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Short-term effects of irregular shelterwood cutting on yellow birch regeneration and habitat use by snowshoe hare

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ABSTRACT

Irregular shelterwood cutting has been recently prescribed to improve the regeneration of semi-tolerant species such as yellow birch (*Betula alleghaniensis* B.), while also maintaining the complexity of natural mixed forests. However, its effects on forest dynamics are poorly known. In this study, we document the short-term effects of three irregular shelterwood cutting patterns on the establishment and composition of regeneration as well as on its use by snowshoe hare (*Lepus americanus* E.). Specifically, we compared uniform, gap, and strip cutting patterns with soil preparation, relative to uncut controls. We counted seedlings, browse, and hare pellets, and measured habitat characteristics after two growing seasons in micro-plots delimited in each of the shelterwood cutting patterns. The mixture of soil and humus resulting from scarification promoted yellow birch establishment. Yellow birch seedlings in gaps were more abundant than in controls, but their abundance was comparable to other irregular shelterwood patterns. All irregular shelterwood patterns promoted competition mainly by pin cherry (*Prunus pensylvanica* L.f.), beaked hazel (*Corylus cornuta* M.), and mountain maple (*Acer spicatum* Lam.). Snowshoe hare browse on yellow birch was low for all irregular shelterwood patterns. Moose browse pressure was higher than that from hare. We found no short-term impact of the snowshoe hare on yellow birch seedling establishment and survival. Snowshoe hare pellet counts suggested a preference for gaps. This result could be explained by increased food and protective cover from higher seedling and shrub densities in gaps than in other treatments. In the short-term, up to three years post-treatment, irregular shelterwood cutting helps to promote yellow birch regeneration, a semi-tolerant species, while maintaining habitat for snowshoe hare.

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1. Introduction

The irregular shelterwood system can maintain or restore irregular stand structures (Raymond et al., 2009). This silvicultural practice is increasingly being used in public land planning in north-eastern North America for forest stands that are affected by partial stand mortality and subject to gap dynamic processes (Raymond et al., 2009). Specifically, irregular shelterwood cutting aims to harvest, regenerate, and improve stands through a series of partial cuts. Irregular shelterwood cutting also aims to ensure that different regeneration patterns are established across stands. This

technique is well suited to mixed stands. Indeed, irregular stands are an integral part of deciduous and mixed forest landscapes (Boucher et al., 2009). Successive partial cuts gradually open the stand canopy with a regeneration period that is greater than 20% of the rotation length. The target is to establish a new regeneration cohort after each cut, under the protective cover of seed trees (Raymond et al., 2009, 2013). Thus, irregular shelterwood practices are recommended to help maintain natural forest complexity and its associated diversity. In northeastern deciduous forests, this management strategy could alleviate the lack of regeneration for several semi-tolerant species (i.e., species with moderate shade tolerance) such as yellow birch (*Betula alleghaniensis* B.) and maintain old-growth structural attributes (Majcen, 2003; Raymond et al., 2009; Nappi and Poulin, 2013). However, this type of intervention is recent and its effects on forest dynamics are poorly understood.

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In mixed forest, yellow birch regeneration is strongly associated with gap dynamics (Kneeshaw and Prévost, 2007; Webster and Jensen, 2007). Silvicultural practices do not always provide suitable conditions for seedlings, in terms of their establishment and survival, comparable to those found in natural gaps (Woods, 2000; Gronewold et al., 2010; Bolton and D'Amato, 2011). The dwindling numbers of yellow birch in managed landscapes has been described as a biodiversity issue that is related to the vegetational composition of hardwood stands (e.g., Grondin and Cimon, 2003). The success of yellow birch regeneration is generally related to the presence of adequate seedbeds (humus–mineral soil mixtures), canopy openings of sufficient size and number, the availability of seeds that are evenly distributed throughout a stand, and the limited presence of understory vegetation (Erdmann, 1990; Raymond, 2012). The availability of seeds depends on yellow birch mast years, which occur every 3 years, on average (Erdmann, 1990). Irregular shelterwood cuts that are followed by mechanical soil disturbance could favour yellow birch regeneration, especially if these treatments are synchronized with mast years (Prévost et al., 2010).

Due to its palatability, yellow birch is an important dietary component of mammalian herbivores such as white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and snowshoe hare (*Lepus americanus*) (Wang, 1968; Hughes and Fahey, 1991; Bouffard et al., 2007). Snowshoe hare is prized by hunters and trappers snaring proponents, but is also considered a key species in forest ecosystem food webs (Boutin et al., 1995; Krebs et al., 1995). Its abundance influences population densities of most predators, including many furbearing mammals such as Canada lynx (*Lynx canadensis*), fisher (*Martes pennanti*) and American marten (*Martes americana*) (Keith, 1990; Etcheverry et al., 2005). Winter is the most critical season in terms of availability of food and cover for hare (Guay, 1994). Protective cover provides both visual protection and physical obstruction against attacks by predators (Keith, 1990). The winter diet of hares consists mainly of twigs and buds of woody species. Hares prefer the twigs of deciduous species such as yellow birch, when they are available (Smith et al., 1988; Keith, 1990). Hares focus on small diameter stems (<3 mm), which have higher nutritional value than stems with larger diameters (Wolff, 1980). As a ubiquitous herbivore, the snowshoe hare has a considerable effect on the vegetation composing its diet (Smith et al., 1988; Murray, 2003; Bouffard et al., 2007). Indeed, observed browsing intensities on twigs are closely related to hare population density estimates. At high densities, hare can remove large quantities of forest biomass (Murray, 2003). Consequently, management practices promoting large hare populations may considerably reduce the regeneration success of highly palatable species, such as yellow birch, because of the adverse effects of browsing.

