

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/m²) was much higher than for yellow birch and white-cedar (mean = 0.10 and 0.25 seedling/m² 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 m²/ha for white-cedar and between 0 and 15.6 m²/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.

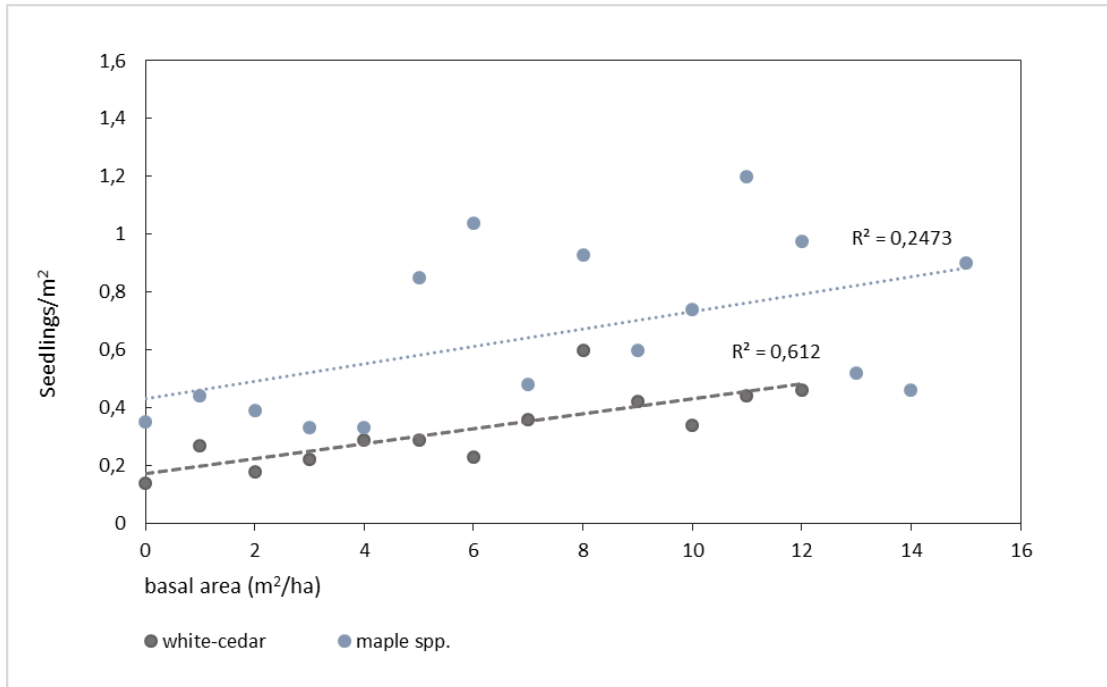


Figure 5: Relationships between seedling density by high class and species merchantable basal area for white-cedar and maple.

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/m²) (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/m²) compared to ecological regions 3a and 4b (mean = 0.11 seedlings/m² for both regions) (table 4). For white-cedar and maple no variations between the three ecological regions were observed on seedling abundance.

