# Northern hardwood regeneration dynamics 10 years after irregular shelterwood and mechanical control of understory American beech

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## ABSTRACT

In northern hardwood stands of the northeastern USA and southeastern Canada, the abundance and occurrence of American beech (*Fagus grandifolia* Ehrh) regeneration have increased substantially over the past decades, to the detriment of other deciduous species such as sugar maple (*Acer saccharum* Marshall) and yellow birch (*Betula alleghaniensis* Britton). To promote the regeneration of these declining species, we established an experimental study near Québec City (Quebec, Canada) to compare the effects of various partial cutting treatments and mechanical control of understory American beech. The design comprises 4 randomized complete blocks, each containing an uncut control, a hybrid single-tree and group selection cutting (SC), two intensities of continuous cover irregular shelterwood (CCIS) and an extended irregular shelterwood (EIS). American beech regeneration, which dominated the sapling layer before cutting, was removed with brush saws in gaps created in the SC and CCIS treatments as well as in the entire understory of the EIS treatment. In addition, gaps and the EIS understory were scarified to favor yellow birch regeneration, and 12 exclosures were built to prevent cervid browsing in CCIS gaps and in entire understory of the EIS treatment. Ten years after cutting, yellow birch regeneration was more abundant in gaps and in the EIS treatment than in the uncut control. These results confirm that increasing the understory light level, eliminating American beech saplings and scarifying the soil can successfully favor yellow birch establishment. However, preferential browsing of yellow birch outside exclosures maintained the overall dominance of American beech in the long term. Thus, under these conditions, damage from repetitive browsing outweighed the positive effects of actions aimed at promoting the regeneration of yellow birch. In the end, despite abundant seed availability, sugar maple remained only a minor component of the regeneration.

## 1. Introduction

Northern hardwood forests consisting primarily of sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh) and yellow birch (*Betula alleghaniensis* Britton) are a predominant forest type in the northeastern United States and in southeastern Canada. They yield important ecological and economic benefits in these regions (Leak et al., 2014). Sugar maple and yellow birch are considered as the most valuable tree species, especially since the spread of beech bark disease (BBD) across eastern North America (Morin et al., 2007; Cale et al., 2017), which reduces the commercial value of American beech (Houston, 1975; Burns and Houston, 1987). Moreover, knowledge gained in the last decades has uncovered another side effect of BBD: American beech has increased in dominance relative to other tree species in the understory (Hane, 2003; Duchesne and Ouimet, 2009; Bose et al., 2017a). Multiple factors have contributed to accentuate this trend, namely the high shade

tolerance of beech (Forcier, 1975; Canham, 1988; Tubbs and Houston, 1990), its capacity to reproduce both sexually and asexually by root suckering (Jones and Raynal, 1987; Beaudet and Messier, 2008), the intense shading caused by beech regeneration (Hane, 2003; Canham et al., 1994) and the preference of cervids for sugar maple (Long et al., 2007; Matonis et al., 2011) and yellow birch (Nyland et al., 2006a; Walters et al., 2016). BBD mortality also indirectly affects the regeneration process, since it promotes beech suckering to the detriment of other species (Houston, 1994; Giencke et al., 2014; Morin and Liebhold, 2015). Beech expansion has also been favored by abiotic factors, such as soil base cation depletion, which negatively affects sugar maple regeneration (Duchesne and Ouimet, 2009; Sullivan et al., 2013) and the current change of climatic conditions (e.g., increases in precipitation, growing season temperature and temperature variability), which have favored the occurrence and abundance of beech over other tree species during the last three decades (Bose et al., 2017b). Forest management

during the last decades has also contributed to promoting this expansion. For instance, the preponderance of low-intensity partial harvests (e.g., single-tree selection cutting) provided low light conditions favorable to very shade-tolerant species such as American beech (Gauthier et al., 2015; Nolet et al., 2008).

The dominance of American beech causes an important management challenge, especially in the context of ecosystem-based management, given its aim of maintaining stand composition and structure of northern hardwoods close to the state of stands regulated by natural disturbances. Since beech often dominates the understory in managed forests, major compositional shifts could occur over time if silvicultural practices are not developed to reverse this trend. Incorporating larger openings into partial harvests or increasing harvest intensity to promote more diverse species regeneration has often been suggested (Leak, 1999; Shields et al., 2007; Nuttle et al., 2013). However, where advance regeneration of shade-tolerant species is abundant, creating large gaps in the canopy by shelterwood cutting may only serve to release advance regeneration (be it desired or not) and favor its development (Reuling et al., 2019). Non-tree vegetation, deer herbivory and the interaction of these two effects may also negate those of gaps on seedlings of desired tree species (Kern et al., 2012, 2013) and limit regeneration to a few species avoided by browsers (Nuttle et al., 2013). Seedbed quality is another important factor affecting the composition and density of seedling composition, since mineral or mixed soil horizons facilitate the germination and early establishment of small-seeded species such as yellow birch (Godman and Krefting, 1960). Such substrates are often scarce in northern hardwood understories, especially when intentional soil scarification is not part of the silvicultural scenario (Shields et al., 2007; Gasser et al., 2010). Hence, regenerating desired species like sugar maple and yellow birch is difficult when beech advance regeneration already dominates the understory. This highlights the importance of doing more than just manipulating the canopy to ensure regeneration of these species (Nyland et al., 2006a; Kern et al., 2016).

This study reports the results of a long-term experiment comparing a hybrid single-tree and group selection cutting (SC) with two variants of the irregular shelterwood system (continuous cover [CCIS] and extended irregular shelterwood [EIS], see Raymond et al., 2009), coupled with understory beech control and soil scarification aimed at improving stand quality and composition, and at favoring the regeneration of yellow birch and sugar maple. SC was the less intensive treatment and was the reference (the most prescribed in northern hardwoods) when the experiment was established, while the two variants of irregular shelterwood were novel treatments for this forest type. This range of treatments represents a gradient of cutting intensities and different residual stand structures. The maintenance of irregular stand structures, which complies with ecosystem-based management, relies on the assumption that each establishment cut enhances micro-environmental conditions to establish a new cohort of seedlings and stimulates the development of older cohorts. We hypothesize that the CCIS and EIS variants of irregular shelterwood, combined with understory beech control and soil scarification, would: 1) increase light transmission, 2) improve seedbed conditions to promote the regeneration of yellow birch and sugar maple, and 3) reduce the proportion of American beech regeneration compared to the reference SC treatment and the control.

## 2. Material and methods

### 2.1. Study site

The study was carried out in 2009 at the Duchesnay Forest (46° 57′ N, 71° 40′ W) near Québec City, Canada. This forest is in the meridional subregion of the balsam fir (*Abies balsamea* (L.) Mill.)–yellow birch bioclimatic domain (Saucier et al., 1998), near the northern edge of the sugar maple–yellow birch bioclimatic domain. Depending on altitude and slope, the forest comprises yellow birch–balsam fir stands or sugar

maple–yellow birch stands. The podzolic soils of this forest developed from deep acidic and stony glacial till derived from the granitic gneiss bedrock of the Canadian Shield. These soils have very poor fertility and show a calcium deficiency (Ouimet et al., 2013). The regional climate is subpolar, subhumid and continental (Robitaille and Saucier, 1998), with a mean annual temperature of 2.5 °C and mean annual precipitations ranging from 1200 mm to 1600 mm. In the past, this forest was partially harvested, mostly for yellow birch, but to our knowledge, the studied stands had not been harvested for at least 3 decades prior to the beginning of this study. The experimental units (EU) contain mostly northern hardwoods dominated by yellow birch, sugar maple and American beech, which respectively occupied 38%, 34% and 23% of merchantable basal area. In 2009, the average merchantable basal area was 26 $m^2 \cdot ha^{-1}$; stands had a reverse J shaped diameter distribution, and the understory was dominated by American beech saplings (see Bédard et al., 2014 for details). Beech defoliation and mortality were observed when the treatments were applied in 2009, but the presence of beech scale (*Neonectria* spp.) was first observed in 2011. Beech bark disease has caused mortality ever since, reducing the proportion of beech in the main canopy.

### 2.2. Experimental design and data collection

The study incorporates 4 completely randomized blocks, each containing: a control (uncut) treatment, a hybrid single-tree and group selection cutting treatment with a residual basal area (BA) of 18 $m^2 \cdot ha^{-1}$ (SC18), two continuous cover irregular shelterwood (CCIS) treatments with residual BAs of either 16 $m^2 \cdot ha^{-1}$ (CCIS16) or 14 $m^2 \cdot ha^{-1}$ (CCIS14), and an extended irregular shelterwood treatment with a residual BA of 14 $m^2 \cdot ha^{-1}$ (EIS14, Fig. 1). The SC18, CCIS16 and CCIS14 treatments created gaps with a mean area of 780 $m^2$, 983 $m^2$ and 1307 $m^2$, respectively, which represented 16%, 20% and 27% of EU area. In the EIS14 treatment, tree marking left a relatively uniform crown cover of 50% (see Bédard et al., 2014). Each block was delimited according to the spatial location of aggregated EUs, which were in 4 different locations and 300 m to 600 m apart.

