Materials and methods

Study sites

This study used 23 sites from a larger network established by the Ministère des Forêts, de la Faune et des Parcs, Quebec, Canada (MFFP) in order to monitor operational effects of selection cutting. The network is composed of 282 stands managed under Timber Supply and Forest Management Agreements. It includes a total of 971 permanent plots distributed in paired treated and control areas. Both areas presented similar characteristics, did not had recent interventions and were located close one to each other. The harvesting activities took place between 1995 and 1999 and were conducted according to operational guidelines. For the study, only groups of permanent plots (treated and control) located in mixedwood stands with a minimum of 10% of the merchantable basal area in white-cedar before harvesting activities were selected. Difficult access to certain areas 20 years after the first data collection allowed a total of 70 permanent plots to be retained for the study. Permanent plots were 400 m^2 in area (circular plot of 11.28 m radius) and were measured by MFFP before harvesting and 0, 5 and 10 years after harvesting. Data from these inventories were provided according to a collaboration agreement between MFFP and Laval University. Additional regeneration and browsing inventories were conducted for this study during summer 2014.

The sites were located in three different regions of western Quebec. Nine sites were located approximately 100 km South East of the town of Ville-Marie in the Témiscamingue Region (47°20'N, 79°26'W), four sites were located 65 km north of the town of Mont-Laurier in the Hautes-Laurentides Region (46°33'N, 75°30'W) and the remaining sites were located 70 km North of the town of Ottawa in the Outaouais Region (45°90'N, 75°62'W). Most of the sites are within the sugar maple-yellow birch bioclimatic domain but the four northernmost lie within the Balsam fir-yellow birch bioclimatic domain (figure 3). Mean annual temperature ranges from 2.5 to 5.0 °C and mean annual precipitation reaches 1000 mm for the sugar maple-yellow birch bioclimatic domain (Saucier et al. 2009). For the Balsam fir-yellow birch bioclimatic domain, the mean annual temperature range is lower (1.5 to 2.5 °C) and the precipitation is slightly higher (1100 mm). Undifferentiated till was the main surface deposit, all sites are mesic and elevation ranged from 260 to 485 meters.