In this study, we document the short-term effects of three cutting patterns of irregular shelterwood (uniform, strips, and gaps) on (1) the establishment and composition of yellow birch regeneration and its competitors, and (2) the use of this new habitat by snowshoe hares. Based on the response of yellow birch to natural gaps, we expected that its regeneration in gap patterns would be greater than in other treatments, although competition would also be greater in these newly created gaps. We also expected that hares use the uniform irregular shelterwood cuts more than strip and gap patterns, and consequently, that browsing pressure would be highest in the uniform shelterwood cuts. Moreover, we expected that hare habitat use, based on pellet counts and browsing inventories, would be lowest in the centre of the openings of strips and gaps, away from the edges that provide protective cover.

2. Methods

2.1. Study area and experimental design

The study was conducted in the Témiscamingue administrative region of northwestern Québec (Canada), within the sugar maple–yellow birch bioclimatic sub-domain (MRNFP, 2003). The experimental site, which is 70 km east of the town of Témiscaming, is located near Petit Lac Caugnawana (46°36' N, 78°26' W) and includes more than 2000 ha. Irregular shelterwood treatments were carried out in winter 2009–2010 in stands that were mostly composed by various proportions of yellow birch, sugar maple, and red maple. Specifically, 118 ha consist of cutted by uniform irregular shelterwood, 416 ha of strip irregular shelterwood cutted by strips, 441 ha cutted of extended gap irregular shelterwood by gaps and, 970 ha of uncut control. Treatments were assigned according to stand characteristics and operational feasibility. The stands selected for this study in this general experimental site were all dominated by yellow birch to minimize inter-stand variability, and represent an area of 215 ha (Fig. S1, Supplementary Materials). A total of 27 ha have been treated by uniform irregular shelterwood cutting, 88 ha by strip cutting, and 38 ha by expanded gap cutting. A total of 62 ha was used as an untreated control. The application of uniform and strip irregular shelterwood cutting was an adaptation of the slow regeneration shelterwood treatment (Raymond et al., 2013).

For uniform irregular shelterwood cutting, each stand was spatially heterogeneous and comprised of different smaller units at least 200 m² that were classified into one of three categories. Each category was subjected to specific silvicultural prescriptions determined according to the stand unit characteristics (Lussier and Meek, 2014). When a unit was not well regenerated and trees were of large dbh (diameter at breast height, 1.3 m; >34 cm), the unit was considered as requiring regeneration establishment. Trees were subsequently marked to obtain a residual forest cover between 50% and 60%, consisting of the desired trees, mainly yellow birch, sugar maple, red maple, and white spruce (*Picea glauca* (Moench) Voss), together with companion trees, such as balsam fir. If a stand unit was composed mainly of small trees (18–32 cm dbh), stand units were thinned to obtain a residual cover of 60–70% to promote future growth. In cases where the desired regeneration was already abundant, regeneration was released by cutting all mature trees. Thus, within a given stand, there could be portions where regeneration was promoted, released, or left to grow. In our study area, 8% of uniform irregular shelterwood stands were well regenerated, 27% were left to grow, and 65% were treated to promote the establishment of regeneration (Joanisse et al., 2011). After tree marking, all unmarked trees with dbh greater than 24 cm were harvested.

Strips of irregular shelterwood consisted of sequences of three 10-m wide strips, oriented east to west and harvested in multiple passes. The first strip of each sequence was clear-cut while adjacent strips remained intact. Harvested strips accounted for 33% of the strips of irregular shelterwood stands when our study was conducted. Expanded gaps consisted in creating 4 gaps per hectare, each having an average size of 400 m² from stem to stem. Gaps were positioned about 50 m apart and separated by permanent trails. All trees in gaps and permanent trails were harvested, while portions outside of gaps and trails remained intact. The canopy openings that resulted from these cuts had an average area of 260 m² (range 86–432 m²). Gaps accounted for 16% of expanded gap irregular shelterwood stands, whereas permanent trails accounted for 14% of stands.

Site preparation by scarification was performed in summer 2010 with an excavator, which mixed the organic layer with the

uppermost 5 cm of mineral soil. For uniform irregular shelterwoods, site preparation was conducted where the excavator could reach without damaging residual trees. In other irregular shelterwood treatments, site preparation was done in harvested strips and gaps. Strips and expanded gap irregular shelterwood treatments were conducted in stands with two types of soil drainage: mesic and subhydryc. In the subhydryc drainage stands, the softwood understory cover is usually more important than in the mesic drainage stands. We expected that areas with a subhydryc drainage could provide a better habitat for hares, which in turn could affect their browsing pressure.

Using aerial photographs, we selected replicates for each irregular shelterwood treatment and control stands. We based our selection on similar characteristics in terms of cover type, age class of the initial stand, as well as slope and drainage classes within the different cut blocks where forest stands had similar attributes before harvesting. The application of these criteria resulted in the final selection of 36 experimental stands. Control stands were not truly spatially replicated because of the availability of the uncut stands in the area. Regeneration inventories for yellow birch and other competitive stems were conducted in autumn 2011, i.e., two growing seasons after cutting. One to three clusters of regeneration micro-plots were established in each stand, depending on the size of stands (Fig. S1, Supplementary Materials). Clusters were distributed with a minimum distance of 75 m between them within each stand. Individual clusters were composed of micro-plots that were spaced at 5 m intervals. Clusters in the uniform irregular shelterwood, controls, and strips were arranged along 60 m transects, for a total of 10 micro-plots per cluster. Given the smaller size of gaps, we used a different micro-plot arrangement in the latter treatment with a total of 5 micro-plots per cluster. The first micro-plot was placed in the gap centre and others were spaced 5 m from the centre along the four cardinal points. Overall, 212 micro-plots were nested in 71 clusters that were spread over our 36 experimental stands.