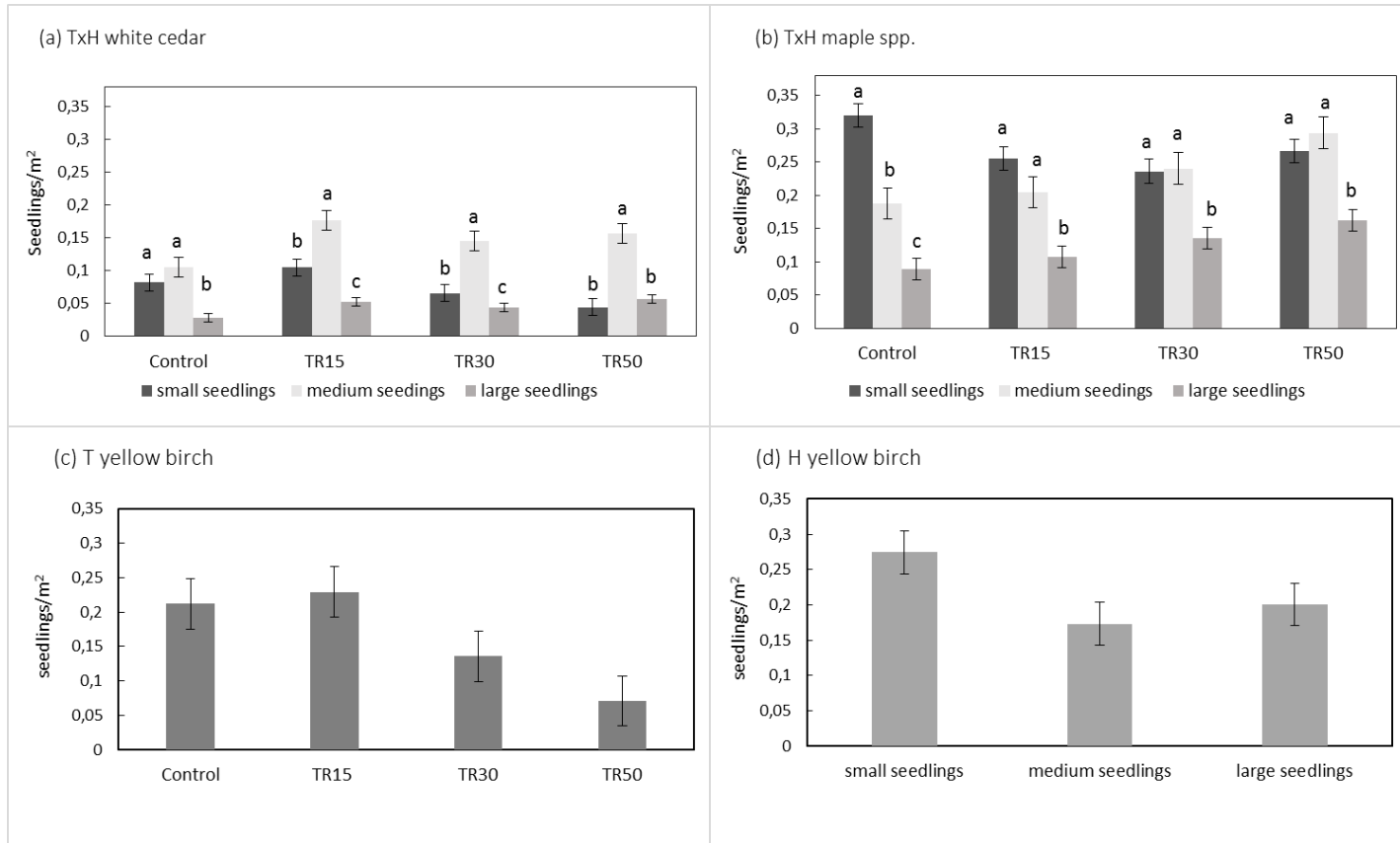


Figure 6: Effect of canopy treatment and height class on the number of seedling per height class. Error bars show 95% confidence intervals.

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).

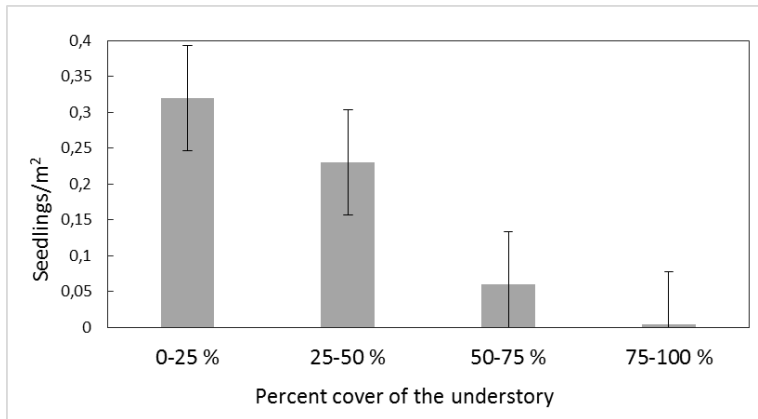


Figure 7: Abundance of white-cedar seedlings in relation with percent cover of the understory. Error bars show 95% confidence intervals.

