%, 20%, and 50% retention corridors (80.6%, $n = 126$) (Fig. 6).

Efficiency of seed trees

The increased stocking with an increase in seed tree den-

Table 1. Analysis of variance of white spruce seedling density, maximum seedling height, and stocking rates 10 years following variable retention harvesting.

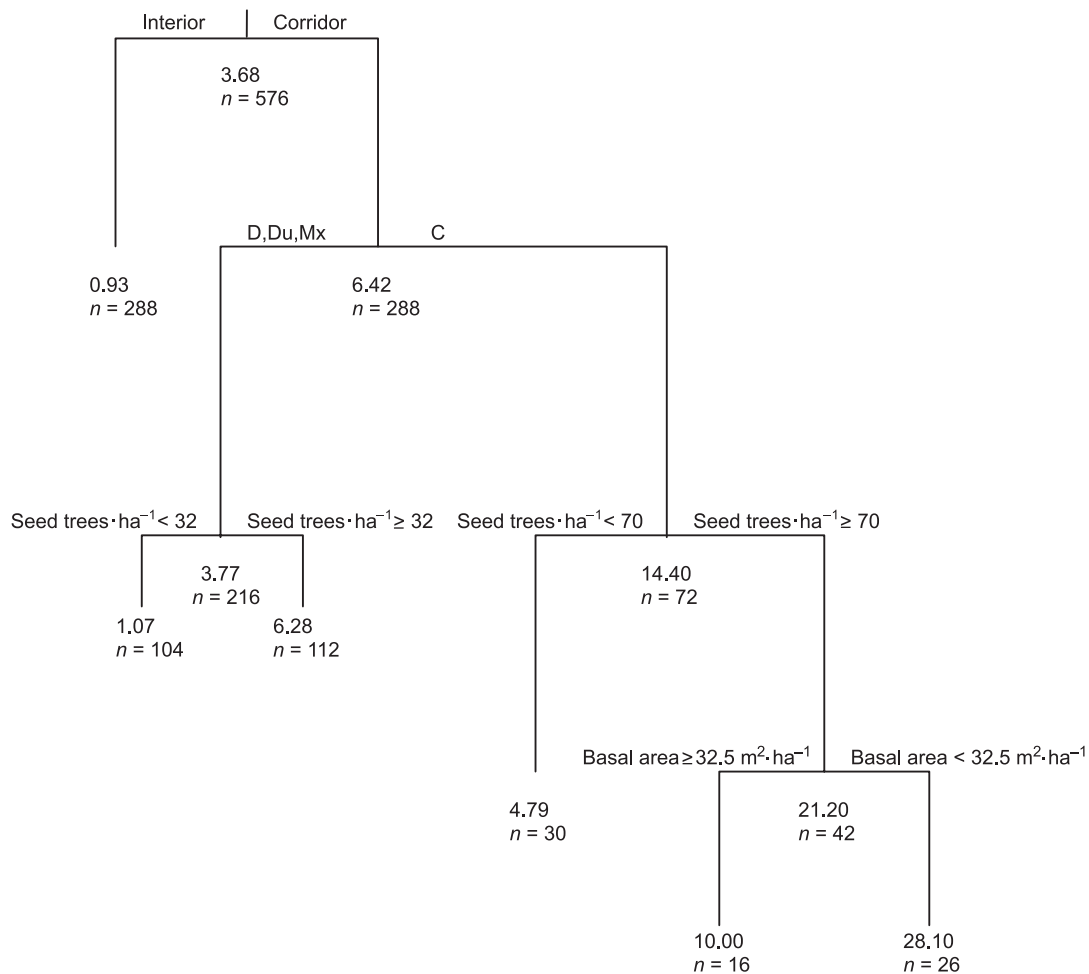
Sources of variation	df	Seedling density*	Max. seedling height	Stocking [†]
Overstory composition	3	0.0015	0.0002	0.0322
Overstory retention	5	<0.0001	0.1591	<0.0001
Composition × retention	15	0.7897	0.8688	0.8030
Error	48			
Total	71			

Note: Effects of overstory composition prior to logging, level of canopy retention, and their interaction are represented. Significant probability values at $\alpha < 0.05$ are in bold.