2.2. Regeneration and browsing

Regeneration sampling was conducted at the end of the second growing season after harvesting. Micro-plots had a 1.13 m radius, which corresponded to an area of 4 m² or 1/2500 ha (MRNF, 2011). We sampled three micro-plots per cluster. All commercial and non-commercial species were recorded, including yellow birch (*B. alleghaniensis* B.), sugar maple (*Acer saccharum* M.), red maple (*Acer rubrum* L.), mountain maple (*Acer spicatum* Lam.), balsam fir (*Abies balsamea* (L.) Mill), pin cherry (*Prunus pensylvanica* L.f.), and beaked hazel (*Corylus cornuta* M.). We considered two seedling height classes for yellow birch, viz., seedlings <25 cm and those ≥25 cm in height, to compare effects on the establishment and development of yellow birch regeneration. Commercial seedlings that were smaller than 25 cm in height were inventoried by the following abundance classes: absent; 1–5 stems; 6–15 stems; and more than 15 stems. Seedlings over 25 cm in height were counted for commercial and non-commercial species, except for raspberry (*Rubus* sp.), for which only its presence was noted. Presence of browsing by cervids (chewed and broken twigs) or hare (sharp cuts) was also noted on the seedlings. The count was exclusive and we only noted the dominant browse type on each seedling.

We conducted timber inventories to characterize initial basal area (m²/ha) among treatments before harvesting, together with residual basal area for seed trees of each species after treatment. We used plots with a fixed 11.28 m radius or with a variable radius employing a factor 2 prism. All tree species with a minimum of 10 cm dbh were recorded. For each micro-plot, seedbed and light environments were also characterized. We created three soil

disturbance classes based on the micro-plot area that was covered by disturbed soil: none; <75%; ≥75%. The type of disturbed ground was also noted as being dominated by humus (>50% humus cover), equal coverage of humus and mineral soil, or dominated by mineral soil (>50% mineral soil cover). For light availability, canopy closure was assessed with a homemade densiometer similar in construction to a Cajanus tube (Ganey and Block, 1994). This instrument consists of a vertical tube, which has a built-in bubble level, an internal mirror that is placed at 45 degrees, and two strings that form a crosshair in the upper opening. We noted if vegetation crossed the intersection of the two strings as observed through the opening in the densiometer. We assessed canopy closure, starting 2 m before the centre of the first micro-plot to 2 m past the last micro-plot, taking measurements every 2 m along the transect, for a total of 31 observation points per cluster. In gaps, canopy closure was recorded above the centre of each of the 5 micro-plots, for a total of 5 observation points per cluster. The ratio of the number of intersections divided by the number of canopy closure measurements gave us an average canopy closure per cluster.

2.3. Habitat use by snowshoe hare

Vegetation density and vertical closure are recognized as the most important variables that explain the distribution of snowshoe hare (Ferron et al., 1996). Wildlife habitat was characterized by vertical and lateral winter cover estimates, and by available browse (food) at each micro-plot. Lateral winter cover was evaluated at the end of winter, after snowmelt and before the vegetation greened up. Because snowshoe hare can reach twigs that are about 60 cm above the ground surface or above the snow surface (Keith et al., 1984), lateral winter cover was measured up to a height of 2 m to account for the accumulated winter snow pack. We estimated lateral cover with a vegetation profile board consisting of a 30 cm-wide panel, which was divided into four sections of 50 cm in height with different bright colours (Nudds, 1977). We assigned a 25% class to each section of the profile board. Vegetation cover was estimated at a 15 m distance along the four cardinal directions in each of the three micro-plots that were sampled in each cluster. We calculated the average percentage cover per micro-plot (four cardinal directions) (Ferron et al., 1996). Vertical winter cover (trees >4 m in height) was based on the presence or absence of vegetation that had been assessed with the densiometer. We conducted these vertical measurements at the end of winter. We measured vertical cover on the same transects that were used for lateral winter cover, from the centre of each micro-plot to the four cardinal directions in 3 m increments to a distance of 15 m. Vertical winter cover was expressed as a percentage of cover occurrences for a total of 21 observation points (Bertrand and Potvin, 2003). Snowshoe hare feed on small twigs (<5 mm diameter) of woody shrubs and trees in winter (Pease et al., 1979). Therefore, we estimated food availability using the regeneration surveys that were previously described for the number of young seedlings >25 cm in height per hectare for each plant species (Bissonnette et al., 1997).

We used pellet counts to assess snowshoe hare occupancy at the experimental sites two and three years after cutting (Litvaitis et al., 1985). Hare pellets persist for several months on the ground and are easily identified by their spherical shape and size (~1 cm diameter). Pellets were counted in the same three permanent micro-plots as those that were used in the regeneration survey, but within a circle of 1 m radius (3.14 m²). We used a circular plot to reduce the error associated with rectangular plots when populations are low (Murray et al., 2005), because we expected populations would be in the low phase of the hare cycle in our study (Assels et al., 2007). These micro-plots were previously cleared in

the autumn (2011 and 2012) to ensure that only pellets produced during the previous winter were counted. Based on the results of Bois et al. (2012), we assumed that the detection probability of pellets varies little from one habitat to another and that pellet counts provide information on fine-scale habitat use by hares.

2.4. Statistical analyses

All statistical analyses were performed in R 3.0.2 (R Core Team, 2013) and incorporated the hierarchical spatial structure of our data with random effects (Gelman and Hill, 2007).

2.4.1. Regeneration

We used linear mixed-effects models to compare total basal area between treatments before harvesting and yellow birch residual basal area after treatment. Treatment was considered as a fixed factor. Stand identity, i.e., the name that designated each treatment replicate, was considered as a random effect. Due to heteroskedasticity among treatments, we explicitly modelled the variance by allowing it to vary with treatment (heteroskedastic variance model; Pinheiro and Bates, 2000).