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%).

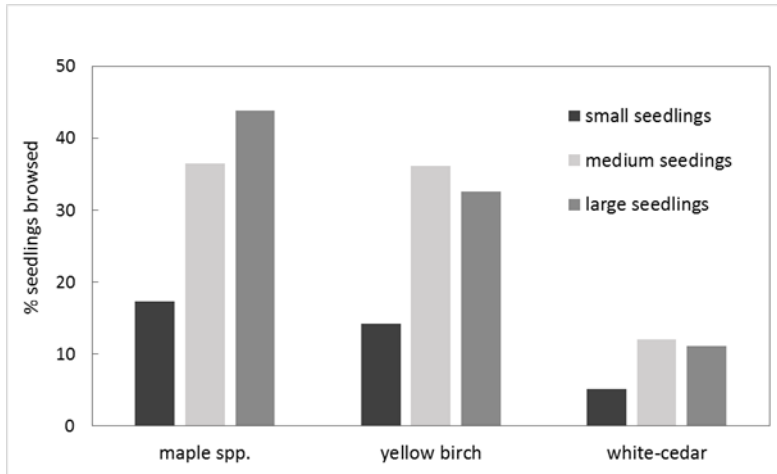


Figure 8: Percent of seedlings browsed for main species throughout all study plots

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.