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

[†]Stocking is the percentage of 10 m² plots with at least one seedling.

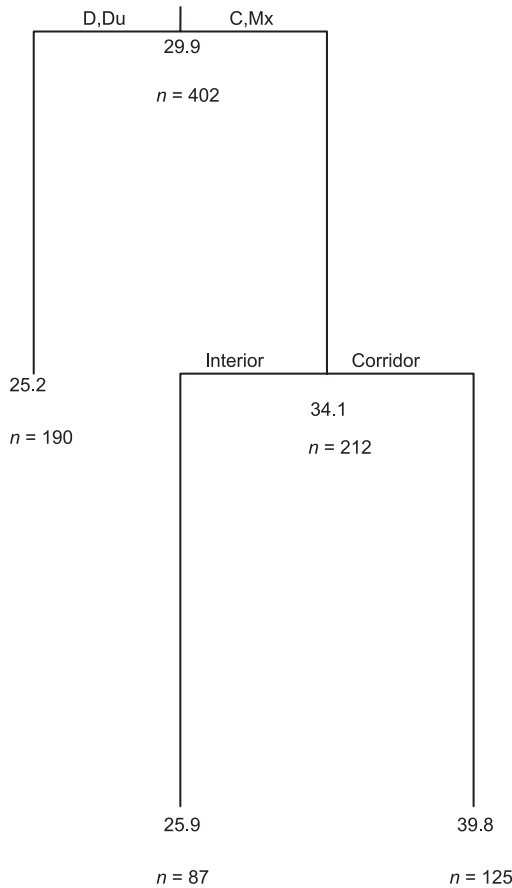
Fig. 4. Regression tree analysis of seedling density per 10 m² for the individual transects from the 10%, 20%, 50%, and 75% retention of mature trees. The explanatory variables considered were corridor and interior location, overstory canopy composition, density of seed trees surrounding the transect, total basal area of residual trees on the transect, decayed and fresh logs, 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.



sity was steepest in the clearcuts (Fig. 7). Retention of only 5 seed trees·ha⁻¹ produced an average of 59% stocking within the clearcuts, which was substantially higher than in any of the partial-harvest compartments (Table 2). Thus, stocking tended to reach higher levels in the clearcuts, 10%, and 20% retentions, while the average stocking peaked at less than 40% in the 75% retention. However, there was

substantial variation in the data (Fig. 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 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 clearcuts.

Fig. 5. Regression tree analysis of seedling maximum height (cm) per 10 m² 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 and interior location, overstory canopy composition, number of seed trees surrounding the transect, total residual basal area, decayed and fresh logs, deciduous cover of saplings, and shrubs and grass cover. This tree explained 18.6% of the total variance, and the vertical depth of each split is proportional to the variation explained. Note, as there were some transects without any seedlings, total sample size was reduced compared with other regression tree analyses.



Discussion

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 the success of white spruce regeneration on an operational scale. It showed that regeneration 10 years after harvest was (i) greater with high numbers of seed trees within 60 m, (ii) greater on machine corridors when the local site had been disturbed at harvest, and (iii) reduced when canopies were dominated by deciduous species (apparently because these sites had few seed trees). Furthermore, stocking was quite high within clearcuts, even with low numbers of seed trees.