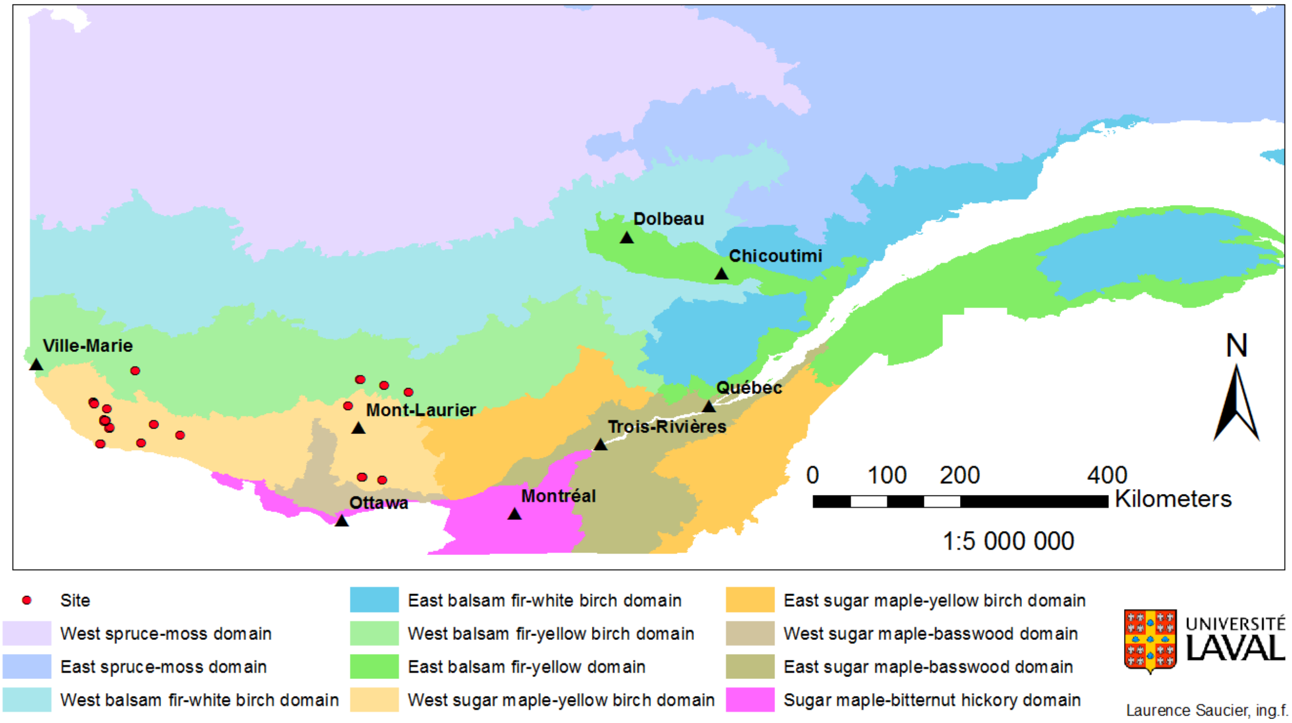

Figure 3: Location of the study sites within bioclimatic subdomains.

Forest description and harvest treatments

The majority of the plots were located in mixedwood stands dominated by deciduous species. The most representative stand types were dominated by yellow birch (*Betula alleghaniensis* Britt.) with a minor component of white-cedar or sugar maple (*Acer saccharum* Marsh.). Mixedwood stands dominated by sugar maple or evergreen species such as hemlock (*Tsuga canadensis* (L.) Carrière) or white-cedar were also found on a few plots. Table 1 presents the main forest stands and the distribution of the plots. Table 2 shows the characteristics before, after, and 10 years after harvesting for the main types of mixedwood stands. Before the treatment, mean diameter at breast height (DBH measured at 1.3 m) was 21.1 cm, mean basal area was 24.3 m^2/ha and mean basal area in white-cedar was 4.6 m^2/ha. After treatment, mean DBH increased by 1.0 cm while mean basal area decreased by 1.5 m^2/ha. The white-cedar basal area has not decreased much, suggesting that very few stems were targeted during the selection cutting. Ten years after treatment, mean DBH increased to 23.0 cm, mean basal area increased to 25.6 m^2/ha and mean basal area in white-cedar increased slightly from 4.2 m^2/ha to 4.4 m^2/ha.

Horizontal stand structure was mostly heterogeneous and the vertical structure was irregular with multiple layers. The understory was composed of a mix of competing species such as striped maple (*Acer pennsylvanicum* L.), mountain maple (*Acer spicatum* Lamb.), squashberry viburnum (*Viburnum edule* (Michx) Raf.) and saplings of species forming the canopy. There was no major disturbance reported, only a few stems were affected by minor windfall.

Table 1 : Number of plots by stand type

Description	Stand code	Secondary species	plots
Mixedwood stands dominated by yellow birch	**BjSb**	balsam fir	7
	BjTo	white-cedar	15
	BjEr	sugar maple	20
	BjPu	hemlock	2
Mixedwood stands dominated by sugar maple	**ErBj**	yellow birch	7
	ErSb	balsam fir	4
	ErTo	white-cedar	2
Mixedwood stands dominated by hemlock	**PuBj**	yellow birch	4
	PuTo	white-cedar	4
Mixedwood stands dominated by white-cedar	**ToBj**	yellow birch	3
	ToEr	sugar maple	2

Table 2: Characteristics before, after and 10 years after harvesting

Stand code	Characteristics	before	after	10 years after
Mean (all stands)	DBH (cm)	21.1 ± 0.5	22.2 ± 0.4	23.0 ± 0.4
	Basal area (m^2/ha)	24.3 ± 0.6	22.8 ± 0.5	25.6 ± 0.4
	white-cedar basal area (m^2/ha)	4.6 ± 0.1	4.2 ± 0.2	4.4 ± 0.2