To determine which parameters best explained the presence of yellow birch regeneration less than 25 cm height on our micro-plots, we used generalized linear mixed models (GLMM) with a binomial distribution for binary responses (package *lme4* version 1.0–5; Bates et al., 2013). We included a random effect of stand and cluster-within-stand to reflect the hierarchical structure of the data. We used GLMM with a Poisson distribution to model the abundance of seedlings over 25 cm in height. Based on a priori knowledge, we developed six candidate models that could explain this variation (Table 1). We ranked these models, based on the second-order Akaike information criterion (AICc) and Akaike weights (w_i), using the *AICcmodavg* package (Burnham and Anderson, 2002; Mazerolle, 2013). The models considered the following habitat parameters and their combinations: residual basal area of yellow birch, which reflected the potential presence of seeds (Seed); canopy closure (Cover); the level of soil disturbance (Dist); and the nature of the dominant soil (Soil). We included a null model, which only contained a constant as an explanatory variable but with the same random effect structure as the other models. We used multimodel inference to compute model-averaged parameter estimates and their unconditional standard errors (Mazerolle, 2013).

Because the treatment was correlated with the level of soil disturbance (all controls had no disturbance), we analysed the difference between treatments with a separate GLMM. We suspected that gaps would be the most favourable sites for regeneration establishment and this treatment was considered as the reference

Table 1

Candidate generalized linear mixed models explaining the presence and abundance of yellow birch (*Betula alleghaniensis*) seedlings during the autumn of 2011 in 26 irregular shelterwood stands and 10 control stands in Témiscamingue, Québec. Explanatory variables are residual basal area of yellow birch (Seed), canopy closure (Cover), the level of soil disturbance (Dist), and the nature of the dominant soil (Soil).

Models	Hypotheses on factors affecting yellow birch regeneration
Null	Intercept only, for comparison with other models
Seed	Residual seed trees of yellow birch (seed availability)
Cover	Canopy closure (light availability)
Dist	Soil disturbance intensity (seedbed quality)
Soil	Nature of the dominant soil (seedbed quality)
Cover + Seed + Dist	Additive effects of closure, seed trees, and disturbance intensity
Cover + Seed + Soil	Additive effects of closure, seed trees, and nature of disturbance

category. No seedling less than 25 cm in height occurred in controls. This problem precluded the convergence of our models. To overcome this problem, we excluded controls from the analysis for seedlings of this height class. The effect of drainage types on the presence and abundance of yellow birch seedlings was evaluated for micro-plots of strips, gaps and controls (only one drainage type in uniform irregular shelterwood) using a GLMM that included the drainage category as an explanatory variable. A similar analysis was performed in the openings of strip and gap cutting patterns to compare the densities of regeneration over 25 cm in height, according to the distance between the micro-plot centres and the edge.

To investigate the effects of treatments on the abundance of competing species to yellow birch, total commercial and non-commercial seedling densities were compared among treatments and with yellow birch densities, using a GLMM.

2.4.2. Habitat use by the snowshoe hare

We used linear mixed models to explain the variation in lateral and vertical winter cover among treatments. Treatment was considered as a fixed factor, whereas stand and cluster within stand were treated as random effects. Due to problems of heterogeneous variances, we modelled the effect of the treatment on the variance with an additional component of the mixed model allowing for heteroskedasticity (Pinheiro and Bates, 2000). We expected that the uniform irregular shelterwood treatment would provide better habitat for snowshoe hare than the other treatments. Thus, we used this treatment as the reference level in the hare analyses. We performed GLMM with a Poisson distribution to quantify the effect of treatment on the number of regenerated stems that were available as food. We assessed differences between treatments based on 95% confidence intervals.

To determine which parameters best explained the number of snowshoe hare pellets that were found in the micro-plots, we used a GLMM with a Poisson distribution for count data. We developed thirteen candidate models potentially explaining the variation in counts of snowshoe hare pellets (Table 2). These models considered the following habitat parameters and their combinations as fixed effects: lateral winter cover (LWC); vertical winter cover (VWC); total available regenerated stems (Food); number of available seedlings of yellow birch (nYB), sugar maple (nSM), red maple (nRM), mountain maple (MM), balsam fir (nBF), pin cherry (nCP), and beaked hazel (nBH); and the presence of raspberry seedlings (pRB). The number of seedlings that were available was reduced to the scale of the pellet inventory micro-plot by multiplying the data by a factor of 0.785, respecting the relative size of the regeneration and the pellet inventories micro-plots. We used GLMM to

Table 2

Candidate mixed models explaining the abundance of snowshoe hare (*Lepus americanus*) pellets and browse during the winter of 2011–2012 in 26 irregular shelterwood stands and 10 control stands in Témiscamingue, Québec. Explanatory variables include lateral winter cover (LWC), vertical winter cover (VWC), total available regenerated stems (Food), number of available seedlings of yellow birch (nYB), sugar maple (nSM), red maple (nRM), mountain maple (MM), balsam fir (nBF), pin cherry (nPC) and beaked hazel (nBH), and presence of raspberry seedlings (pRB).

Models	Hypotheses on factors affecting snowshoe hare presence
LWC	Protection by lateral cover obstruction
VWC	Protection by vertical cover obstruction
LWC + VWC	Habitat structure
Food	Food available
LWC + VWC + Food	Habitat structure + Food available
LWC + VWC + nX ^a	Habitat structure + number of X seedlings
LWC + VWC + pRB	Habitat structure + presence of raspberry seedlings

^a X = YB, SM, RM, MM, BF, PC, BH.

evaluate the effect of a further growth season (2 vs 3 years after treatment) on the abundance of snowshoe hare pellets among treatments. Models were ranked using the second-order Akaike information criterion (AICc).

We analysed the number of seedlings over 25 cm in height that had hare browse marks for every species using the same models as those used for the pellet counts. Linear mixed models were used to compare the variation in the proportion of browsed seedlings between wildlife species (snowshoe hare and cervids), treatments, and the wildlife species by treatment interaction. Here again, we explicitly modelled the heterogeneity of variances among treatments by including an additional component in the linear mixed model. The potential effect of drainage was evaluated on the proportion of seedlings that were browsed by hare and the hare pellets in a manner similar to the one that was used for the presence of yellow birch seedlings. In strips and gaps, we used a GLMM that included the distance between the micro-plot centre and the nearest edge as an explanatory variable both for hare browsed seedling proportions and for pellets.

