Data analysis

Abundance of seedlings and sapling density

To characterize regeneration dynamics following partial harvesting, the first step was to model seedling abundance and sapling density for the main species of interest (i.e. white-cedar, sugar maple and yellow birch) after treatments. Seedling and sapling analyses were conducted separately because we assumed that the establishment of seedlings was the result of the canopy treatments and that the saplings were probably established before the interventions. All analyses were conducted using SAS (version 9.1, SAS Institute Inc., Cary, NC, USA). Mixed linear models were developed to examine the effects of canopy treatments on each species abundance using the GLIMMIX procedure. This procedure was selected because of the presence of hierarchical random effects. To reflect this hierarchical structure of variance, subplots nested within plots, which were themselves nested within sites, were considered as random effects. For the abundance of seedlings, the CLASS statement integrated canopy treatments, height class, browsing, and ecological region as classification variables. Canopy treatments were divided into four categories according to harvested basal area: three intensities of selection cutting and control (table 4). The Ecological Region was included into the model to reflect composition and vegetation dynamics of the sites. In the MODEL statement, basal area after harvesting, percent cover of the understory, and year of harvesting were also used as explanatory variables. Only the basal area of the modeled species was integrated in each model to test the importance of seed trees in the stand. Percent cover was used as an indicator of understory competition. Only the presence or absence of browsing in the subplot was integrated into the model because of the small number of observations. For sapling density, essentially the same parameters were used in the model except the percentage of cover that was replaced by the density of non-commercial tree species and the height class by DBH class. In addition, there were not enough observations of browsing on white-cedar saplings to integrate this variable into the model. Abundance of seedlings and sapling density data followed a negative binomial distribution due to the high presence of zeroes in the data set. The distribution followed by the data set was specified in the DIST statement.

Table 4: Number of plots by canopy treatments

Canopy treatments	Code	Plots	Description
Low intensity selection cutting	**TR15**	20	10 to 20% of the harvested basal area
Medium intensity selection cutting	**TR30**	23	21 to 40% of the harvested basal area
High intensity selection cutting	**TR50**	12	41 to 60% of the harvested basal area
No treatment (control)	**TE**	15	No recent harvesting activity

Establishment microsite

For each height class, the distribution of available microsites (litter and microtopography type) was compared with the distribution of microsites used by white-cedar seedlings using χ^2 test. This comparison provides information on establishment microsites preferred by white-cedar and their availability in the stand. The abundance of seedlings should be more important in areas with more favorable microsites available.

Results

Abundance of seedlings

White-cedar seedlings were present in more than 85% of the plots while maple and yellow birch seedlings occurred in 90% and 65% of the plots respectively. Likewise, throughout the study area, maple seedling density (mean = 0.61 seedling/m^2) was much higher than for yellow birch and white-cedar (mean = 0.10 and 0.25 seedling/m^2 respectively). Softwood species seedlings were present in 96% of the plots for balsam fir (*Abies balsamea* (L.) Mill.), 21% for white pine (*Pinus strobus* L.) and less than 10% for hemlock (*Tsuga canadensis* (L.) Carrière). The presence of other species like paper birch (*Betula papyrifera* Marsh.), American beech (*Fagus grandifolia* Ehrh.), red oak (*Quercus rubra* L.), black ash (*Fraxinus nigra* Marsh.), white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.) was marginal (< 5%).

Local abundance of seed trees, measured by the species merchantable basal area, was significant for white-cedar and maple seedlings densities (table 5). Basal area in the plots ranged between 0 and 12.2 m^2/ha for white-cedar and between 0 and 15.6 m^2/ha for maple. Seedling abundances increased with the basal area of the species but the coefficient of determination is higher for white-cedar (figure 5).