The plots are located in the northern part of the distribution of white-tailed deer (*Odocoileus virgianus* Zimmerman) populations (Hébert et al. 2013). In the Témiscamingue region, densities of white-tailed deer are difficult to evaluate because there is no hunting record. In the Outaouais and the Hautes-Laurentides regions, the population densities of white-tailed deer in 2011 were estimated at about 0 to 2 deer/10 km^2 (Hébert et al. 2013). However, moose (*Alces alces* Gray) are also present in the study area and the populations in 2008 were estimated as 2.8 ± 0.3 moose/10 km^2 for the Témiscamingue region and slightly lower (2.4 ± 0.3

moose/10 km^2) for the Outaouais and Hautes-Laurentides regions (Lefort and Massé 2015). Hare (*Lepus americanus* Erxleben) was not abundant in the study sites, only occasional and random browsing was observed on regeneration in a few sites.

Plots implementation

Regeneration and browsing inventory

In each 400 m^2 permanent plot, a regeneration survey was carried out between June and August 2014, 15 to 19 years after harvesting activities depending on the sites. The seedlings (DBH < 1.1 cm) were numbered in 10 circular 4 m^2 subplots and all the saplings, including non-commercial tree species, were counted by species in 2 cm DBH classes (DBH between 1.1 and 9.0 cm) in one circular 100 m^2 plot (figure 4). The distance between each center of 4 m^2 subplots was 5 meters. As the requirements of the seedlings are not the same according to their stage of development, it became interesting to distinguish the seedling height classes. We distinguished three demographic categories for the regeneration based on seedling height. We classified all the regeneration between 15 to 30 cm tall as "small seedlings", those from 31 to 100 cm as "medium seedlings" and those higher than 101 cm but smaller than 1.1 cm DBH as "large seedlings". Seedlings between 0 and 15 cm were not inventoried because they were not considered as established. The establishment phase extends from seed germination until juvenile mass mortality is no longer to be feared and seedlings are able to react to canopy opening (Larouche 2009). No distinction between sexual and asexual reproduction was made because of the difficulties in differentiating both types on established seedlings without destroying them. Percent cover of the understory layer was estimated in each subplot to evaluate understory competition. Percent cover includes all concurrent species taller than seedlings (> 15 cm) such as herbaceous, shrubs and abundant species of the understory like striped maple, mountain maple, squashberry viburnum and saplings of species forming the canopy. Browsing was assessed on each seedling in subplot by herbivore type (deer or moose, and hare) and by percentage of the foliage consumed. For each white-cedar seedling, characterization of the establishment microsite was carried out according to microtopography and litter type at the rooting site (table 3). Characterization according to the same categories was also made for the center of each 4 m^2 subplot to estimate microsite and litter availability.

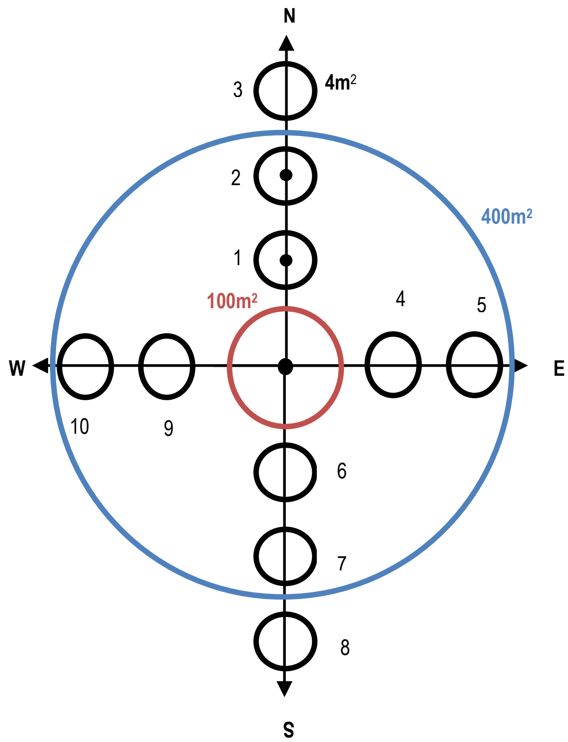

Figure 4: Illustration of the subplots distribution in one 400 m² study plot.