Compartment level

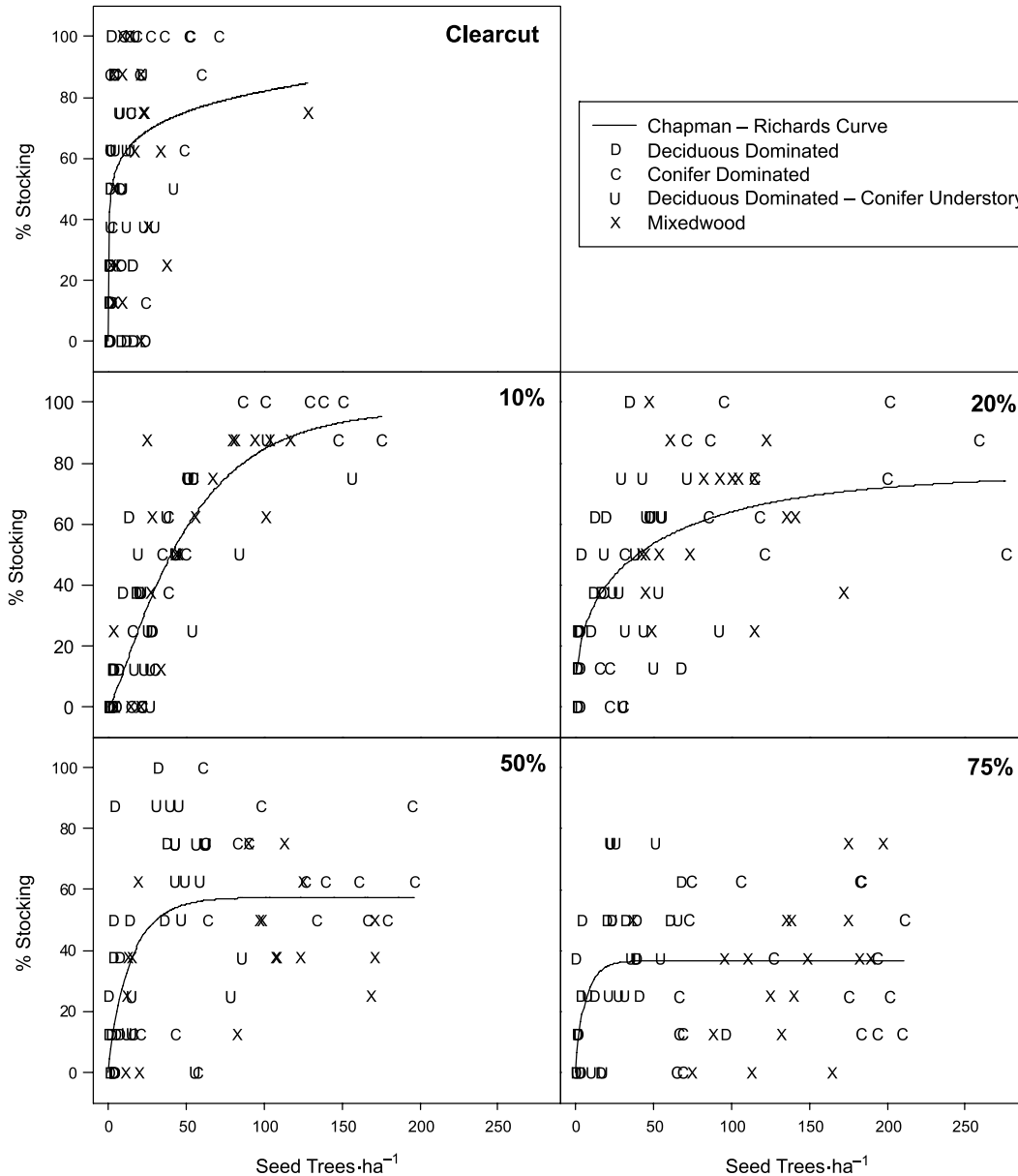
Surprisingly, there was little benefit to spruce regenera-

Table 2. Summary of nonlinear regression for stocking in relation to seed tree density for the different levels of retention (see eq. 1).

Overstory retention	Parameter estimate					% Stocking at a retention rate of:				
	a	b	c	MSE	Pseudo R ² *	5 seed trees·ha ⁻¹	10 seed trees·ha ⁻¹	25 seed trees·ha ⁻¹	50 seed trees·ha ⁻¹	
Clearcut (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	

Note: 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. *Pseudo R² calculated by 1 - (SS_{residual}/SS_{total corrected}) (Schabenberger et al. 1999).