Table 5: Test III of fixed effects for seedling abundance of main species

Source of variation	dfn[a]	white-cedar			maple spp.			yellow-birch		
		dfd[b]	F value	Pr>F	dfd	F value	Pr>F	dfd	F value	Pr>F
Canopy treatment (T)	3	170.9	2.04	0.1106	83.03	0.61	0.6078	129	3.70	**0.0136**
Height class (H)	2	2079	59.55	**<.0001**	1649	38.89	**<.0001**	2078	22.05	**<.0001**
T x H	6	2079	2.54	**0.0187**	1648	4.01	**0.0005**	2078	1.96	0.0686
White-cedar basal area	1	128.6	29.28	**<.0001**	-	-	-	-	-	-
Maple basal area	1	-	-	-	67.87	17.60	**<.0001**	-	-	-
Yellow birch basal area	1	-	-	-	-	-	-	91.2	2.31	0.1316
Percent cover of the understory (C)	1	2079	13.66	**0.0002**	2078	0.04	0.8507	1516	0.18	0.6701
Browsing (B)	1	688	0.08	0.7725	2078	15.05	**0.0001**	1103	9.86	**0.0017**
Year of cut (Y)	1	178	10.89	**0.0012**	83.77	0.52	0.4711	78.06	0.20	0.6542
Ecological region (E)	2	165.7	2.19	0.1146	77.25	1.60	0.2087	133.6	3.55	**0.0313**

Note:
[a] *Numerator degrees of freedom.*
[b] *Denominator degrees of freedom.*

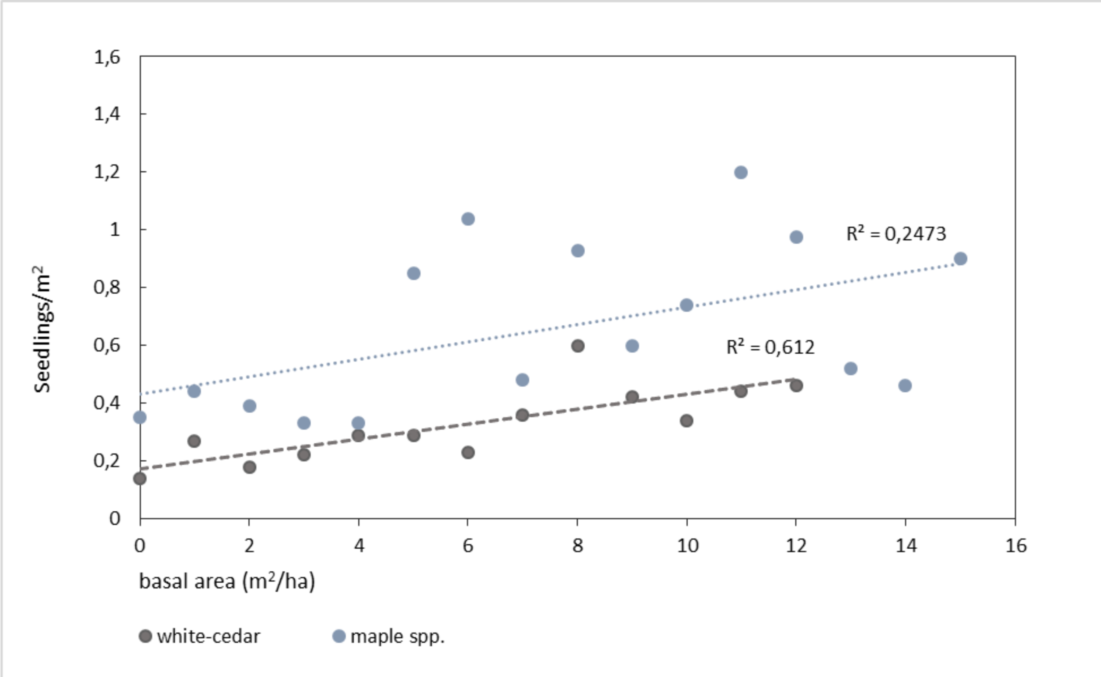

Figure 5: Relationships between seedling density by high class and species merchantable basal area for white-cedar and maple.