Table 3: Characterization of the establishment microsites according to microtopography and litter type

	Code	Description
Microtopography type		
Mound	MT	
Depression	DP	
Level ground	TU	
Litter type		
Hardwood	LF	Litter mostly composed of hardwood leaves
Softwood	LR	Litter mostly composed of softwood needles
Mixed	LM	Litter composed of softwood needles and hardwood leaves
Decaying wood	BM	All coarse woody debris, boles, stumps, or branches

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

		white-cedar			maple spp.			yellow-birch		
Source of variation	dfn[a]	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.*

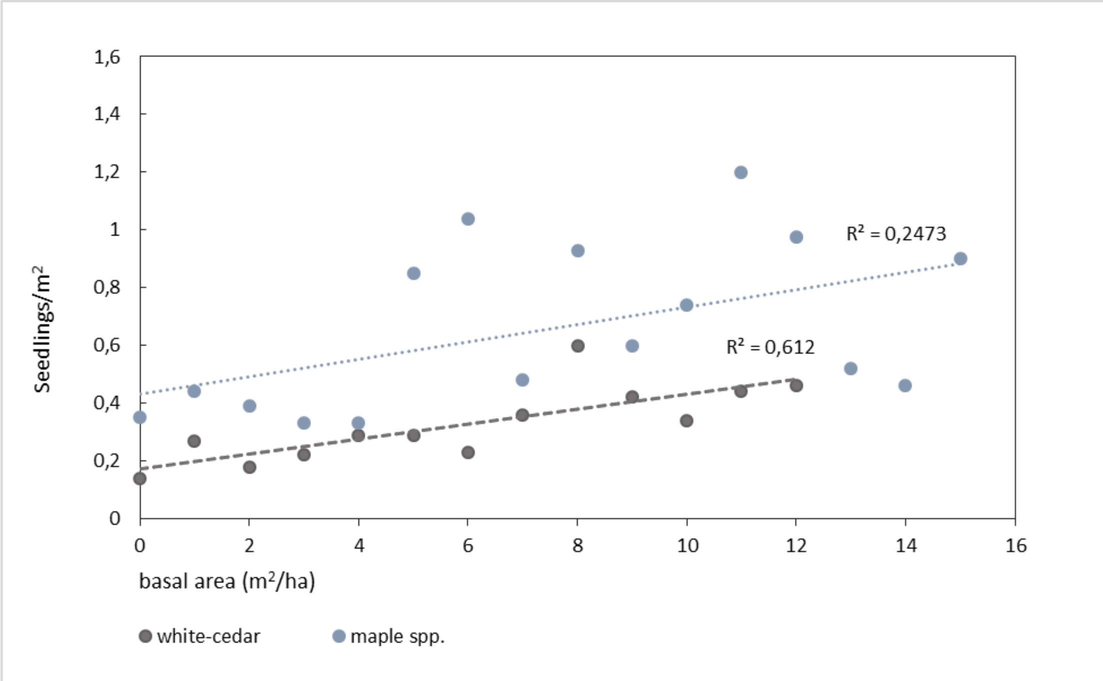

Figure 5: Relationships between seedling density by high class and species merchantable basal area for white-cedar and maple.

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.