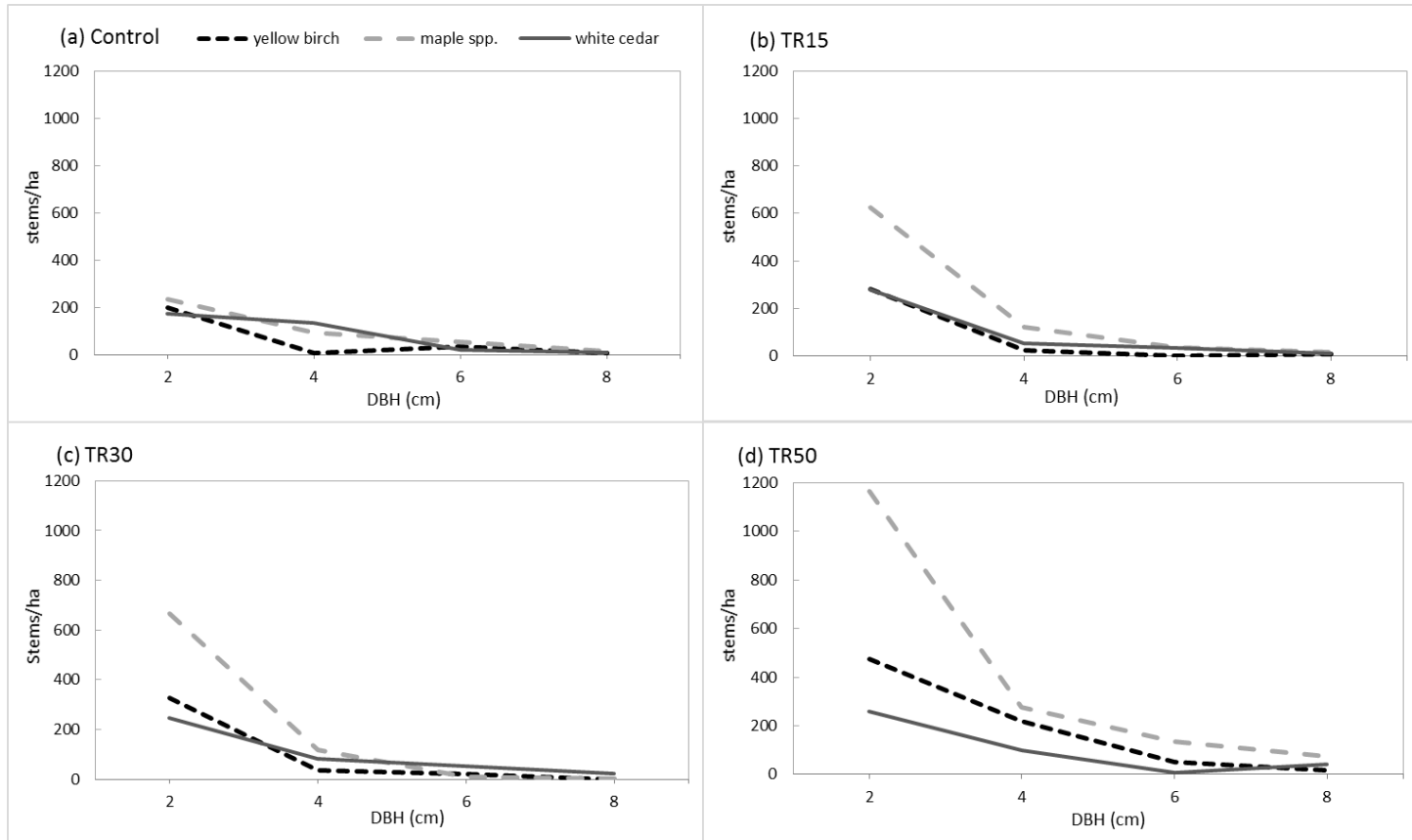


Figure 9: Sapling density for main species by DBH class for each canopy treatment.

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).

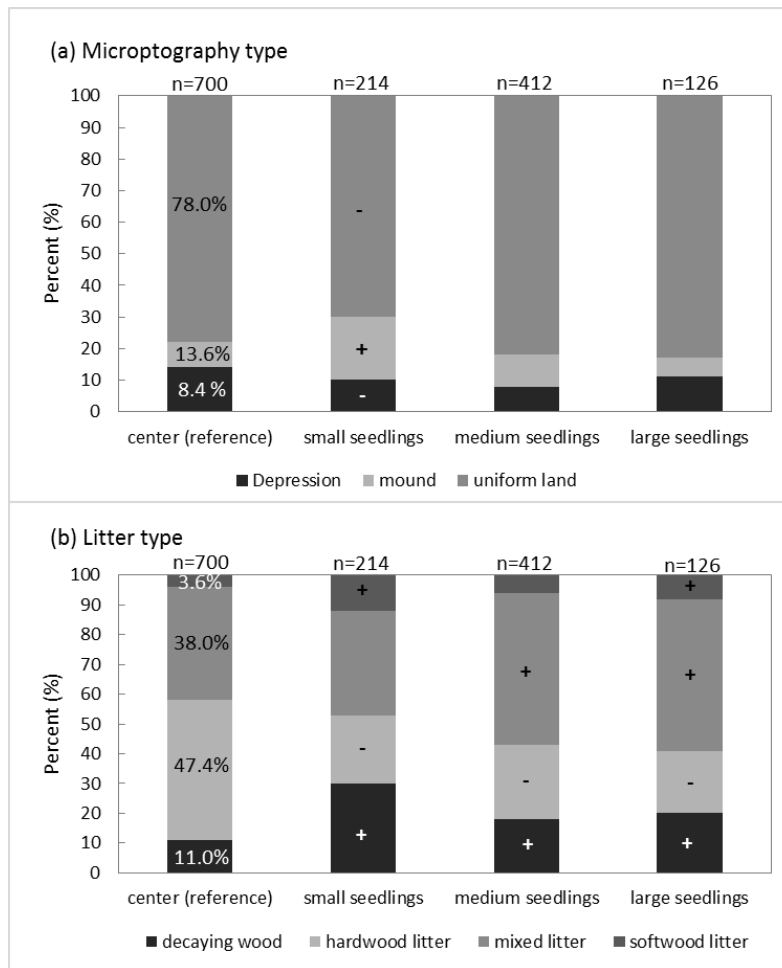


Figure 10: Distribution of white-cedar seedlings by height class and microsite availability; (a) relationship with microtopography type, (b) relationship with litter type.