3. Results

We analysed data from 212 micro-plots: 30 in uniform irregular shelterwood; 62 in strips; 60 in gaps; and 60 in control stands. Mean initial stand basal area did not differ among treatments ($F_{3,34} = 0.44$; $P = 0.727$), ranging between 20 and 23 m²/ha. On average, basal area consisted of 34% of yellow birch, 18% of sugar maple, 7% of red maple, 17% of balsam fir, 18% of other softwood species, and 6% of other hardwood species. Mean residual basal area of seed trees was 7.9 m²/ha (range 0–20) for yellow birch, 3.7 m²/ha (range 0–11.4) for sugar maple, 1.6 m²/ha (range 0–6.7) for red maple, and 3.2 m²/ha (range 0–14) for balsam fir. The mean residual basal area of yellow birch was similar among treatments ($P = 0.386$). Canopy closure averaged 39% (range 0–93%) across clusters. All micro-plots in strips and gaps were scarified. Since machinery avoided unharvested areas and regenerating islets, only half of the uniform irregular shelterwood micro-plots were scarified. All treatments combined, only 6% of micro-plots had experienced less than 75% soil disturbance, whereas 57% had more than 75%. The remaining micro-plots had soil with a dominance of undisturbed humus. Most of the microplots with soil disturbance were composed of a mixture of humus–mineral (121/133 micro-plots). The average distance between the furthest micro-plots (closest to the middle of the openings) and the edge was 5.25 m (3.7–7.9 m) in strips and 8.6 m (7.3–10.8 m) in gaps.

3.1. Regeneration

3.1.1. Occurrence of yellow birch seedlings under 25 cm in height

Yellow birch seedlings less than 25 cm tall were present on 43% of uniform irregular shelterwood micro-plots, 84% of the strip micro-plots, and 78% of the gap micro-plots, but were absent in control micro-plots (Fig. 1). The probability of yellow birch seedling presence was higher in gaps (Beta: 3.93; 95% CI: 0.6, 7.26) and strips (4.03; 0.84, 7.22) than in uniform irregular shelterwood. The occurrence of yellow birch seedlings did not differ between strips and gaps (0.10; –2.78, 2.98). We found no difference in yellow birch presence between the mesic and subhydryc environments in strips and gaps (1.07; –5.71, 7.85). Two models explaining yellow birch regeneration had the greatest support, with $\Delta\text{AICc} < 2$, and could be considered equally plausible. Their combined Akaike weight is 0.96 (Table S1, Supplementary Materials). These models considered an effect of yellow birch residual basal area (seed availability), degree of canopy closure (light availability), intensity of soil disturbance, and soil

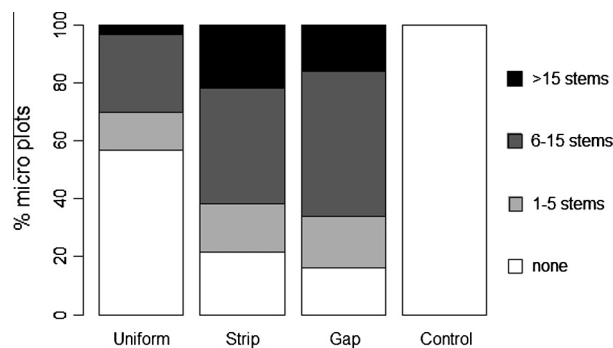


Fig. 1. Proportion of micro-plots within each treatment containing increasing numbers of yellow birch seedlings under 25 cm in height.

composition (seedbed availability) on the presence of yellow birch seedlings. As expected, soil disturbance promoted the presence of yellow birch seedlings and was higher when the disturbed area was greater than 75% (Dist, Table S2, Supplementary Materials). The dominance of a humus–mineral mixture was also more favourable to the occurrence of yellow birch seedlings than soil that was dominated by humus (Dom, Table S2, Supplementary Materials). Furthermore, the presence of yellow birch seedlings decreased with increasing canopy closure (Cover, Table S2, Supplementary Materials) (Fig. 2).

3.1.2. Density of yellow birch seedlings over 25 cm

The mean density of yellow birch seedlings that were over 25 cm tall after two growing seasons was 1000 ($\pm 95\%$ CI: ± 957) seedlings/ha in uniform irregular shelterwood, 726 (± 412) seedlings/ha in strips, and 1708 (± 971) seedlings/ha in gaps, whereas natural regeneration in the control portions was 83 (± 115) seedlings/ha. Yellow birch seedlings were more abundant in gaps than in controls (–2.81; 0.83, 4.79), but there was no difference among irregular shelterwood treatments. We found no difference between mesic and subhydryc drainages (0.24; –0.94, 1.42). Two models had the greatest support in explaining the abundance of yellow birch seedlings over 25 cm tall, with a combined Akaike weight of 0.68 (Table S3, Supplementary Materials). These models considered an effect of canopy closure (light availability), yellow birch residual basal area, and seedbed type. Although no parameter

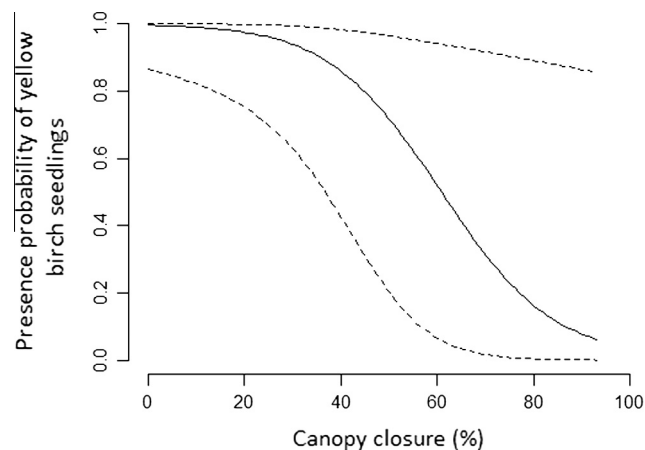


Fig. 2. Model-averaged predictions of presence of yellow birch seedlings under 25 cm, depending upon canopy closure. Mean values for other variables that were included in the models were 7.95 m²/ha for yellow birch basal area, soil disturbance over 75% of micro-plot area, and dominance of a humus–mineral soil mixture. Dashed lines represent 95% confidence intervals.