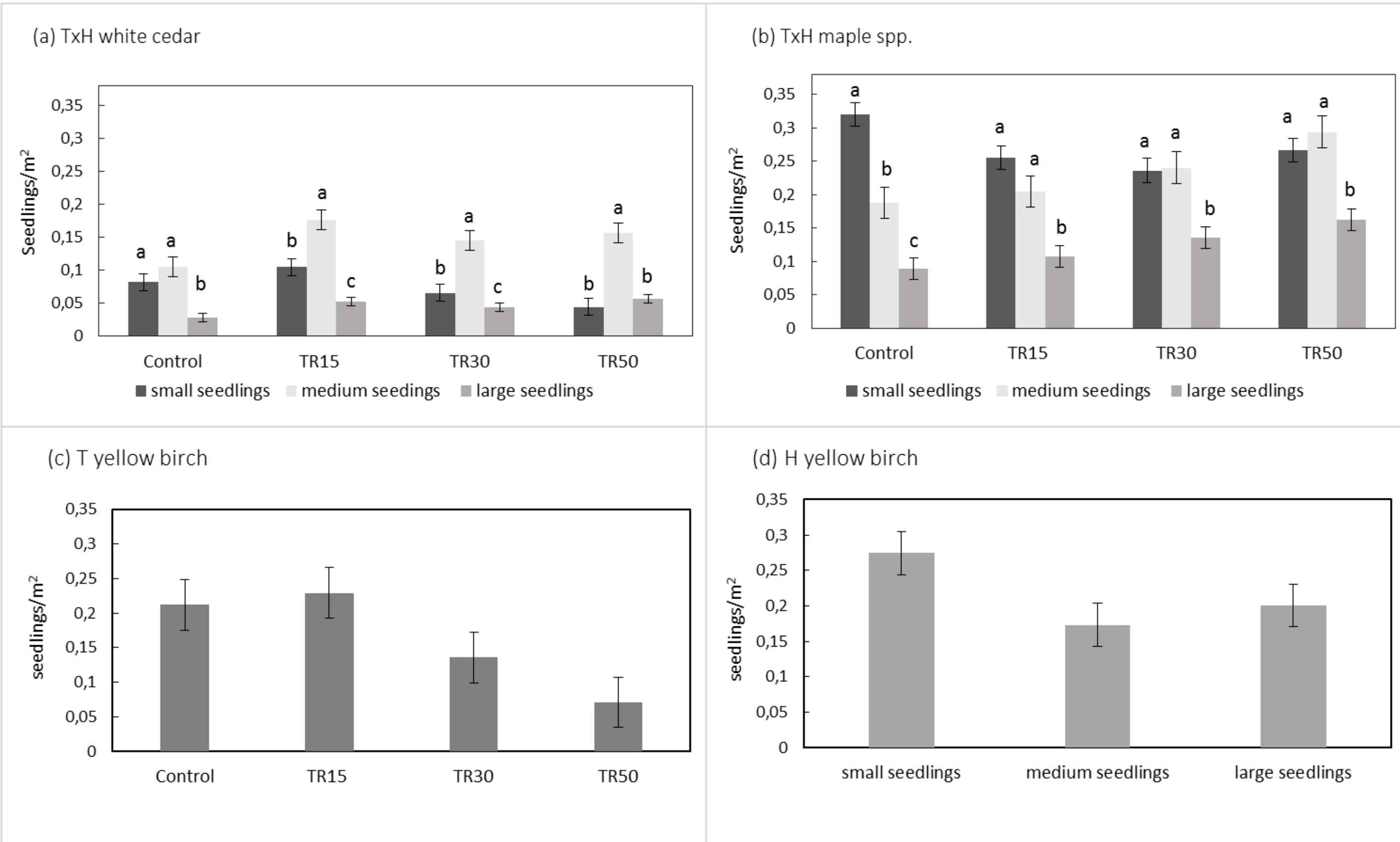

Figure 6: Effect of canopy treatment and height class on the number of seedling per height class. Error bars show 95% confidence intervals.

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).

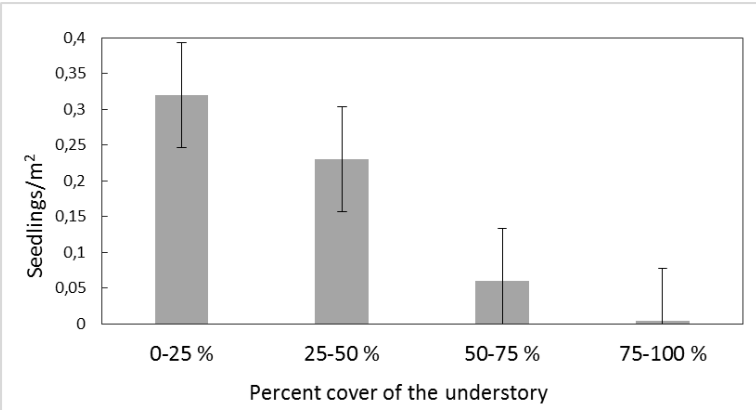

Figure 7: Abundance of white-cedar seedlings in relation with percent cover of the understory. Error bars show 95% confidence intervals.