Fig. 7. Percent stocking in relation to density of seed trees for clearcuts, 10%, 20%, 50%, and 75% residuals. Data were fit with the Chapman–Richard’s function using data from the interior and corridors combined, weighted by their area. Data from the uncut control were excluded from the analysis. $N = 72$, parameters are in Table 2.



those seedlings within the C stands. This contrasts with the results of Gradowski et al. (2008) who showed 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 have warmer soils (Macdonald and Fenniak 2007) than C stands, and thus, higher temperatures should have increased the 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 m² plot. With fewer seedlings in a plot, the plot is less likely to have a seedling with superior genetics, found on a superior microsite and (or) one that is recruited early after logging (Fig. 1). Thus, maximum seedling height may have been confounded with seedling density.

Transect level

Our transect-level analyses corroborated many features of the compartment-level analysis but also contributed new insights. Firstly, there was a sixfold increase in seedling density in machine corridors relative to interior positions (Fig. 4). As all overstory trees had been removed on corridors, the resulting higher light availability could have positively influenced seedling survival and height growth (Fig. 5). As in clearcuts, skidding will have exposed mineral soil in corridors. Surprisingly, variation in seedling densities within the retention strips (Fig. 4) was not further explained by the number of seed trees, overstory canopy composition, or level of overstory retention, further underscoring the overwhelming importance of a receptive seedbed in natural regeneration of spruce after harvest (Nienstaedt and Zasada

1990; Prévost and Pothier 2003). Secondly, the importance of seed trees in producing seedlings (Fig. 4) and in increasing stocking (Fig. 6) was also evident in our data, thus supporting other findings (Greene et al. 1999, 2002; Martin-DeMoor et al. 2010). Thirdly, maintaining very high levels of overstory cover reduced regeneration success, measured in terms of either density (Fig. 4) or stocking (Fig. 6), even if residual cover was composed of potential seed trees (Fig. 7). It is likely that long-distance dispersal of seed was better in clearcuts (Greene et al. 1999) because of greater ground-level wind speeds than in partial cuts. Fourthly, dense canopies will result in low light illumination and low temperatures in these stands that may reduce survival of white spruce (Constabel 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 and (or) interior locations were considered; it must also be remembered that seedlings located with corridors had better growth and stocking, but corridors also had higher rates of grass and deciduous cover. This is unexpected given the literature describing reduced growth in relation to competition from aspen regeneration (Groot 1999) or grass competition (Lieffers et al. 1996; Cater and Chapin 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 Fig. 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 decayed or fresh logs. It has long been recognized that decayed logs can provide improved local microhabitats 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 decayed logs. Also, while removal of fresh logs on corridors likely created more seedbeds immediately after logging, the presence of fresh logs (inappropriate as seedling microsites) in the interior may have removed seedbeds.

Advanced 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 multicohort stands of white spruce and aspen. CLAAG (careful logging around advanced growth), CPRS (Coupe avec protection de la régénération et de sols) (e.g., Ruel et al. 2000; Greene et al. 2002; Chen and Wang 2006), and 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.

Management implications

This study illustrates, firstly, that on average, leaving ≥ 30 trees-ha⁻¹ can produce 55% stocking, and stocking is further increased on the systematic machine corridors employed in partial retention harvests. In clearcuts, 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 the use of partial retention would not be met on clear-cut blocks. Nonetheless, in this region, clear-cutting and passive site preparation are an acceptable means of producing natural white spruce regeneration, provided that seed trees are retained within 60 m; and this method should be considered 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 six times more regeneration occurring on the corridors than on the wider area of undisturbed substrates between the corridors. Intentionally disturbing the forest floor of these interior positions could potentially increase the overall stocking of these stands. We also found natural regeneration in an understory protection cut is possible (Fig. 3), suggesting that multicohort stands can be produced by understory protection system using defined machine corridors.

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