The EUs of the same block had to have a similar forest composition, stand structure and site characteristics (slope, exposition, drainage and surface deposit). Treatments were randomly assigned within each block. For each treatment, tree marking aimed at removing the less vigorous trees of all species and at reducing the amount of American beech. In addition, the SC treatment considered a target diameter distribution (maximum diameter at breast height [DBH] of 55 cm), a residual BA of 18 $m^2 \cdot ha^{-1}$ and 2 q factors calculated by 2 cm classes: 1.12 for pole-size trees (9 cm ≤ DBH ≤ 19 cm) and 1.09 for larger trees, following the marking guide of Majcen et al. (1990). Small gaps were also created to increase light transmission and reduce beech abundance and favor the regeneration of yellow birch and sugar maple over beech. For the two CCIS treatments, the objectives were to maintain an irregular stand structure (*sensu* Smith et al., 1997) and to create conditions that would decrease understory beech abundance and facilitate yellow birch and sugar maple regeneration. The lower target residual BAs (14 or 16 $m^2 \cdot ha^{-1}$) in these treatments led to the marking of a higher proportion of low-vigor trees and of a higher proportion of American beech than in the SC18 treatment. Larger gaps and more gaps were also created. For the EIS treatment, tree marking left a residual BA of 14 $m^2 \cdot ha^{-1}$, with a relatively uniform crown cover of 50%. To preserve potential seed trees at a uniform spacing, the surrounding merchantable size trees (DBH ≥ 9.1 cm) were removed to increase light penetration to the forest floor.

Treatments were applied in October 2009 using a cut-to-length system with a single-grip harvester and a forwarder. In gaps and across the entire EIS understory, American beech saplings were removed using brush saws immediately after harvesting. A site preparation was performed within the gaps and between the residual trees in the EIS treatment, using a skidder equipped with a fixed-tooth blade to remove harvesting debris and to expose mineral horizons just after mechanical
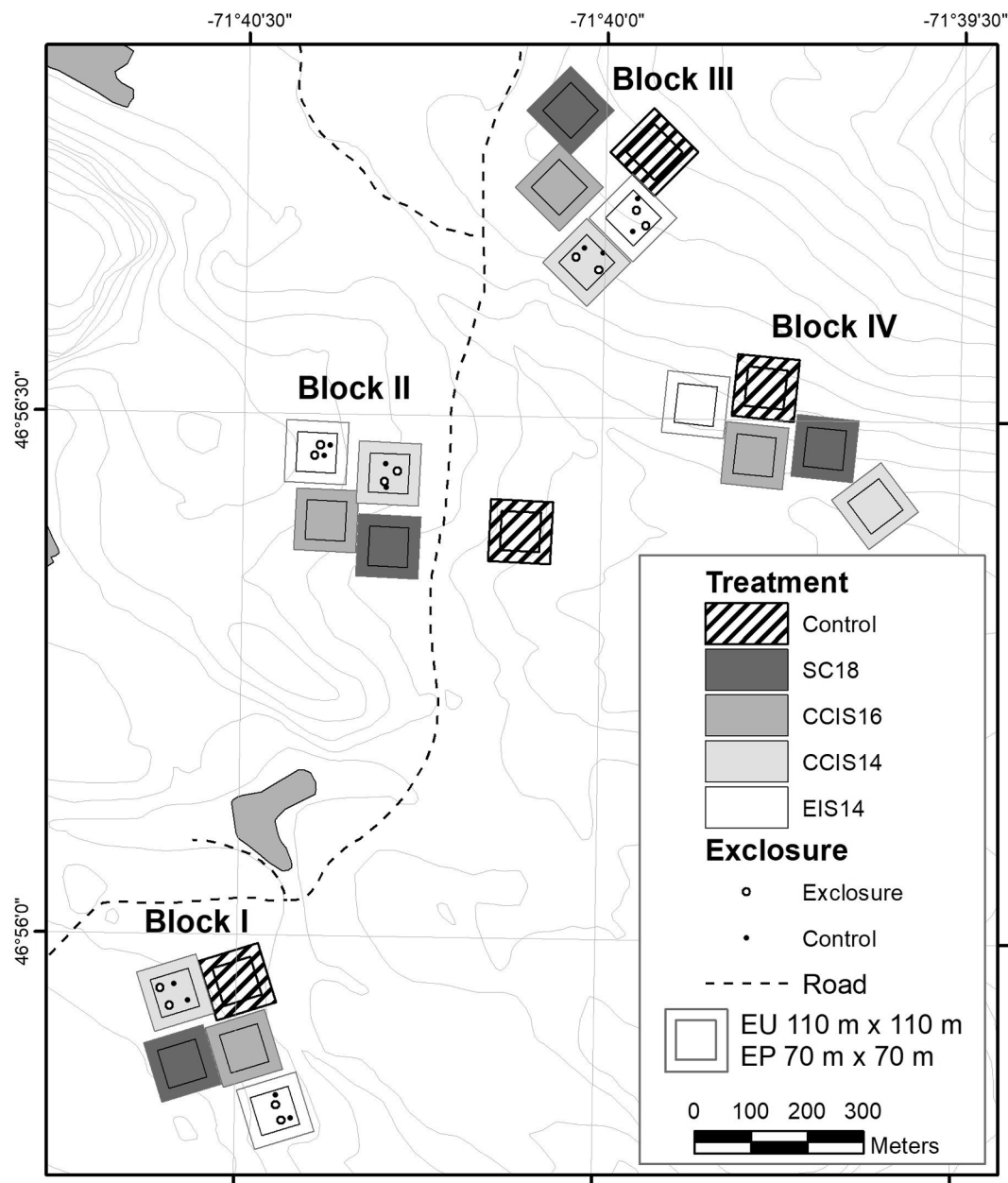
**Fig. 1.** Layout of the experimental design. Each block included 5 randomized treatments: uncut control (control), hybrid single-tree and group selection (SC18), continuous cover irregular shelterwood (CCIS16 and CCIS14) and extended irregular shelterwood (EIS14). The number following treatment abbreviation corresponds to the target residual basal area after cutting (m²·ha⁻¹). At the beginning of the second growing season, 12 exclosures and adjacent control areas were installed in 3 blocks, within gaps of the continuous cover (CCIS14) treatment and in the understory of extended (EIS14) treatment to assess the effects of ungulate browsing on tree regeneration. EU = experimental unit, EP = experimental plot.

beech control.

Each EU measures 110 m × 110 m (1.2 ha), with a 70 m × 70 m central plot in which merchantable trees (DBH > 9 cm) were numbered, mapped, and characterized for species, DBH, and a combined risk (vigor) and product class (Majcen et al., 1990). The central plot was also divided into a grid of 10 m × 10 m squares. Regeneration was recorded in 2 fixed-area plots centered on each of the grid's 36 inner intersection points. First, a regeneration plot (1.13 m radius; 4 m² area) was used to record all seedlings of commercial species and of main non-commercial species, by height class (≤5 cm, 6–30 cm, 31–60 cm, 61–100 cm, 101–200 cm and > 200 cm, with DBH ≤ 1.0 cm). Seedlings were recorded in years 0, 1, 3, 5 and 10 after cutting. However, in year 10, we only recorded seedlings larger than 30 cm, using the same height classes as described above. We used the same regeneration plots (radius: 1.13

m) to assess the percent coverage of seedbeds in year 1, immediately after cutting, according to 7 classes: undisturbed humus, disturbed litter, mix of mineral and organic horizons, exposed mineral horizon, woody debris, rocks and water. Second, we recorded and measured saplings (1 cm < DBH ≤ 9 cm) in years 0, 5 and 10 in a larger plot (2.82 m radius; 25 m² area) with the same center point, using a tally by species and 2 cm DBH classes. To estimate total transmitted light, a hemispherical photograph was taken 1.5 m above the ground over each plot center, before and after cutting, using a Nikon Coolpix 4500 digital camera (Nikon, Tokyo, Japan) and an 8 mm fisheye lens (Nikon, FC-E8) on a self-leveling mount, during midsummer, before sunrise or under overcast conditions.

In the spring of 2011, 12 exclosures made of galvanized steel wire fence (10 m × 10 m × 3 m height) were installed in 3 blocks within gaps

of the continuous cover (CCIS14) treatment and in the understory of extended (EIS14) treatment to protect these areas from browsing by white-tailed deer (*Odocoileus virginianus*), moose (*Alces americanus*) and snowshoe hare (*Lepus americanus*). In each of the 6 selected EUs, we measured the regeneration in the exclosures as well as in 10 m × 10 m areas located outside exclosures and beside them. This area had similar total transmitted light and seedbed conditions. We established four 4 m$^2$ plots (plot radius: 1.13 m) inside each exclosure and 4 others in the adjacent control area to record all seedlings. The centre of each regeneration plot inside the exclosure was located 3 m from each corner of the fence. This space left a 1.9 m buffer zone to avoid potential browsing. In the adjacent area, the nearest seedlings plots were located at least 10 m outside the fence around the exclosure. For saplings, we used one large plot (2.82 m radius; 25 m$^2$ area) inside and outside exclosures and in the middle of each of the 4 seedlings plots. We used the same sampling protocol for regeneration as mentioned earlier to tally seedlings and saplings. Regeneration was recorded in years 2 (immediately after exclosure installation), 5 and 10 after cutting.

### 2.3. Data analysis

BA and regeneration were calculated on a per hectare basis, for each EU and measurement year. Percentage of cover for seedbed types was also averaged by EU. All hemispherical photographs were analyzed using GLA software (Frazer et al., 1999) in order to calculate the percentage of total transmitted light, which is the percentage of diffuse and direct radiation of transmitted light in the open field; the values obtained for each photograph were also averaged by EU for each measurement year.