Harvesting intensity ranged between 10 and 58% of the merchantable basal area depending on the plots. The effect of canopy treatments was significant for yellow birch seedlings with no significant interaction with height class (table 4). The lowest abundance of seedlings was observed in high intensity selection cutting compared to low intensity selection cutting and control plot (figure 6c). Maple and white-cedar seedling abundances were both influenced by the interaction between height class and canopy treatment (table 4). Total density of white-cedar seedlings was slightly higher in all canopy treatments than in the control. For maple seedlings, total density was slightly higher in the high intensity selection cutting. For white-cedar, medium seedlings were the most abundant in all canopy treatments and the highest abundance was observed in the low intensity selection cutting (0.14 seedlings/m^2) (figure 6a). Maple seedling abundance was higher than yellow-birch and white-cedar abundance for most height classes in all canopy treatments, with the exception of large seedlings, where yellow-birch density was higher than maple. Except in the control, abundance of small and medium maple seedlings was practically the same in each canopy treatment (figure 6b). The control showed a different distribution of maple seedlings, with a higher abundance of small seedlings and lower abundance of large seedlings.

Analysis showed that plots in ecological region 3b had a lower abundance of yellow birch seedlings (mean = 0.04 seedlings/m^2) compared to ecological regions 3a and 4b (mean = 0.11 seedlings/m^2 for both regions) (table 4). For white-cedar and maple no variations between the three ecological regions were observed on seedling abundance.