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 competitiveness 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 as 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

soil moisture at a suitable level for seedlings survival (Raymond et al. 2013). In fact, treatments with a canopy cover are more suitable for early survival of white-cedar seedlings than treatments with full sunlight conditions (Larouche et al. 2011). In the control, abundances of medium and large seedlings of all studied species were lower than in all other canopy treatments. These results confirm that available light had a positive influence on seedling height growth. However, in this study, abundance of large seedlings were not significantly higher in the medium and high intensity selection cutting than in the low intensity selection cutting for the white-cedar. As no regeneration inventory was carried out before harvesting activities, it is difficult to know whether seedlings were already established. Thus, if the pre-established regeneration was scarce and small as in the control or if there was no pre-established regeneration, it is not surprising that the effects of treatments on the saplings number are not significant. Moreover, this lower abundance of white-cedar large seedlings and saplings can be explained by the presence of more competition by other species in treatments with higher harvesting intensity.

Selection cutting also promoted hardwood regeneration (Majcen 1996; Malenfant and Patry 2002; Meunier et al. 2002; Majcen and Bédard 2003). The results showed an increase of sugar and red maple medium and large seedlings abundance and sapling recruitment with the increase of harvesting intensity. For yellow birch and white-cedar, control and low intensity selection cutting showed higher abundance of seedlings, all height classes combined, than medium and high intensity selection cutting. In the latter two treatments, the lower abundance of seedlings may be due to the a better recruitment to the sapling stage. Several studies showed that yellow birch establishment is favored by soil disturbance while growth is influenced by canopy openness (Malenfant and Patry 2002; Meunier et al. 2002; Prévost et al. 2010). The passage of the machinery during the harvesting activities may not have been sufficient to disturb the organic horizon and improve seedbed receptivity (Blouin et al. 2011). Scarification spot in the gaps has been recommended to obtain a higher density of well-developed yellow birch seedlings (Malenfant and Patry 2002; Majcen and Bédard 2003; Prévost et al. 2010). Yellow birch abundances of seedlings and saplings were also influenced by ecological region which was not the case for maple and white-cedar. Ecological regions are distinguished by the unique character of their geomorphology, geology, climate, soils, water resources, fauna and flora (Robitaille and Saucier 1998). Plots located in ecological region 3b presented lower general abundance of yellow-birch seedlings and saplings in the stands than ecological regions 3a and 4b.

Results showed that understory competition decreased the abundance of white-cedar seedlings. Competition restricted the access of white-cedar seedlings to resources (water, light, nutrients) and compromised their growth and survival. The highest percent cover of the understory (> 75%) was found in gaps of the high intensity selection cutting. High harvesting intensity created larger gaps and fast-growing species took advantage of access to light. Striped maple, mountain maple, squashberry viburnum were abundant when harvesting intensity was higher. Low intensity selection cutting allowed better control of the competition of the understory and the results showed a higher abundance of white-cedar seedlings.