We performed all analyses of variance (ANOVA) with linear mixed models (MIXED procedure; SAS statistical software version 9.4, SAS Institute Inc., Cary, North Carolina, USA), using cutting treatment as a fixed effect factor and block as a random effect factor. We used Kenward-Roger's method to approximate the denominator degrees of freedom. For analyses with repeated measurements, we introduced year and the year × cutting treatment interaction in the model as fixed effect factors, as well as the block × cutting treatment interaction (corresponding to the whole EU) as a random effect factor. Regarding data from exclosures, we compared exclosures and adjacent areas by adding a third fixed effect factor and all its interactions with other fixed effect factors in the model. Subplots, defining by the two repetitions of exclosures and adjacent areas within each EU, were also considered as a random effect factor.

We conducted ANOVAs with repeated measurements for seedling density of commercial species (treated separately) as well as non-commercial species, for two combined height classes (≤30 cm and >30 cm) and for saplings (1.1 cm ≤ DBH ≤ 9 cm) when their density was sufficient. For the cutting treatments that included gaps (SC18, CCIS16 and CCIS14), gap and non-gap areas within each treatment were considered separately so the cutting treatment factor in the model had 8 levels (Control, SC18_1, SC18_0, CCIS16_1, SSCI16_0, CCIS14_1, CCIS14_0 and EIS14 with prefixes _1 and _0 corresponding to gap and non-gap areas respectively). Analyses were done on values of gap and non-gap areas within each EU. For the exclosure data, we also used ANOVAs with repeated measurements to compare seedling and sapling densities among cutting treatments (CCIS14_1 and EIS14) and exclosures/adjacent areas, for each main species in years 5 and 10.

Because potential differences at the beginning of the experiment can affect future vegetation responses, we tested precut % light transmission and precut seedling density as covariates in their respective analyses. We did the same with the first measurement after installation (2011, 2 years after cutting) for the analysis of exclosure data. Interactions between the covariate and the other factors were also tested, but they were never retained in the models.

For ANOVAs with repeated measurements, we used a variance-covariance matrix to take into account the correlation between measurements made on the same EUs, gap and non-gap areas within EUs or subplots. This matrix was chosen to minimize the likelihood value of the model while involving as few parameters as possible and while considering consistency across sets of analyses. The unstructured matrix with null covariances (banded main diagonal UN(1)) was used for all analyses except that for American beech seedling regeneration, for which we chose the compound symmetry (CS) matrix, and that for the exclosure effect on yellow birch saplings, for which we chose the unstructured (UN) matrix. When a factor or an interaction was statistically significant ($p < 0.05$), we used a simulation-based approach (ADJUST = SIMULATE option of the LSMEANS statement in the MIXED procedure) to make pairwise comparisons and to assess differences while considering test multiplicity (Westfall et al., 1999; Edwards and Berry, 1987). For significant interactions between main factors, all mean values that related to the levels of one factor were compared at a fixed level of the other factors. When the cutting treatment factor was significant in the regeneration analyses, we included a total of 19 pairwise comparisons: those among the 5 main treatments (control, SC18, CCIS16, CCIS14 and EIS14) (10 comparisons), those of the control vs. both gap and non-gap areas for each of the SC18, CCIS16 and CCIS14 treatments (6 comparisons), and finally, gap vs. non-gap areas for the SC18, CCIS16 and CCIS14 treatments (3 comparisons).

For all models, the homogeneity of variance of residuals and the presence of outliers were verified graphically. Normality of residuals was also verified graphically and tested with the Shapiro-Wilk test. Most of the seedling and sapling density data were square-root transformed to meet these underlying assumptions, but are presented in their original scale in the results section. When none of the transformations allowed the data to meet underlying assumptions, we used the nonparametric randomization test (Cassell, 2002).

## 3. Results

### 3.1. Merchantable basal area before and after cutting

Before the cuts, the overall mean BA of merchantable (DBH ≥ 9.1 cm) trees was 26.1 m$^2$·ha$^{-1}$, with 37.8% yellow birch, 34.3% sugar maple, 23.4% American beech, 2.7% red maple (*Acer rubrum* L.), and 1.8% softwoods (*Picea rubens* Sarg. and balsam fir). Postcut merchantable BA slightly exceeded the prescribed target basal area (by 0.4 to 0.6 m$^2$·ha$^{-1}$), because losses during logging operations were less than expected. Immediately after cutting, the proportion of yellow birch increased, while that of sugar maple remained constant. The postcut proportion of American beech varied among treatments: its BA decreased in all cutting treatments, but more so in the CCIS14 and EIS14 treatments. (Table 1).

### 3.2. Transmitted light

The percentage of transmitted light varied among treatment ($p < 0.001$, Table S1 in Supplementary material). All cutting treatments significantly increased the percentage of transmitted light (mean values ranging from 23.1% to 33.6%) compared to the uncut control ($p ≤ 0.003$, mean value: 14.6%). On average, total transmitted light percentages for the cutting treatments can be divided in two groups: those of the SC18 and CCIS16 treatments were similar (23.1% vs. 25.2%, $p = 0.779$), but significantly less ($p ≤ 0.007$) than those of the CCIS14 (32.9%) and EIS14 (33.6%) treatments, which did not differ significantly from one another ($p = 0.995$). The overall distribution of % transmitted light shows that the cutting treatments widened the range of % transmitted light, which went from 0% to 25% before cutting to much higher percentages (Fig. 2). After cutting, the shape of the distribution for this variable was similar for the SC18 and CCIS16 treatments: asymmetric, with higher frequencies in the 10%–25% range. In contrast, the distribution was more symmetric for the CCIS14 and EIS14 treatments, resembling a normal curve with a mode in the 25%–50% range.

**Table 1**
Basal area (standard error in brackets) and species composition of merchantable trees (DBH ≥ 9.1 cm), by treatment, for precut and postcut periods.

| Treatment | Period | Basal area (m$^2$·ha$^{-1}$) | Species composition (%) | | | | |
|---|---|---|---|---|---|---|---|
| | | | Yellow birch | Sugar maple | American beech | Red maple | Softwoods* |
| Control | Start of the experiment | 25.7 (1.0) | 40.0 | 32.0 | 23.1 | 3.0 | 1.9 |
| SC18 | Precut | 26.6 (1.3) | 39.8 | 33.5 | 22.7 | 2.9 | 1.0 |
| | Postcut | 18.4 (0.1) | 48.1 | 33.9 | 16.0 | 1.3 | 0.7 |
| CCIS16 | Precut | 25.3 (0.3) | 35.5 | 35.7 | 24.6 | 2.4 | 1.8 |
| | Postcut | 16.4 (0.2) | 43.3 | 37.3 | 16.2 | 1.9 | 1.3 |
| CCIS14 | Precut | 26.9 (1.1) | 37.3 | 37.0 | 19.3 | 3.1 | 3.4 |
| | Postcut | 14.5 (0.1) | 47.7 | 38.9 | 9.0 | 1.1 | 3.2 |
| EIS14 | Precut | 26.2 (0.6) | 36.2 | 33.2 | 27.5 | 2.1 | 1.0 |
| | Postcut | 14.6 (0.1) | 52.3 | 41.2 | 4.4 | 1.0 | 1.0 |
| **All** | **Precut** | **26.1 (0.4)** | **37.8** | **34.3** | **23.4** | **2.7** | **1.8** |
| | **Postcut** | **17.9 (1.0)** | **45.5** | **36.0** | **15.0** | **1.8** | **1.6** |

*Softwoods include balsam fir and red spruce.
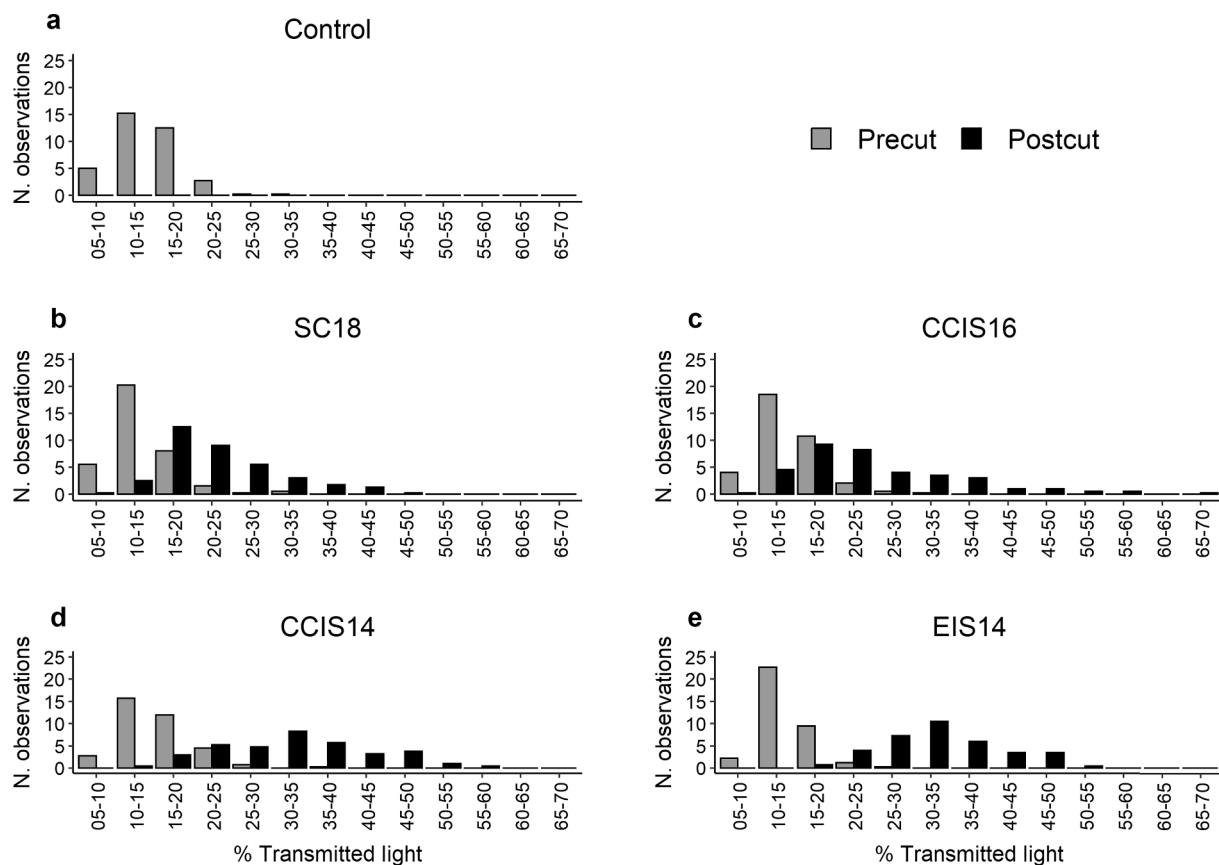