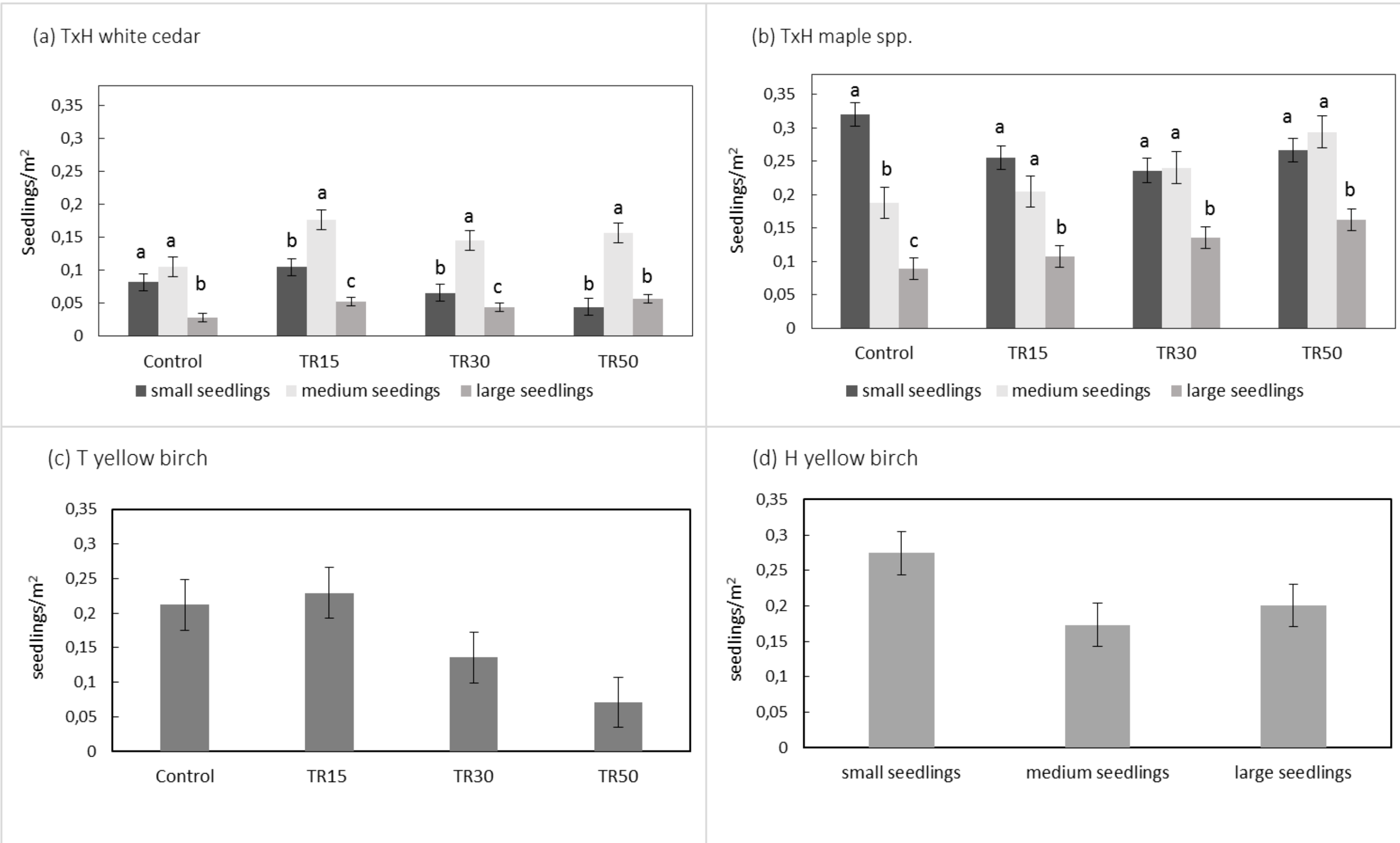

Figure 6: Effect of canopy treatment and height class on the number of seedling per height class. Error bars show 95% confidence intervals.

Letters indicate significant differences between the mean density of height classes in each canopy treatment.

T, treatment; H, height class; T X H, interaction between treatment and height class
TR15, low intensity selection cutting; TR30, medium intensity selection cutting; TR50 high intensity selection cutting.
Maple spp. included sugar maple and red maple

The abundance of white-cedar seedlings was influenced by the percent cover of the understory (table 4). The abundance of seedlings decreased drastically when percent cover was high (>50%). Over 75% of percent cover, only a few small seedlings were present in the subplot (figure 7).

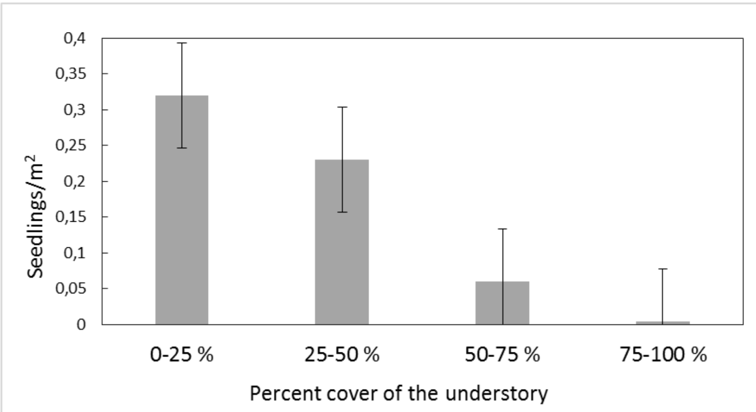

Figure 7: Abundance of white-cedar seedlings in relation with percent cover of the understory. Error bars show 95% confidence intervals.

The presence of browsing had a significant effect on maple and yellow birch seedling abundance (table 4). For these two species, the proportion of seedlings browsed increased with each height class, and over 40% of the large seedlings showed some browsing damage (figure 8). However, most of the damage observed was not severe, with an average of only 25% of the foliage consumed for the majority of the browsed seedlings. Only a few of the large seedlings (<5%) were classified as "moribund" because >50% of their branches were dead or dying. Only a very small percentage of white-cedar seedlings presented signs of browsing (< 10%) and their survival did not appear to be compromised by these damages (figure 8). Differences between browsing by moose and deer were difficult to evaluate. However, presence of moose faeces was observed on the majority of sites. Some signs of browsing by hare and other small mammals were also observed but they were marginal (<5%).

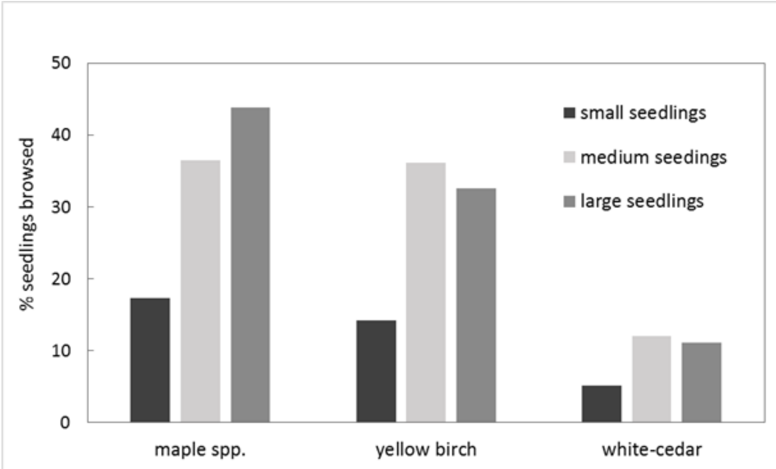

Figure 8: Percent of seedlings browsed for main species throughout all study plots