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%).

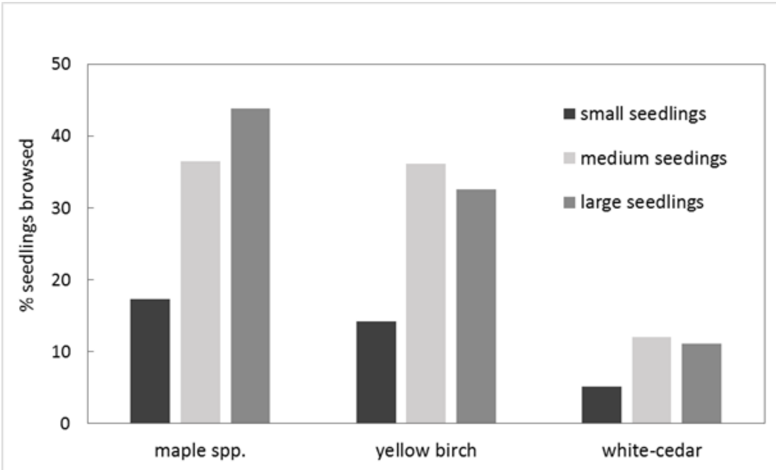

Figure 8: Percent of seedlings browsed for main species throughout all study plots

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

		white-cedar			maple spp.			yellow-birch		
Source of variation	dfn[a]	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*.