**Fig. 2.** Distribution of light transmission before and after cutting, by treatment (SC18 = single-tree and group selection [residual BA: 18 m$^2$·ha$^{-1}$]; CCIS16 = continuous cover irregular shelterwood [residual basal area (BA): 16 m$^2$·ha$^{-1}$]; CCIS14 = continuous cover irregular shelterwood [residual BA: 14 m$^2$·ha$^{-1}$]; EIS14 = extended irregular shelterwoood [residual BA: 14 m$^2$·ha$^{-1}$]).

### 3.3. Seedbed coverage

The proportions of undisturbed, disturbed and scarified soil surface varied among treatment ($p < 0.001$, Table S1 in Supplementary material). The undisturbed organic layer was, by far, the dominant seedbed type in control plots (83%), but its coverage decreased in the cutting treatments (57%–68%, Fig. 3). Overall, the abundance of disturbed and scarified horizons increased significantly in all cutting treatments (18%–24%) compared to the control (0.3%, $p \leq 0.002$). However, their coverage did not differ among cutting treatments ($p \geq 0.352$). The proportion of decaying wood was similar among all treatments (treatment factor, $p = 0.054$, Table S1 in Supplementary material).

### 3.4. Regeneration

#### 3.4.1. Seedlings ≤ 30 cm in height.

Analysis results of seedlings ≤ 30 cm in height for the first 5 years revealed that yellow birch seedling density was affected by both treatment and year ($p < 0.001$), but that year was the only significant effect for the other species ($p < 0.001$, Table 2). The density of yellow birch seedlings was greater in the cutting treatments (SC18, CCIS16, CCIS14 and EIS) than in the control ($p \leq 0.003$, Fig. 4a). We observed that yellow birch seedling density progressed from the SC18 to the EIS14 treatment, but that there was no significant difference between cutting treatments ($p \geq 0.224$). Density was greater in gaps (mean: 55,300 stems·ha$^{-1}$ for the SC18_1, CCIS16_1 and CCIS14_1 treatments) than in
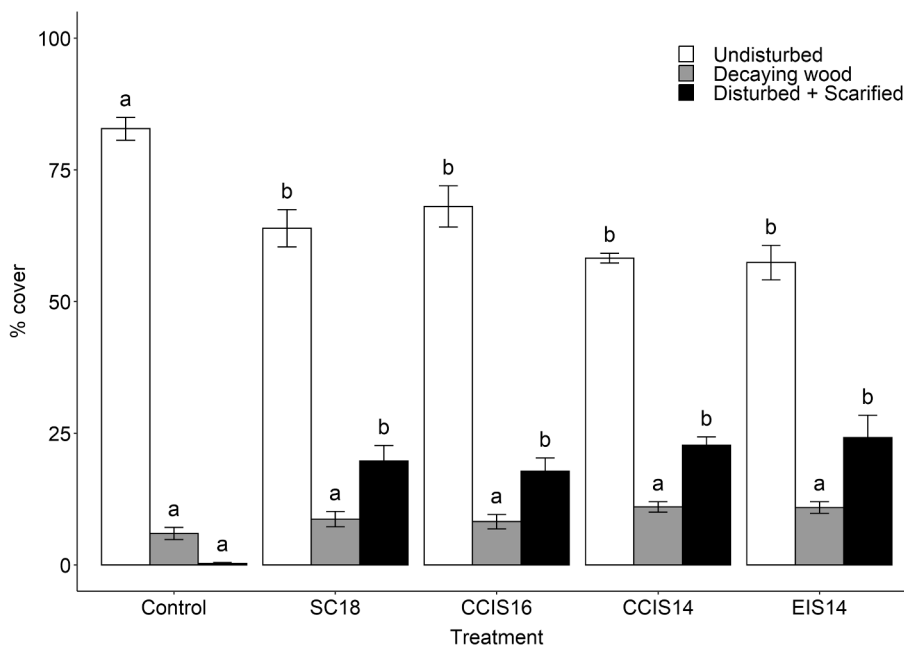
**Fig. 3.** Mean proportion of seedbed coverage by treatment immediately after cutting (2010). Different letters indicate significant differences among treatments for a given seedbed (SC18 = single-tree and group selection [residual BA: 18 m$^2$·ha$^{-1}$]; CCIS16 = continuous cover irregular shelterwood [residual basal area (BA): 16 m$^2$·ha$^{-1}$]; CCIS14 = continuous cover irregular shelterwood [residual BA: 14 m$^2$·ha$^{-1}$], EIS14 = extended irregular shelterwoood [residual BA: 14 m$^2$·ha$^{-1}$]; the disturbed and scarified seedbed included disturbed litter, a mix of mineral and organic soil and exposed mineral soil). Error bars represent standard errors.

**Table 2**

ANOVA results (*p*-values) for seedling density (stems·ha$^{-1}$) according to height ($\leq$30 cm and > 30 cm) for the main commercial and non-commercial species after cutting (a square-root transformation was used for all species. The banded main diagonal variance–covariance matrix UN(1) was retained, except for American beech, for which we used the compound symmetry matrix. T = treatment; ndf = numerator degrees of freedom; ddf = denominator degrees of freedom; N.S. = non-significant).

| | Seedlings $\leq$ 30 cm* | | | | Seedlings > 30 cm | | | |
|---|---|---|---|---|---|---|---|---|
| | T | Year (Y) | T $\times$ Y | Covariate** | T | Year | T $\times$ Y | Covariate** |
| ndf | 7 | 2 | 14 | 1 | 7 | 3 | 21 | 1 |
| ddf[†] | 32.8 | 21.0 | 38.6 | 26.1 | 47.6 | 86.6 | 64.6 | 90.3 |
| Yellow birch | <0.001 | <0.001 | 0.778 | N.S. | <0.001 | <0.001 | <0.001 | N.S. |
| Sugar maple | 0.337 | <0.001 | 0.513 | <0.001 | 0.315 | 0.025 | 0.296 | <0.001 |
| American beech | 0.460 | <0.001 | 0.078 | 0.003 | 0.002 | <0.001 | <0.001 | <0.001 |
| Red maple | 0.078 | <0.001 | 0.884 | <0.001 | <0.001 | <0.001 | 0.042 | <0.001 |
| Non-commercial species[‡] | 0.499 | <0.001 | 0.052 | 0.012 | <0.001 | <0.001 | 0.023 | <0.001 |

\* Seedlings $\leq$ 30 cm in height were measured from year 0 to year 5 only.

\*\* The covariate corresponds to the precut seedling density.

[†] The ddf values presented are those for American beech, as a representative example.

[‡] Non-commercial species include mountain maple (*Acer spicatum* Lamb.), striped maple (*Acer pensylvanicum* L.) and pin cherry (*Prunus pensylvanica* L.).

the control (1,900 stems·ha$^{-1}$, *p* < 0.001, Fig. 4a). For the CCIS16 treatment, yellow birch seedling density was significantly greater inside gaps than outside (*p* = 0.003), while for the SC18, this difference was near the significance threshold (*p* = 0.052). Yellow birch seedling density increased significantly in year 3 (*p* < 0.001), then returned to a level comparable to year 1 by year 5 (*p* = 0.242). The density of American beech seedlings was lower than that of yellow birch; it increased from year 1 to year 3 (*p* < 0.001), then decreased in year 5 (*p* < 0.001) to a level similar to that of year 1 (*p* = 0.839, Fig. 4b). For sugar maple, the second most important species after yellow birch, density of seedlings peaked in year 3 after cutting at a level significantly greater than in year 1 (*p* < 0.001), then decreased significantly in year 5 (*p* = 0.035), while still remaining higher than in year 1 (*p* < 0.001, Fig. 4c). For red maple, seedling density increased significantly from year 1 to year 3 (*p* < 0.001, Fig. 4d), then remained stable until year 5 (*p* = 0.110). For non-commercial species, seedling density was lower than other species; values remained stable from year 1 to year 3 (*p* = 0.129), then decreased significantly from year 3 to year 5 (*p* < 0.001, Fig. 4e).

### 3.4.2. Seedlings > 30 cm in height

The density of seedlings varied in response to a treatment $\times$ time

interaction for yellow birch, American beech, red maple and non-commercial species (*p* $\leq$ 0.042, Table 2). The covariate (precut sapling density) was significant for sugar maple, American beech, red maple and non-commercial species (*p* < 0.001, Table 2).