Sapling density

The effect of canopy treatments was significant for maple sapling density (table 5). Density of maple saplings increased significantly with harvesting intensity. In high intensity selection cutting, the density of small maple saplings was nearly five times higher than in the control (mean = 1167 and 233 stems/ha respectively). The same result was not observed for the density of yellow birch and white-cedar saplings. Significant differences were observed only between DBH classes and there was no significant interaction between DBH classes and treatments for all species. Basal area in seed trees in the plot are significant for maple and yellow birch but not for white-cedar. For those two species, sapling density increased with the basal area. The results showed a slight increase of white-cedar sapling density with the year of cut. Plots that have been harvested in 1995 showed higher saplings density than the others. Analysis showed the same results for yellow birch seedlings and saplings densities concerning the ecological regions. Plots in ecological region 3b had a lower abundance of sapling compared to ecological regions 3a and 4b.

Table 6: Test III of fixed effects for sapling density of main species

Source of variation	dfn[a]	white-cedar			maple spp.			yellow-birch		
		dfd[b]	F value	Pr>F	dfd	F value	Pr>F	dfd	F value	Pr>F
Canopy treatment (T)	3	57.4	0.96	0.416	80.3	3.06	**0.0328**	90.4	0.46	0.709
DBH class (C)	1	9.1	55.6	**<.0001**	127	102.8	**<.0001**	61.7	61.8	**<.0001**
T x C	3	9.5	0.36	0.782	103.3	1.98	0.122	60.2	0.27	0.847
Basal area (BA)	1	44.8	1.02	0.318	63.9	7.36	**0.0086**	75.7	6.00	**0.0166**
Non-commercial sapling density	1	44.6	0.05	0.823	52.6	0.07	0.796	43.3	0.89	0.350
Year of cut (Y)	1	116.1	8.21	**0.0049**	64.4	1.19	0.279	59.7	0.30	0.585
Ecological region (E)	2	101.4	2.40	0.096	61.85	1.26	0.292	62.1	2.85	**0.0653**

Note:
[a] *Numerator degrees of freedom.*
[b] *Denominator degrees of freedom*.