Abundance of white-cedar seedlings also appears to be influenced by the available establishment microsites. As expected in the hypothesis, white-cedar small seedlings were found more often on decaying wood compared to other available substrates (Scott and Murphy 1987; Cornett et al. 1997). Small seedlings were most abundant on mounds created by coarse woody debris. The results showed that the proportion of white-cedar seedlings on mounds declines as plants grow larger. However, the rooting substrate of medium and large seedlings were strongly associated with highly decomposed woody debris (Hébert 2007). In fact, medium and large seedlings have been established for a longer period therefore their deadwood substrates had more time to decompose. Decayed logs and stumps are reported to be preferred seedbeds for white-cedar germination and survival, particularly when moisture availability is limiting and areas are undisturbed which was the case in our study sites (Cornett et al. 2000b; Cornett et al. 2001). Hardwood litter was the most available substrate but was proportionally less used by white-cedar seedlings. In fact, litterfall can smother slow-growing seedlings like white-cedar and compromise their survival (Simard et al. 2003). Mounds seem more suitable for seedlings installation because of the thinner forest floor formed on these microsites (Ruel et al. 1988). In this study, the distinction between sexual and asexual reproduction has not been established. The asexual mode has the advantage to increase seedling establishment and survival success even when favorable microsites are scarce (Simard et al. 2003; Larouche 2009).

Browsing has been identified elsewhere has a predominant cause of low recruitment of white-cedar large seedlings and saplings (Cornett et al. 2000b; Rooney et al. 2002; Forester et al. 2008; Hofmeyer et al. 2009; Larouche 2009; Palik et al. 2014; Larouche and Ruel 2015). The impact of browsing can be very variable depending on deer density. Seedlings between 30 and 130 cm tall are more vulnerable to deer browsing (Larouche and Ruel 2015). In this study, the presence

of a well-developed stratum of white-cedar medium seedlings (30 to 100 cm) suggests a low density of deer in the study area. In all plots, only few seedlings presented some signs of browsing (<10%) and their survival did not appear to be compromised. Moose were present in all study sites and mainly browsed hardwood species. Maple and yellow birch seedlings presented signs of browsing by moose especially in the larger size classes. However, percent of foliage consumed was low and the damage did not appear to affect seedling height growth. The hypothesis that abundance of seedlings taller than 30 cm and recruitment of small saplings are affected by deer density was not supported in this study.

The results showed that maple sapling density increases significantly with harvesting intensity. In the high intensity selection cutting, densities of maple saplings were five times superior to the densities in the control. Pre-disturbance advance regeneration species like red maple and sugar maple took advantage of the increase of light availability to dominate the stratum (Bolton and D'Amato 2011). This high density of maple saplings creates a competitive environment for other species like white-cedar. White-cedar is a shade-tolerant species that can live in the understory for many decades until release (Johnston 1990; Hofmeyer 2008). In this condition of suppression, growth of stems is considerably reduced. However, white-cedar can respond well to release even after extended periods of suppression (Hofmeyer et al. 2009).

Silvicultural implications

To ensure regeneration of white-cedar in mixedwood stands, Larouche and Ruel (2015) recommend to use partial cutting to open up the stand sufficiently to increase canopy transmittance on the forest floor to 20%–35% of full sunlight. Even if there is no significant results concerning the effect on canopy treatments on white-cedar seedlings density, the recommendations of this study are consistent with the previous results. Treatments with less than 40% of the basal area harvested are suitable to promote the establishment and growth for white-cedar small and medium seedlings. In fact, low intensity selection cutting allows good light conditions for white-cedar seedlings establishment and provides favourable conditions for height growth without stimulating the understory. Single-tree selection cutting allowed better controls the concurrent species than group selection cutting. In fact, the abundance of white-cedar seedlings in the low intensity selection cutting than in the other canopy treatments. In high intensity selection cutting, results showed that gaps favor the growth of fast-growing species and create a competitive environment for white-cedar seedlings that are often oppressed. However, white-cedar in inferior canopy positions could still respond to release, even after extended periods of suppression (Hofmeyer et al. 2009). Consequently, advance regeneration must be carefully protected during harvesting activities to ensure a return of white-cedar in upper stratum after canopy opening (Larouche 2009). Presence of seed trees, availability of establishment microsites are also important to consider during the planning of silvicultural treatment to ensure the success of regeneration of white-cedar in mixedwood stands.