In year 1, the density of yellow birch seedlings did not differ significantly between cutting treatments. However, one notes the absence of seedlings in the SC18_1, CCIS16_0 and CCIS16_1 treatments (Fig. 5a). In year 3, values in the SC18_1 and CCIS16_1 treatments were significantly higher than in the control (*p* $\leq$ 0.026, Fig. 5a). In years 5 and 10, a progression of yellow birch seedlings density from SC18 to EIS14 was observed; values were higher in the CCIS14 and EIS treatments (respective mean values: 18,500 stems·ha$^{-1}$ and 26,600 stems·ha$^{-1}$ for year 5, and 10,000 and 13,000 stems·ha$^{-1}$ for year 10) and in all gaps (SC18_1, CCIS16_1, CCIS14_1, mean values: 29,000 stems·ha$^{-1}$ for year 5 and 15,300 stems·ha$^{-1}$ for year 10) than in the control (*p* $\leq$ 0.042, mean values: 500 stems·ha$^{-1}$ for year 5 and 240 stems·ha$^{-1}$ for year 10, Fig. 5b).

For American beech, seedling density in year 1 was lower in the CCIS16 treatment (2,700 stems·ha$^{-1}$), CCIS14 (1,800 stems·ha$^{-1}$), EIS14 (1,800 stems·ha$^{-1}$) and in gaps (SC18_1, CCIS16_1, CCIS14_1, mean: 1,500 stems·ha$^{-1}$) than in the control (*p* $\leq$ 0.019, 8,200
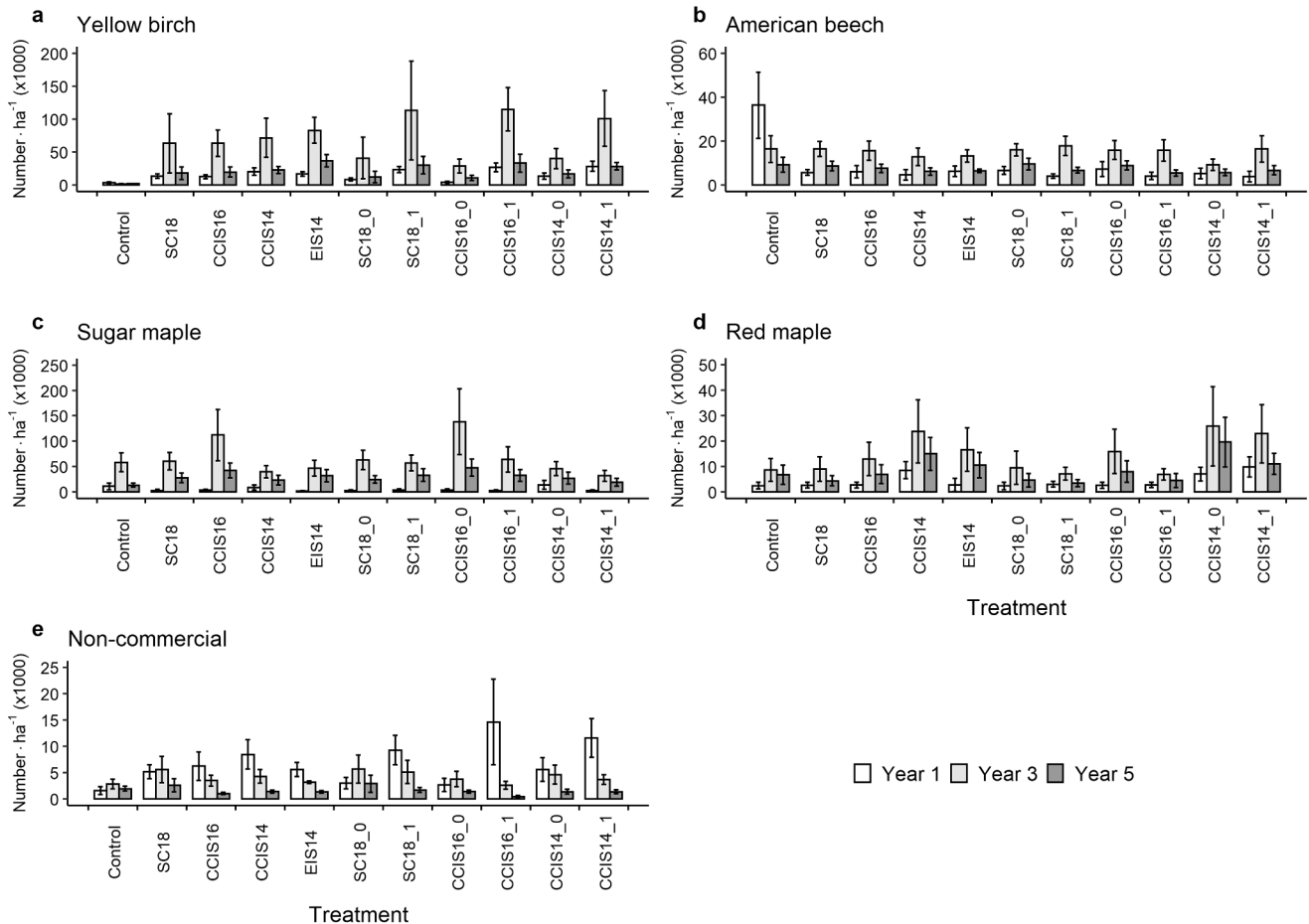
**Fig. 4.** Mean density of seedlings ≤ 30 cm in height, by species and treatment, for years 1, 3 and 5 after cutting (SC18 = single-tree and group selection [residual basal area (BA): 18 m²·ha⁻¹]; CCIS16 = continuous cover irregular shelterwood [residual basal area (BA): 16 m²·ha⁻¹]; CCIS14 = continuous cover irregular shelterwood [residual BA: 14 m²·ha⁻¹]; EIS14 = extended irregular shelterwood [residual BA: 14 m²·ha⁻¹]; treatment abbreviations followed by "_1" refer to locations within gaps for a given treatment, and those followed by "_0" refer to locations outside gaps). Error bars represent standard errors.

stems·ha⁻¹, Fig. 5b). However, by years 3 and 5, seedling density in the EIS14 treatment had increased to levels significantly higher than in the SC18, CCIS16 and the control ((p ≤ 0.035). In addition, American beech seedling density was higher in the SC18_1, CCIS14_1 treatments than in the control (p ≤ 0.037). By year 10, however, values for the EIS14 treatment had returned to levels that no longer differed significantly from other cutting treatments or the control (p ≥ 0.992, Fig. 5b).

For sugar maple, only year had a significant effect on seedling density (p = 0.025, Table 2). It was higher in year 5 (mean: 1,900 stems·ha⁻¹) than in year 1 (p = 0.035, mean: 1,300 stems·ha⁻¹), whereas comparisons among other years showed no significant differences (p ≥ 0.076, Fig. 5c).

For red maple, seedling density was higher in the CCIS14 and the CCIS14_1 treatments than in the control from years 3 to 10 (respective means: 4,800 stems·ha⁻¹ and 6,700 stems·ha⁻¹ vs. 1,300 stems·ha⁻¹, p ≤ 0.017, Fig. 5d). There was no marked trend for non-commercial species. Nonetheless, seedling density was lower in the CCIS14_1 treatment than in the control in year 1 (p = 0.011, Fig. 5e), and in year 3, density was higher in the SC18_1 treatment than in the control (p = 0.010), but this difference was no longer significant in subsequent years (p ≥ 0.921). In year 5, red maple seedling density was higher in the EIS14 treatment than in the CCIS14 and CCIS16 treatments (p ≤ 0.013), but by year 10, it had decreased and was no longer significantly different than in the other treatments (p ≥ 0.866).

### 3.4.3. Sapling density

Sapling density was very low for yellow birch, sugar maple, red

maple and non-commercial species (Fig. 6a, c, d, e). Considering this result, no statistical tests were performed for these species. However, sapling density was higher for American beech; our analysis revealed that it varied according to a treatment × year interaction, and that the covariate was significant (p < 0.001, Table 3). In years 1 and 5, American beech sapling density was lower in the cutting treatments (SC18, CCIS16, CCIS14 and EIS14) than in the control (p ≤ 0.050). The density in the EIS14 treatment was also lower than in the CCIS16 and SC18 treatments (p ≤ 0.008). In addition, American beech sapling density was lower in gaps (SC18_1, CCIS16_1 and CCIS14_1, respective mean values: 70 stems·ha⁻¹ and 240 stems·ha⁻¹) than outside gaps (SC18_0, CCIS16_0 and CCIS14_0, p < 0.001, respective mean values: 910 stems·ha⁻¹ and 1,500 stems·ha⁻¹) and in the control (p < 0.001, respective mean values: 1,400 stems·ha⁻¹ and 1,700 stems·ha⁻¹, Fig. 6b). However, by year 10, the density of American beech saplings had increased for all the treatments compared to the control; this difference was significant in the EIS14 and CCIS14_1 treatments (p ≤ 0.024, Fig. 6b). Also in year 10, American beech sapling density was higher in the EIS14 treatment than in the SC18 treatment (p = 0.029).