had an effect on the number of yellow birch seedlings over 25 cm tall, the degree of canopy closure had a weak negative effect ($-1.75; -3.59, 0.09$). The number of yellow birch seedlings in gaps increased with the distance between the centre of micro-plot and the nearest edge ($0.27; 0.09, 0.45$) (Fig. 3), but we did not observe this relationship in strips ($0.18; -0.19, 0.55$).

3.1.3. Seedling densities of competing species over 25 cm tall

Mean densities of yellow birch, total commercial excluding yellow birch and non-commercial seedlings over 25 cm tall in the different treatments are summarized in Fig. 4 (Fig. 4). In each pattern of irregular shelterwood, there was more non-commercial than commercial seedlings over 25 cm tall, and more commercial than yellow birch seedlings. In controls, there was more non-commercial and commercial than yellow birch seedlings over 25 cm tall. As an index of competition, the numbers of seedlings of all other species were combined but we found no difference between treatments. In uniform irregular shelterwood, the average total density of all other species over 25 cm was 14,750 (± 5546) seedlings/ha, which included 28% as mountain maple and 18% as beaked hazel seedlings. In strips, the average was 17,863 (± 4790) seedlings/ha, which consisted of 41% pin cherry, 21% red maple, and 21% beaked hazel seedlings. In gaps, the average was 18,667 (± 5858) seedlings/ha, including 39% pin cherry, and 27% beaked hazel seedlings. In controls, there was an average of 15,958 (± 3352) seedlings/ha, composed of 30% sugar maple and 24% mountain maple seedlings.

3.2. Browse

For all browse species that were studied, the proportion of total seedlings that had been browsed did not differ among treatments. Identification of cervid pellets in the field determined that only moose (*A. alces*) was present in our study site. Analyses further revealed that the proportion of seedlings that were browsed by moose did not differ among treatments. The proportion of seedlings that were browsed by snowshoe hare was lower in strips than in controls ($0.07; 0.03, 0.11$). The average proportion of seedlings over 25 cm tall that showed evidence of browsing was 15% ($\pm 3\%$), but only 3% ($\pm 2\%$) were browsed by snowshoe hare. Moose browse was more abundant than snowshoe hare browse ($0.09; 0.07, 0.11$) for all seedlings over 25 cm in height that we counted ($n = 1524$). Moose browse was significantly higher than snowshoe hare

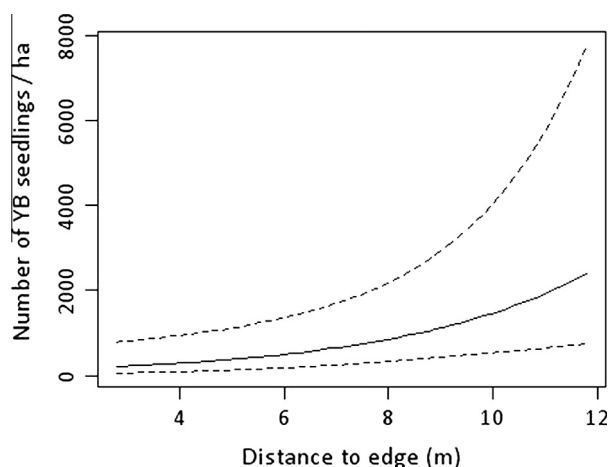


Fig. 3. Model-averaged abundance of yellow birch seedlings that were over 25 cm in height, converted to density (seedlings/ha), depending upon the distance between plot centre and the nearest gap edge. Dashed lines represent 95% confidence intervals.

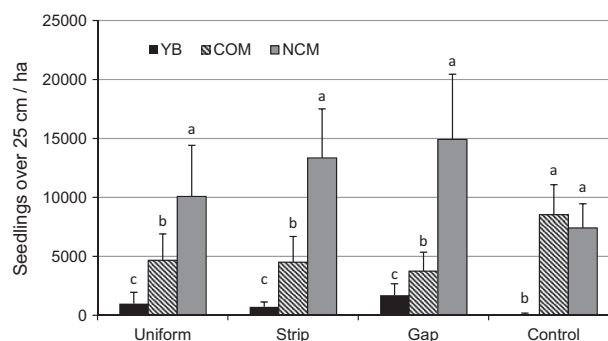


Fig. 4. Average density of seedlings over 25 cm tall (seedlings/ha) by species group and treatment in irregular shelterwood cuts in northwestern Québec, Canada. Treatments are uniform, strips, and gap patterns of irregular shelterwoods, together with controls. Species groups are yellow birch (YB), commercial excluding YB (COM) and non-commercial (NCM) species. Error bars indicate a 95% confidence interval. Means with different letters are significantly different (Tukey's HSD, $p < 0.01$).

browse in all irregular shelterwood treatments (uniform: 0.07; 0.01, 0.13; strips: 0.13; 0.07, 0.19; gaps: 0.11; 0.05, 0.17), but not in controls ($0.03; -0.03, 0.09$). Moose browse represented 71% of total browse in uniform irregular shelterwood (number of total seedlings with browse marks $n = 41$), 98% in strips ($n = 98$), 82% in gaps ($n = 68$), and 62% in controls ($n = 60$). Browsed seedlings were mainly mountain maple in uniform irregular shelterwood (32%) and controls (27%), whereas pin cherry was mainly browsed in strips (61%) and gaps (54%). Pin cherry seedlings were browsed only by moose in strips ($n = 60$), whereas the snowshoe hare was responsible for 19% of browsed pin cherry seedlings ($n = 37$).