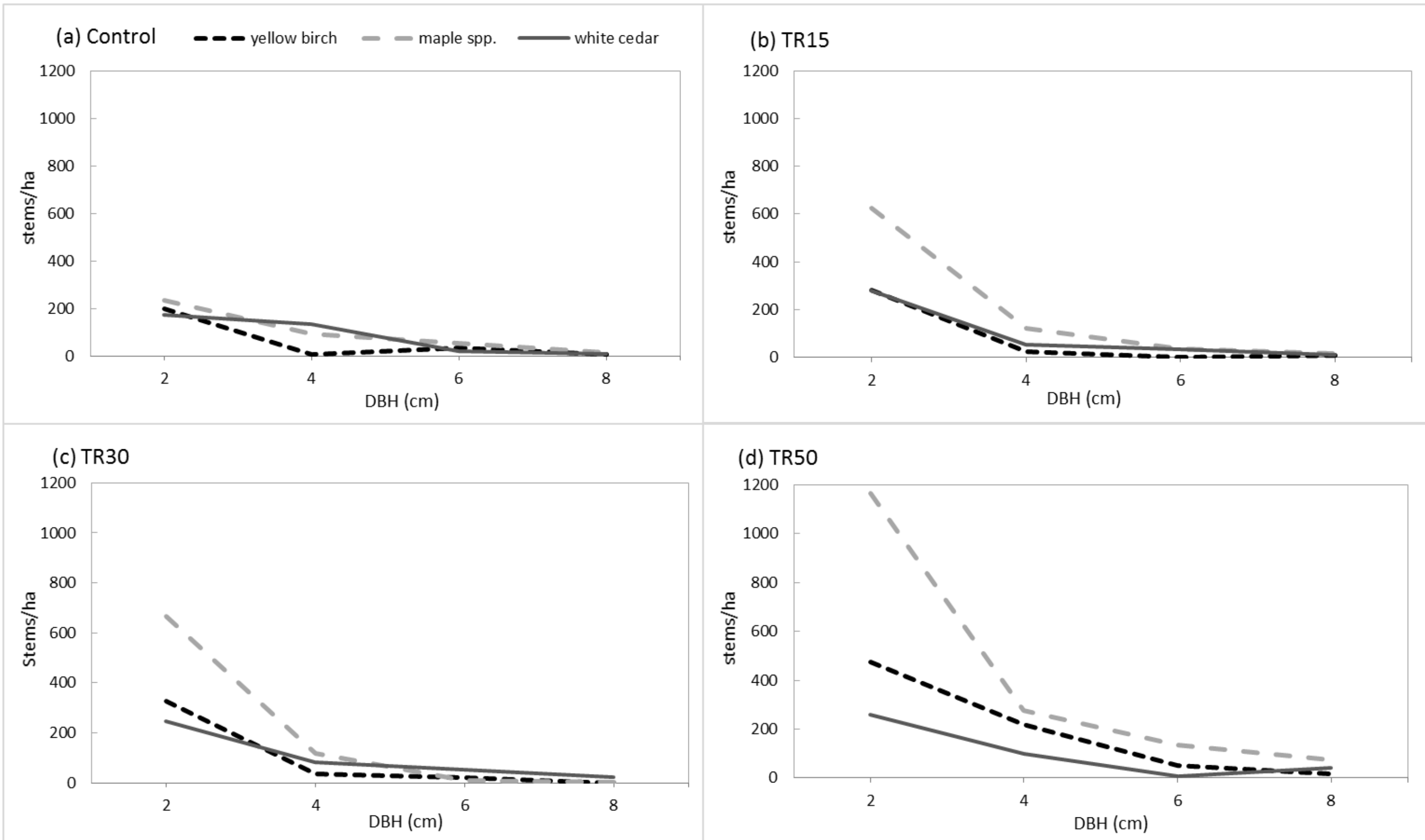

Figure 9: Sapling density for main species by DBH class for each canopy treatment.

Same legend as figure 5.

Establishment microsite of white-cedar seedlings

Relative frequency of microtopography types at the subplot center showed only 8% of mounds available (table 6a). However, more than 20% of the small seedlings were found on mounds (figure 10a). Medium and large seedlings followed the pattern of site availability for microtopography types (table 6a). Important differences were found when the proportion of white-cedar seedlings in a given height class were compared to litter type availability (table 6b). The relative frequency of all height classes of white-cedar seedlings were proportionally higher on decaying wood than on all other substrates when compared to the litter type availability (control), especially for small seedlings (figure 10b). Hardwood litter was the most available substrate but was proportionally less used by white-cedar seedlings (table 6b).