### 3.5. Effects of exclosures on the main species

#### 3.5.1. Seedlings > 30 cm in height

Seedling density was low inside and outside exclosures for sugar maple, red maple and non-commercial species (Fig. 7c, d, e). Considering this result, we limited our statistical analysis of the effects of exclosures to yellow birch and American beech, for which seedling
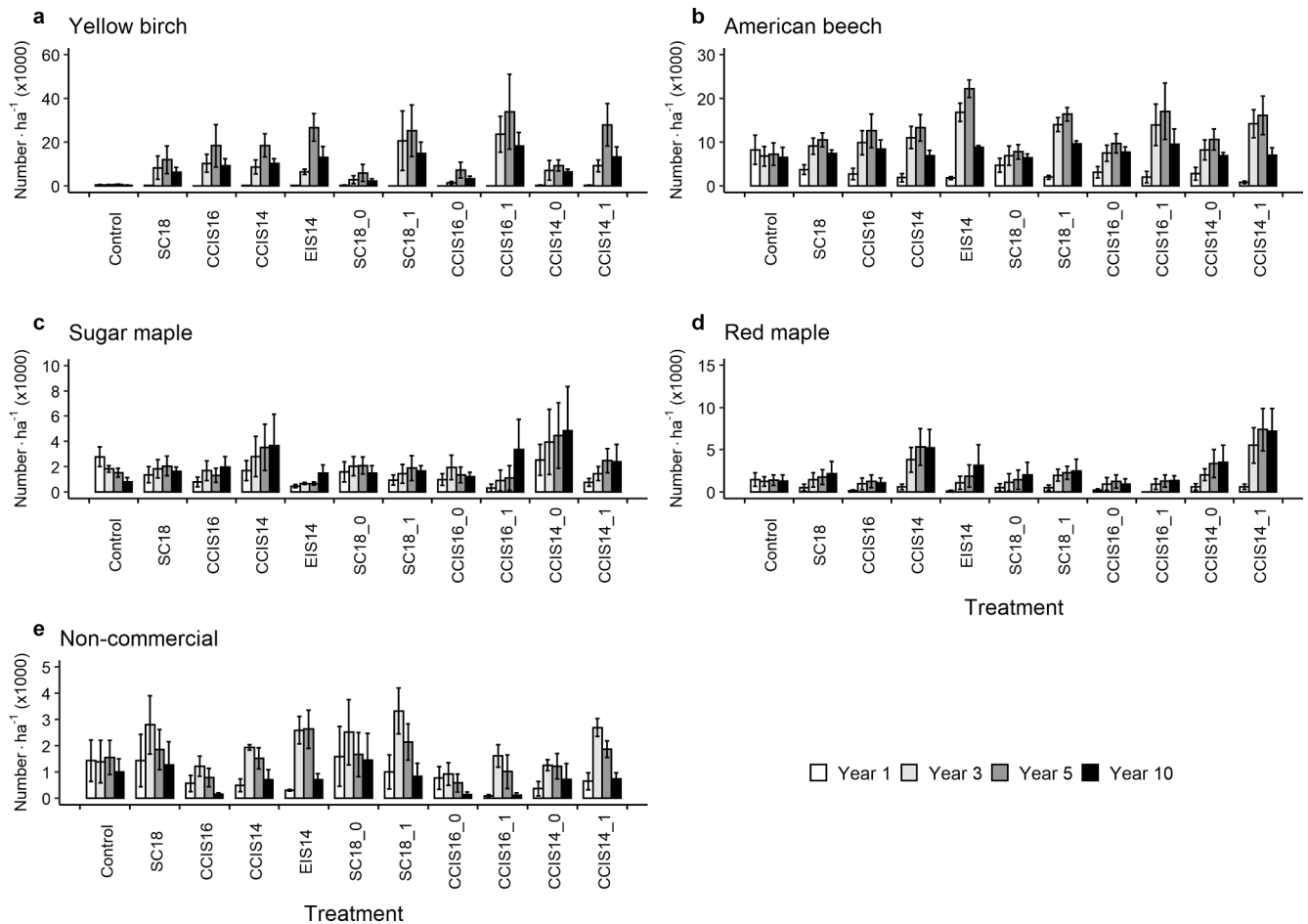
**Fig. 5.** Mean density of seedlings > 30 cm in height by species and treatment, for years 1, 3, 5 and 10 after cutting (SC18 = single-tree and group selection [residual basal area (BA): 18 m²·ha⁻¹]; CCIS16 = continuous cover irregular shelterwood [residual basal area (BA): 16 m²·ha⁻¹]; CCIS14 = continuous cover irregular shelterwood [residual BA: 14 m²·ha⁻¹]; EIS14 = extended irregular shelterwoood [residual BA: 14 m²·ha⁻¹]; treatment abbreviations followed by "_1" refer to locations within gaps for a given treatment, and those followed by "_0" refer to locations outside gaps). Error bars represent standard error.

density was much higher. Our analysis reveals that for both species, this variable was unaffected by the cutting treatments ($p \geq 0.617$, Table 4) and by exclosures ($p \geq 0.061$, Table 4); it varied only according to year ($p < 0.001$, Table 4). For yellow birch, seedling density was higher in year 5 than in year 10 ($p < 0.001$, respective mean values: 48,100 stems·ha⁻¹ and 14,800 stems·ha⁻¹, Fig. 7a). American beech followed the same trend ($p < 0.001$, mean of 18,400 stems·ha⁻¹ in year 5 and of 7,000 stems·ha⁻¹ in year 10, Fig. 7b).

*3.5.2. Saplings*

Sapling density was low inside and outside exclosures for sugar maple, red maple and non-commercial species (Fig. 8c, d, e). Considering this result, no statistical tests were performed for these species. For yellow birch and American beech, sapling density varied according to a year × exclosure (inside or outside) interaction ($p < 0.001$, Table 4). For yellow birch mean value was higher inside than outside the exclosures in years 5 and 10 ($p \leq 0.003$, Fig. 8a) and density also increased inside the exclosures between years 5 and 10 ($p < 0.001$), but not outside the exclosures ($p = 0.905$). For American beech, sapling density in year 5 was not significantly different inside or outside exclosures ($p = 0.157$, Fig. 8b), but in year 10, it was higher outside than inside exclosures ($p < 0.001$).

## 4. Discussion

### 4.1. Light and seedbed conditions

One objective of hybrid single-tree and group selection cutting and of the irregular shelterwood methods is to create conditions favorable for regenerating a diversity of tree species, including less shade-tolerant species such as yellow birch. The combination of high light and adequate seedbed conditions are major factors known to favor yellow birch regeneration (Erdmann, 1990; Tubbs, 1969; Godman and Krefting, 1960). Several studies in northern hardwoods indicate that creating canopy gaps should favor the regeneration of trees with lower shade tolerance (Leak, 1999; Webster and Lorimer, 2005; Shields et al., 2007). However, other studies have found that gaps have little effect on less shade-tolerant species when advance regeneration is abundant or shrub density is high (Shure et al., 2006). Moreover, growth of advance regeneration of shade-tolerant species can also respond well to release after gap creation. Thus, gap creation could be ineffective for the regeneration of less shade-tolerant species if advance regeneration is not reduced or removed (Kelty et al., 2003).

Results of the present study show that the experimental treatments created more diverse understory light and seedbed conditions, and that removing American beech saplings also allowed for better control of understory vegetation composition. All the cutting treatments increased total transmitted light by a factor of 1.6 to 2.2 (mean values: 23% to 34% transmitted light) compared to precut conditions and to those in the
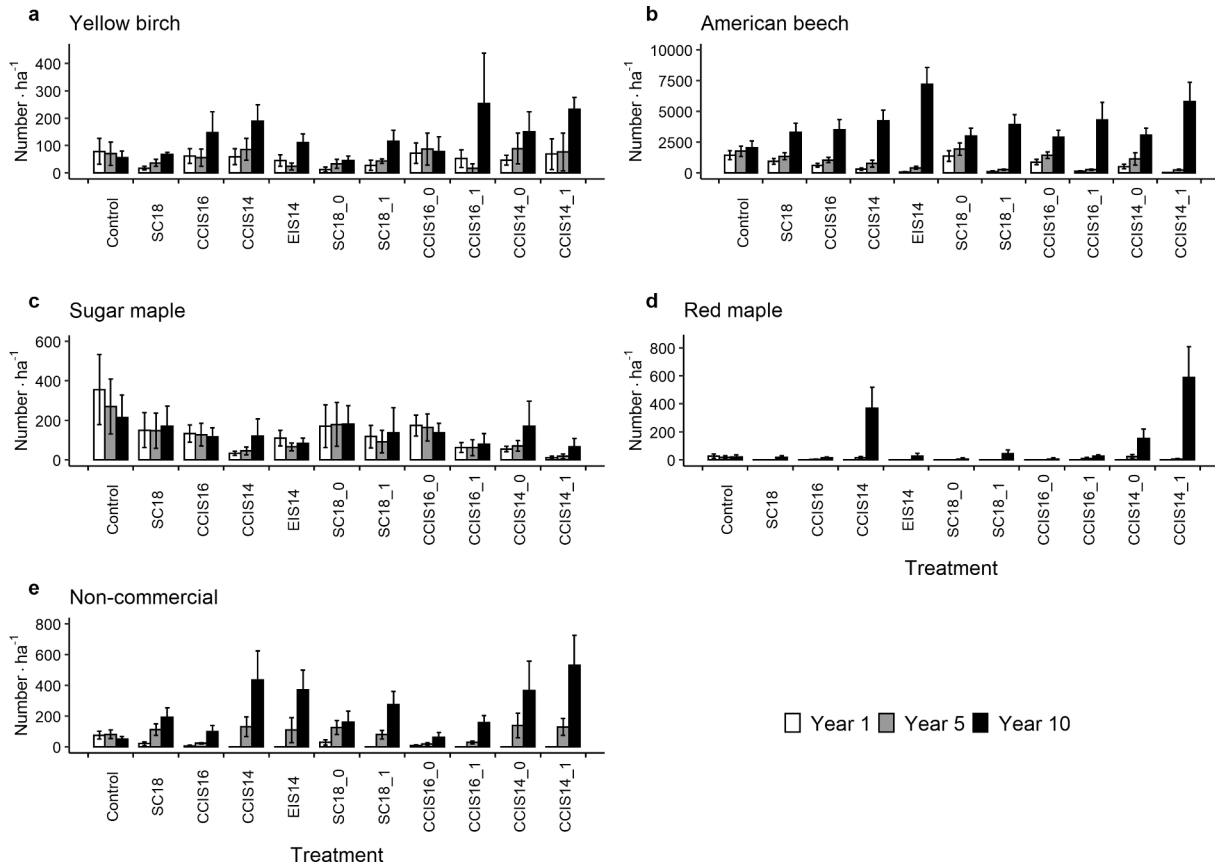
**Fig. 6.** Mean density of saplings (1.1 ≤ DBH ≤ 9.1 cm), by species and treatment, for years 1, 5 and 10 after cutting (SC18 = single-tree and group selection [residual basal area (BA): 18 m²·ha⁻¹]; CCIS16 = continuous cover irregular shelterwood [residual basal area (BA): 16 m²·ha⁻¹]; CCIS14 = continuous cover irregular shelterwood [residual BA: 14 m²·ha⁻¹]; EIS14 = extended irregular shelterwoood [residual BA: 14 m²·ha⁻¹]; treatment abbreviations followed by _1 indicate groups within the treatment, and those followed by "_0" refer to locations outside gaps). Error bars represent standard errors.