Only one yellow birch seedling had a snowshoe hare browse mark in each treatment and one seedling exhibited signs of moose browsing in a gap. Therefore, the occurrence of browsing was not significant after the second year of growth for yellow birch. Drainage and distance to the edge had no effect on the proportion of stems that were browsed by hares, for yellow birch and for total species.

3.3. Habitat use by snowshoe hare

As expected, the uniform irregular shelterwood provided better vertical winter cover than other irregular shelterwoods, gaps ($-0.18; -0.28, -0.08$), or strips ($-0.27; -0.35, -0.19$), but less cover than controls ($0.25; 0.17, 0.33$). Average lateral winter cover was 51% (range: 12–86) in uniform irregular shelterwood, 40% (20–75) in strips, 39% (10–65) in gaps, and 46% (6–95) in controls. Lateral winter cover did not differ among treatments (mean 43%, range 6–95). The numbers of seedlings that were available for food also did not differ among treatments (mean: 5.5 stems/3.14 m² plot; range: 0–33).

Drainage type did not influence the number of hare pellets ($-0.11; -1.07, 0.85$). One model garnered most support for explaining the number of snowshoe hare pellets in 2012, with an Akaike weight of 0.84 (Table S4, Supplementary Materials). This model considered the effects of lateral and vertical winter cover. The model with availability of balsam fir seedlings over 25 cm tall was also plausible for explaining some of the observed variation in the abundance of snowshoe hare pellets ($\Delta AICc < 4$). The total number of seedlings that were present on the plot had a positive effect on the number of hare pellets (Fig. 5a). Similarly, hare pellets increased with the number of balsam fir, mountain maple and pin cherry seedlings, and with the presence of raspberry seedlings (Table S5, Supplementary Materials). As expected, lateral winter

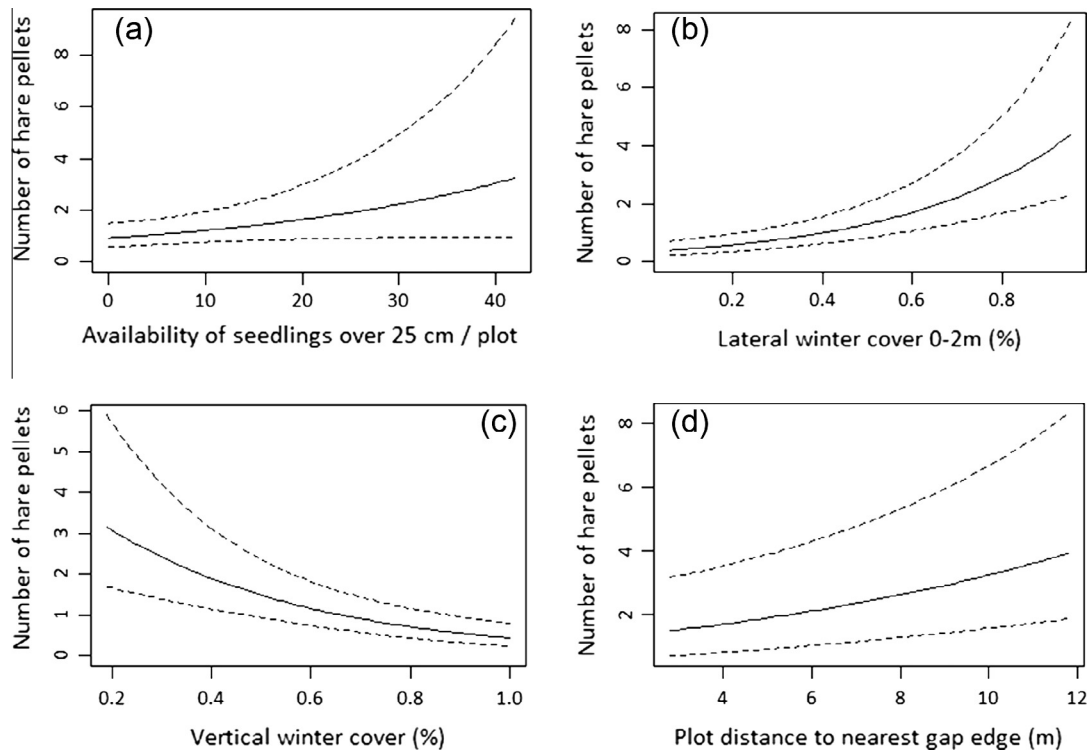


Fig. 5. Predicted number of hare pellets per plot (3.14 m² area) that was related to (a) availability of seedlings over 25 cm tall, (b) lateral winter cover at 0–2 m (%), (c) vertical winter cover (%), and (d) distance between micro-plot centres and nearest gap edges. Dashed lines represent 95% confidence intervals.

cover at 0–2 m had an important positive effect on snowshoe hare pellet abundance (Fig. 5b), whereas vertical winter cover had a negative effect (Fig. 5c).

The number of snowshoe hare pellets per micro-plot was lower overall in 2013 (−0.23; −0.33, −0.13) compared to 2012. Analysis by treatment revealed that the number of pellets decreased in strips (−0.29; −0.56, −0.02) and controls (−1.72; −2.01, −1.43), but it increased in uniform irregular shelterwood (0.59; 0.18, 1.0) and gaps (0.24; 0.08; 0.40). The number of hare pellets was lower in strips than in gaps both in 2012 (−1.51; −2.74, −0.27) and in 2013 (−2.13; −3.89, −0.37). The distance between the centres of the micro-plots and their nearest edges ranged from 2.3 to 11.80 m in gaps and from 1 to 7.9 m in strips. The number of hare pellets increased with distance in gaps in both 2012 (0.11; 0.05, 0.17) and 2013 (0.12; 0.08, 0.16) (Fig. 5d), but did not vary strongly in strips in 2012 (0.13; −0.02, 0.28) or 2013 (0.03; −0.19, 0.25).