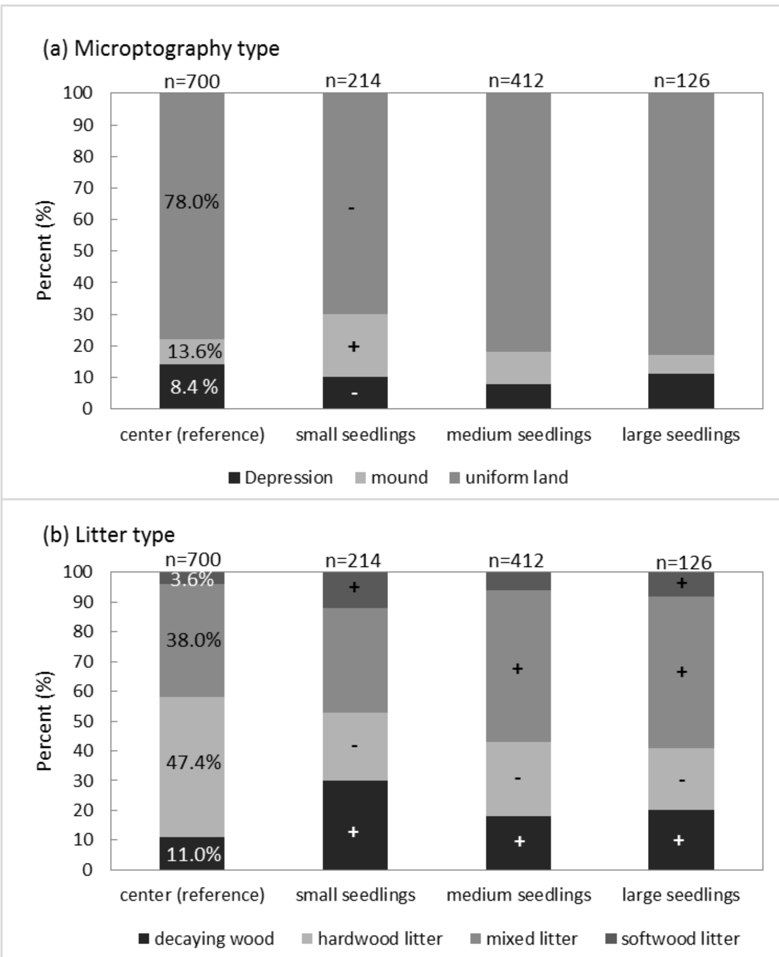

Figure 10: Distribution of white-cedar seedlings by height class and microsite availability; (a) relationship with microtopography type, (b) relationship with litter type.

Note: + or – indicates a significant difference superior or inferior to the general distribution (a) $\chi^2=12.99; p<0.01$
(b) $\chi^2=21.86; p<0.01$
n= number of observations

Discussion

Results showed that white-cedar seedlings can be regenerated by operational scale selection cutting. White-cedar seedlings were present in all plots independently of the canopy treatment. However, operational scale selection cutting generated a very important variation in harvesting intensity. At the plot level, basal area harvested varied between 10 and 58%. Consequently, this has certainly created an important gradient of light availability in residual stands (Palik et al. 1997, Beaudet et al. 2011). This heterogeneous light environment likely contributed to the observed variation of the white-cedar seedlings abundance between height classes.

Abundance of seed trees is an important criteria for the establishment of white-cedar seedlings. The results obtained confirm our hypothesis. Abundance of white-cedar seedlings increase with the residual basal area of white-cedar in the plot. Seed tree abundance is even more important because the seed dispersal distance of white-cedar is relatively short, around 60 meters (Rooney et al. 2002). Also, seed viability on the forest floor is very short (less than one year) and hence, there is no white-cedar seed bank in the soil (Johnston 1990; Béland et al. 2013). Thus, without seed trees in the stand, the establishment of white-cedar seedlings is compromised. Approaches using low intensity selection cutting like single-tree selection cutting could favor the conservation of seed trees in the stand for many decades, allowing the progressive build-up of the seedling bank, despite the lower competitively of cedar over other species (Miller 1992; Schaffer 1996; Cornett et al. 1997; Asselin et al. 2001 Rooney et al. 2002). The abundance of seed trees was also significant for maple but not for yellow birch. The fact that yellow birch seeds can disperse over a longer distance may explain that the presence of regeneration was not directly related to the presence of seed trees in the plot. Maple, like white-cedar, also has a relatively short seed dispersal distance that explains the close relation between the presence of seed trees in the plots and the abundance of seedlings.

The light requirements of white-cedar seedlings are not the same for the establishment and for the growth of established seedlings (Larouche et al. 2011). White-cedar seedlings need 11 to 13 years to reach 30 cm height and another 8 to 20 more years to reach more than 1 meter (Larouche 2009). Fifteen to 19 years after harvesting activities, the majority of the white-cedar seedlings were classified has medium seedlings, between 30 and 100 cm tall. The highest abundance of white-cedar seedlings, all height classes combined, was observed in the low intensity selection cutting. In this canopy treatment, partial shading maintains temperature and