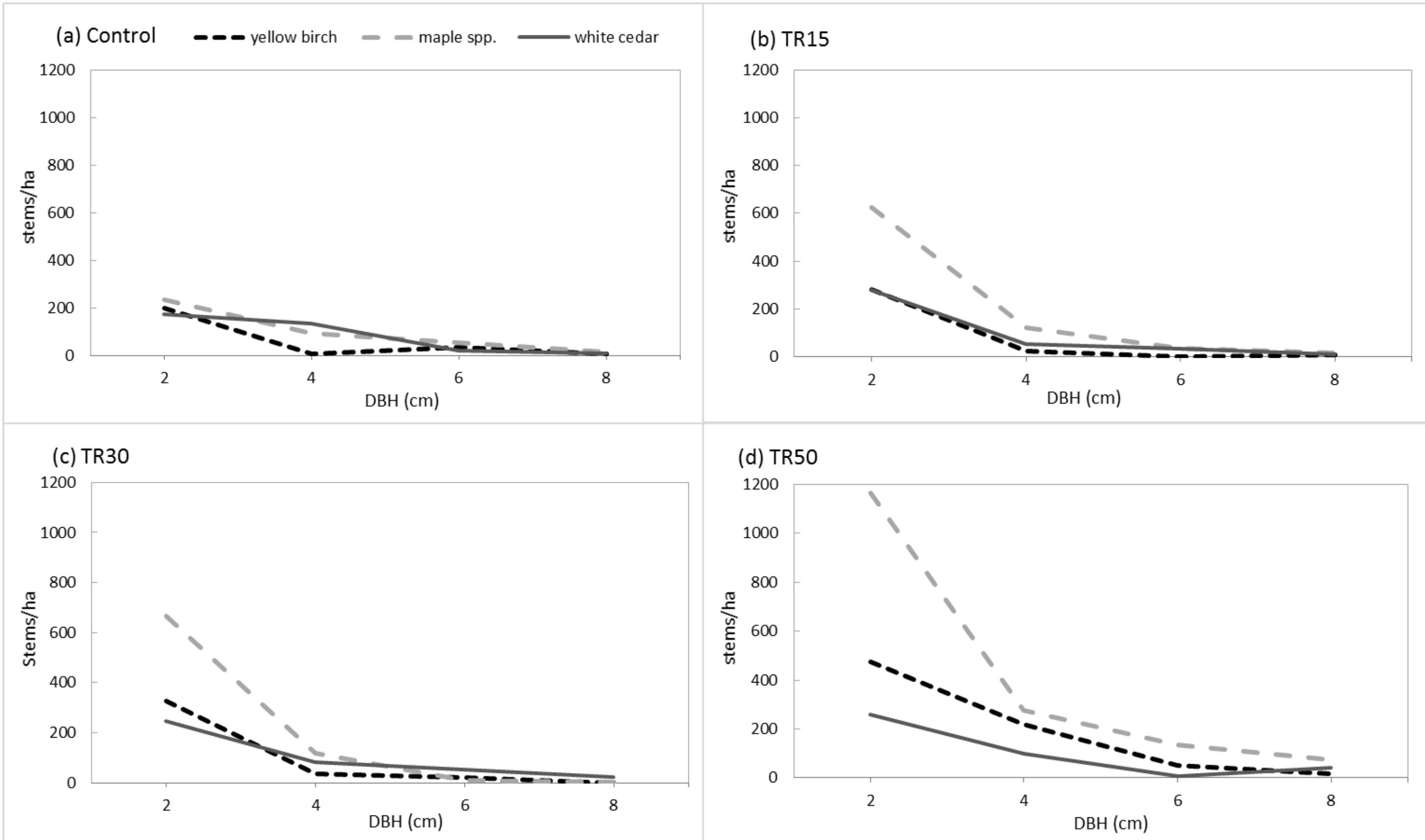

Figure 9: Sapling density for main species by DBH class for each canopy treatment.

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).

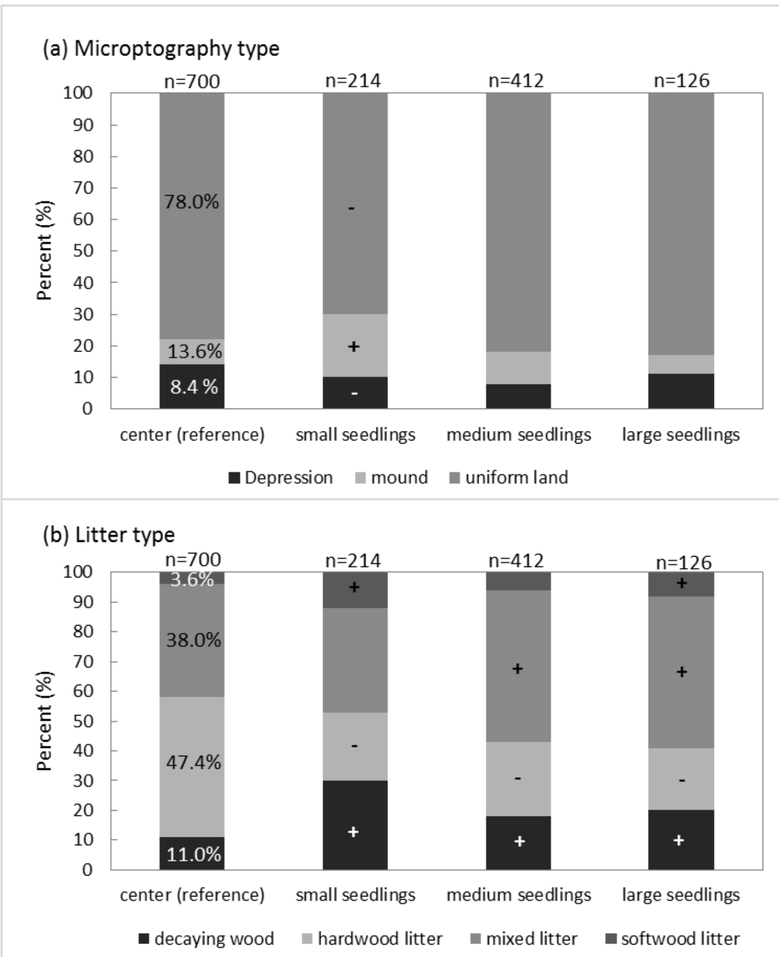

Figure 10: Distribution of white-cedar seedlings by height class and microsite availability; (a) relationship with microtopography type, (b) relationship with litter type.

Note: + or – indicates a significant difference superior or inferior to the general distribution (a) χ^2=12.99; p<0.01 (b) χ^2=21.86; p<0.01

n= number of observations