**Table 3**
ANOVA results (*p*-values) for sapling density (stems·ha⁻¹) of American beech (square-root transformation and banded main diagonal variance–covariance matrix UN(1) used; ndf = numerator degrees of freedom; ddf = denominator degrees of freedom).

| Source of variation | ndf | ddf | American beech |
|---|---|---|---|
| Treatment (T) | 7 | 41.9 | <0.001 |
| Year (Y) | 2 | 47.1 | <0.001 |
| T × Y | 14 | 50.8 | <0.001 |
| Covariate* | 1 | 55.6 | <0.001 |

* The covariate corresponds to the precut sapling density.

control (mean: 15% transmitted light). Gap creation and the removal of understory beech saplings in the SC18 and CCIS treatments contributed the most to the increase in light. In the EIS14 treatment, cutting intensity coupled with understory beech removal also contributed to the increase in light. As expected, treatments with the lowest residual BA (14 m²·ha⁻¹) allowed better light transmission (CCIS14 and EIS14; 33%–34%) than the others (SC18 and CCIS16; 23%–25%). The proportion of microsites where transmitted light reached 45%, which is the optimal threshold reported by Logan (1965), increased in all cutting treatments, especially in those with the lowest residual BA (CCIS14 and EIS14). Interestingly, the range of light intensities was similar among these two treatments, despite our intention of creating different cutting patterns (Fig. 2d, e). This result highlights that at low residual BAs, the difference between a patchy harvest (combining gaps and single trees) and a more uniform cutting pattern may be subtle, particularly in stands with an initial irregular structure that prevents a perfect uniform spacing

between residual trees.

Other studies have highlighted the importance of scarification and exposed mineral soil (Godman and Krefting, 1960; Raymond et al., 2003; Willis et al., 2015; Gauthier et al., 2016). In support of this, our results show that soil scarification improved the proportion of favorable seedbeds (disturbed and scarified) for species with lightweight seeds such as yellow birch. The greater coverage of these receptive seedbeds observed in the gaps suggests that it is more effective to scarify inside gaps than between trees under a uniform cover. Results obtained outside gaps are mostly related to passive scarification during logging. We found that receptive seedbeds represented a smaller area within the gaps (36%) than in other studies with a similar forest composition and treated with similar equipment (Bédard and DeBlois, 2010 [55%], Gauthier et al., 2016 [50%]). Our result is also lower than the 50% coverage recommended to ensure the successful establishment of birch (Godman and Krefting, 1960). This result was likely caused by a very stony soil in this study, which limited the scarification that could be done using a skidder with a blade rake. Nevertheless, receptive seedbed coverage was greater than what was obtained by Shields et al. (2007) and by Gasser et al. (2010) in gaps of similar size without intentional scarification (≤18%).

*4.2. Regeneration*

As expected, treatments creating gaps and lowering BA, coupled with soil scarification and American beech control, did the most to promote yellow birch regeneration, both of seedling and sapling size. The study's design does not allow for separating the effects of the main treatments from the understory treatments (i.e., removing American beech and
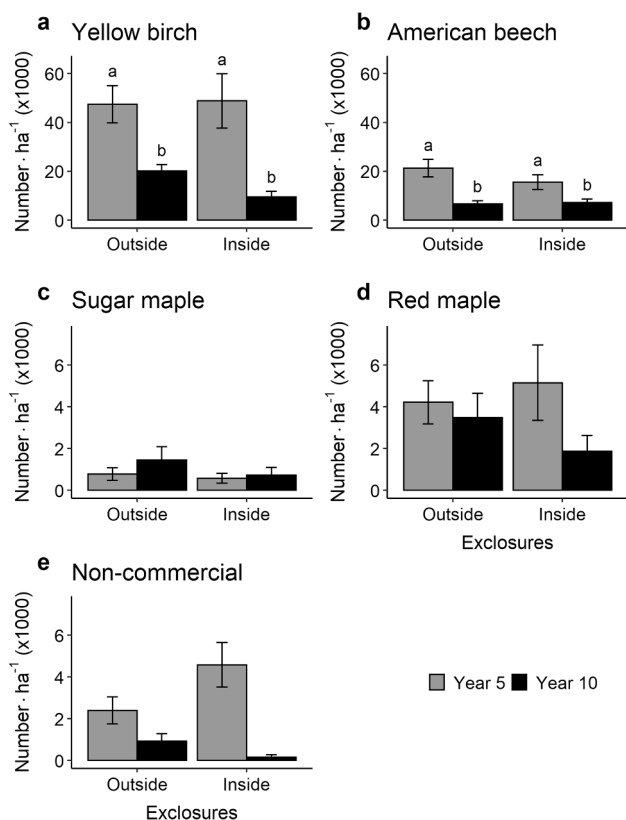
**Fig. 7.** Mean density of seedlings > 30 cm in height inside or outside exclosures, by species, in years 5 and 10. Error bars represent standard errors, and different letters indicate a significant difference between years for a given level of exclosures (outside or inside).

scarifying the soil) because these were carried out on all cutting treatments. This design was retained on the basis of other studies, which had already highlighted that opening the canopy or creating silvicultural gaps alone often led to the promotion of advance regeneration. Since advance regeneration in this study was largely dominated by American beech saplings, additional treatments (scarification and removal of beech) were viewed as necessary to favor the development of yellow birch and sugar maple since these two species were an important component of the canopy and nearly absent as advance regeneration.

The density of yellow birch regeneration increased with cutting intensity, but no significant differences were found among cutting treatments. After 5 and 10 years, the density of large seedlings (height > 30 cm) was significantly greater in the CCIS14 and the EIS14 treatments and in gaps (SC18_1, CCIS16_1, CCIS14_1) compared to the control.

After 10 years, however, despite its dominance at the seedlings stage, yellow birch did not reach the sapling class as fast as American beech. Indeed, beech abundance decreased in the short term after mechanical control, but increased significantly over 10 years in the EIS14 and CCIS14_1 treatments, compared to the control. According to our field observations, the re-emergence of American beech in the sapling class and the failure of yellow birch to reach this class can be explained by two main factors: 1) the vegetative reproduction of cut beech by stump sprouts and root sprouts, and 2) the browsing preference of deer and moose for yellow birch seedlings. The simultaneous action of both factors is known to promote beech development (Nyland et al., 2006a) and has probably contributed to the large-scale expansion of beech in the northern hardwood range. Where beech had been controlled in our study, we observed stump sprouting on about 1/3 of saplings (often with more than a single stem per stump) and root sprouting on another 1/3 of saplings. The high proportion of stump sprouts from cut saplings could be related to the fact that treatments were applied during the fall. During the dormant season, carbohydrate reserves are known to concentrate in root systems and to fuel future stump sprout development (Nyland et al., 2006b). By contrast, other studies in which beech saplings were mechanically removed during the growing season with brush saws (Nyland et al., 2006b) or with lopping shears (Nyland and Kiernan, 2017) have resulted in a high beech mortality rate. However, to our knowledge, no other studies have documented beech sapling mortality and sprouting after mechanical control for longer than one growing season. Moreover, soil scarification and logging operations may also have contributed to root sprout formation after root damage (Jones and Raynal, 1987).

Contrary to our expectations, cutting treatments coupled with soil scarification and American beech control did not promote sugar maple at the seedling or the sapling stage. Even though sugar maples represented an important proportion of merchantable trees after cutting (36%) and a similar proportion (40%) of the seedlings class (≤30 cm), these did not develop into larger seedlings and saplings. Sugar maple was probably subject to heavy competition from the dense beech sapling layer, which is known to hinder the development of other species by reducing light and other resources (Kobe et al., 1995; Hane, 2003). Within the gaps, scarification operations could have contributed to hindering the regeneration process through the destruction of advance sugar maple seedlings or saplings. Furthermore, competition with yellow birch may also have played a role in the gaps, since we observed that yellow birch quickly overtopped sugar maple during the first year due to its faster initial growth. This is consistent with the findings of Beaudet and Messier (1998) and of Gasser et al. (2010) in similar gap conditions. Another factor that may have limited sugar maple development is the poor soil exchangeable Ca at the study site. Sullivan et al. (2013) showed that the proportion of sugar maple regeneration is low (0%–20%) where soil base saturation is <20% in the upper B horizon. At Duchesnay forest, in a study site located near our study, Ouimet et al. (2013) reported that soil base saturation of the upper B horizon was 2.08% to
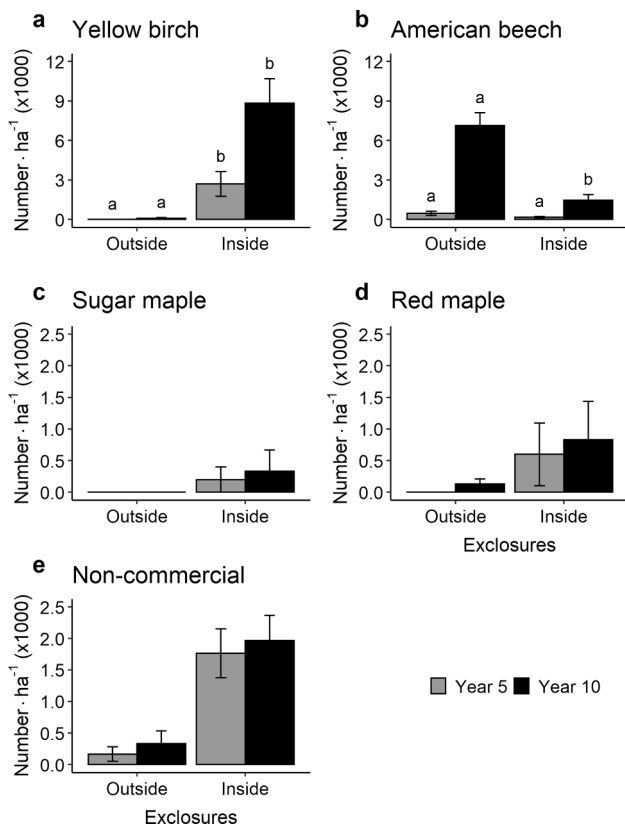
**Table 4**

ANOVA results (*p*-values) for density (stems·ha$^{-1}$) of seedlings > 30 cm in height and of saplings (1.1 cm ≤ DBH ≤ 9.1 cm) for the main commercial species, considering that the factor related to treatment (T) is defined as EIS14 and CCIS14_1, and that exclosure (E) is defined as inside or outside exclosures. A square-root transformation was used for yellow birch seedlings, whereas yellow birch saplings were analyzed using the randomization test. The banded main diagonal variance-covariance matrix UN(1) was retained, except for yellow birch saplings, for which we used the unstructured (UN) matrix. ndf = numerator degrees of freedom; ddf = denominator degrees of freedom.

| Source of variation | Seedlings (height > 30 cm) | | | | Saplings (1.1 cm ≤ DBH ≤ 9.1 cm) | | | |
|---|---|---|---|---|---|---|---|---|
| | ndf | ddf* | Yellow birch | American beech | ndf | ddf* | Yellow birch | American beech |
| Treatment (T) | 1 | 13.9 | 0.659 | 0.617 | 1 | 1.1 | 0.533 | 0.837 |
| Exclosure (E) | 1 | 17.8 | 0.061 | 0.263 | 1 | 18.0 | <0.001 | <0.001 |
| T × E | 1 | 17.8 | 0.394 | 0.059 | 1 | 18.0 | 0.330 | 0.703 |
| Year (Y) | 1 | 17.8 | <0.001 | <0.001 | 1 | 20.0 | <0.001 | <0.001 |
| T × Y | 1 | 17.8 | 0.337 | 0.910 | 1 | 20.0 | 0.187 | 0.977 |
| E × T | 1 | 17.8 | 0.141 | 0.182 | 1 | 20.0 | <0.001 | <0.001 |
| T × E × Y | 1 | 17.8 | 0.728 | 0.108 | 1 | 20.0 | 0.179 | 0.746 |

*The ddf values presented are those for yellow birch, as a representative example.

**Fig. 8.** Mean density of saplings inside or outside exclosures, by species, in years 5 and 10. Error bars represent standard errors and different letters represent a significant difference between levels of exclosures (inside or outside) for a given year.

4.2%. The low available Ca in this northern temperate ecosystem is probably attributable to the combination of high levels of acid deposition, significant Ca leaching, and relatively low Ca replenishment through mineral weathering in the soils (Houle et al., 1997; Ouimet and Duchesne, 2005). Thus, soil Ca may be a limiting factor for sugar maple survival and growth in such conditions (Long et al., 1999; Duchesne et al., 2005; Juice et al., 2006). In situations such as this, Ca addition could improve survivorship and abundance of sugar maple regeneration (Kobe et al., 2002; Juice et al., 2006; Moore et al., 2012). American beech has a better tolerance than sugar maple for soils with lower Ca content in the upper mineral layers (Long et al., 1997; Sullivan et al., 2013; Duchesne et al., 2013). Sugar maple is also susceptible to deer browsing in northern hardwood stands (Long et al., 2007; Matonis et al., 2011). Thus, cervid browsing may also have contributed to the low observed density of sugar maples in the seedling and sapling classes.

In our study, red maple was a marginal species in terms of relative abundance, which is typical for this forest type. This shade-tolerant species has a high capacity to regenerate sexually or asexually after a disturbance. Our results show that gap conditions and lower residual density promoted its regeneration in one treatment (CCIS14). Mean relative density of seedlings reached 13% in year 5 and stayed at this level until year 10. This proportion is higher than what was observed in the main canopy before and after cutting (2%–3%). In year 10, the relative seedling density of non-commercial species was only 5%.

### 4.3. Effects of browsing

At the seedling stage, the exclosures did not affect yellow birch and American beech abundance, probably because a proportion of the seedlings reached the sapling stage and the remaining proportion may have suffered from competition by the saplings. However, the contrasting results obtained inside and outside the exclosures for saplings clearly show the negative effects of browsing on yellow birch development. Contrary to the results obtained outside the exclosures, yellow birch dominated the sapling class inside exclosures and reached a density similar to that of beech outside exclosures. Our field observations indicate that yellow birch was repetitively browsed during the 10-year period, so much that the majority of seedlings did not exceed 1 m in height, and very few reached the saplings class. Negative impacts on the height growth of yellow birch planted in silvicultural gaps have also been reported in northern hardwoods where deer density varies from 5.4 to 12 deer·km$^{-2}$ (Kern et al., 2012; Walters et al., 2016). Walters et al. (2016) also found that yellow birch seedling height stagnated at about 1 m in unfenced areas due to browsing. They also found that sugar maple and American beech height were not affected by deer. Data on deer and moose density is not available in our study site, but it is likely that densities exceeded critical thresholds for successful yellow birch regeneration. It is worth mentioning that hunting is prohibited over the entire 8,900 ha area of Duchesnay Forest. Game cameras installed from 2014 to 2019 in the EUs with exclosures (n = 6) showed that mostly deer, and occasionally moose, frequently pass in our study during the snow-free season. Deep snow generally restricts deer movements from January to March in the area.

## 5. Implications for forest management

Our 10-year results indicate that regenerating yellow birch and sugar maple can be challenging under contemporary conditions, despite all the efforts made to favor their regeneration over American beech. Creating receptive seedbeds and favorable light conditions has contributed to establishing a new cohort of yellow birch seedlings in the gaps and under EIS treatment, but deer browsing limited their height development and prevented them from reaching the sapling stage. Preferential browsing of yellow birch, combined with vegetative American beech reproduction, has favored the return of the latter and allowed it to dominate most of the understory. The high browsing pressure observed in our experiment could be related to the absence of deer density control through hunting, but also to current forest management practices. During the last two decades, single-tree selection cutting was the main silvicultural system used in the area; this approach did not create conditions promoting the generation of new seedling patches in gaps like those experimented in our study. Consequently, the relative scarcity of patches of young regeneration cohorts in the landscape probably exacerbates the browsing pressure in our study. Increasing the frequency of early-successional forest conditions by creating silvicutural gaps or more open canopy conditions at the landscape scale could probably mitigate browsing pressure on our targeted species by providing more forage to cervids (Royo et al., 2017). Our results also suggest that the hunting prohibition could have major effects on future forest composition. We propose that deer and moose harvesting be considered along with silvicultural treatments to favor regeneration (Béguin et al., 2016). Another factor to consider is the effectiveness of American beech mechanical control. Realizing the intervention during the growing season could probably yield better results (Nyland and Kiernan, 2017). However, we hypothesize that this method would only be effective if the regeneration of the target species could grow faster in height than American beech stump sprouts arising from the saplings that were cut and if the browsing pressure on these species was lower than in this study. Finally, the sugar maple regeneration failure in this study is not well understood and might be related to site characteristics. Consequently, other strategies combining canopy and understory manipulation as well as soil amendments with lime should be considered to favor sugar maple regeneration where the soil shows severe base cation depletion.

## Declaration of Competing Interest

## Acknowledgements

## Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120142.

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