4. Discussion

4.1. Yellow birch regeneration in irregular shelterwood

The presence of seed trees, adequate light conditions, and appropriate seedbeds are essential for the establishment of yellow birch (Erdmann, 1990; Raymond et al., 2013). Our results indicate that light and seedbed quality are more limiting than the presence of seed trees, regardless of the irregular shelterwood cutting pattern employed. Indeed, yellow birch seeds are light-weight and can be dispersed over large distances, usually at 100 m, but up to over 400 m (Erdmann, 1990). The residual basal area of yellow birch was similar among treatments and seemed sufficient for seed production and dissemination (Erdmann, 1990). Further, a field visit during site preparation confirmed that these treatments were conducted during a good seed year in our study area. Soil disturbance that created a humus–mineral mixture was beneficial to

the establishment of yellow birch seedlings in all irregular shelterwood patterns. This result concurs with those of previous studies (Godman and Krefting, 1960; Tubbs and Oberg, 1966; Wang, 1968). Synchronizing the year of soil disturbance and a good seed year was a key element for yellow birch regeneration (Crcha and Trottier, 1991).

As expected, yellow birch seedlings were more frequently present in gaps and strips than in uniform irregular shelterwood. Strips provided environments that were similar to natural gaps, the latter favouring yellow birch establishment (Kneeshaw and Prévost, 2007; Prévost et al., 2010). This result can be explained by the combination of canopy openings and preparation of suitable seedbeds, which were available in the strip and gap treatments. Most of the micro-plots had experienced soil disturbances that created humus–mineral mixtures in strips and gaps. However, growing seedlings, released saplings, and regenerating portions in uniform irregular shelterwood also can influence yellow birch establishment. In our study, scarification was applied only when regeneration was deficient and where the machinery could move without injuring residual trees. Moreover, uniform irregular shelterwood allowed us to distribute seedbeds over the entire surface of the stands, whereas seedbeds were located at specific locations in strip and expanded gap irregular shelterwood treatments. As a result, yellow birch regeneration in uniform irregular shelterwoods was lower across treated areas than in other treatments, but it had a better distribution across the entire stand.

No other difference was observed among treatments in the number of yellow birch seedlings over 25 cm in height after two growing seasons. We expected that greater light availability in gaps and strips could induce better seedling growth that would compete with pre-established seedlings in uniform irregular shelterwood (Godman and Krefting, 1960; Erdmann, 1990). Indeed, a high degree of canopy closure had a negative effect on the presence of yellow birch seedlings. It is possible that the size of the seedlings increased with light availability, but our ability to detect such an

effect was limited by the use of only two height categories (seedlings <25 cm and those \geq 25 cm). Furthermore, we found a higher density of yellow birch seedlings inside gaps at the farthest distance from the edge, where light is available for a longer period in the day (Prévost and Raymond, 2012). Strip micro-plots were oriented diagonally throughout the 10 m-wide strips. Consequently, the distance between each micro-plot and the edge was smaller in strips than in gaps. This could explain why the distance to the edge was not related to yellow birch seedling densities in the strips.

Overall, yellow birch seedling stocking and densities were higher in irregular shelterwoods than in untreated stands. In the short-term, each irregular shelterwood treatment contributes to the establishment of abundant yellow birch regeneration but at a different spatial scale.

All irregular shelterwood treatments in our study created structural complexity and spatial heterogeneity such as variable density thinning (Harrington et al., 2005). Although uniform irregular shelterwood creates spatial heterogeneity, the silvicultural objectives were somewhat different than those of variable density thinning. Uniform irregular shelterwood treatment in multi-cohort stands adapts to make the most of the timber-producing potential and each unit is recognized and treated accordingly (Smith et al., 1997). In contrast, variable density thinning generally produces a grid pattern of different thinning intensities. Nevertheless, after the first cutting cycle, all three treatments created heterogeneity within treatments and among treatments.

4.2. Potential inter-specific competition

To promote semi-tolerant species regeneration while limiting the regeneration of intolerant species, the canopy cover must be either partially opened or partially composed of small openings. Shade-intolerant species are considered aggressive but partial shading reduces their ability to compete and could enhance yellow birch seedling development. Canopy openings on the order of 40–50% can be appropriate for regenerating yellow birch, while limiting intolerant species (Godman and Krefting, 1960). In this study, tree marking in the uniform irregular shelterwood had aimed to maintain a residual cover from 50% to 60% in portions where regeneration was to be facilitated. The small size of gaps (1 tree height) and strips (10 m width) aim to limit incoming light in the openings. Strip orientation, which was East–West, also contributes to limit direct light (Lessard et al., 1999).

The abundance of competing species did not differ between treatments but tended to be higher in the gap pattern compared to others patterns. The small sizes of the openings that were created did not reduce regeneration of competitor species. In contrast, the uniform irregular shelterwood treatment, which tends to minimize competitor species regeneration, had the greatest potential for maximizing the development of yellow birch regeneration, at least in the short term. Measuring the density of competing species 5 years after treatment would document the extent of this threat to the development of birch seedlings and help identify the appropriate thinning strategies required in the future.

4.3. Short-term browse pressure

Hares tend to gnaw or cut entire seedlings at their base, resulting in the death of the plants (Gill, 1992a). In contrast, cervids browse the top parts of the seedlings, rarely killing the entire plant, though they may instead impede its growth or cause forking and offshoot growth (Gill, 1992b). The damage induced by mammalian herbivores can severely degrade the monetary value of the timber through growth defects. In this short-term study, the proportion of total browsed stems did not vary among treatments, drainage

types, or distance to nearest edges. Browsing pressure on young yellow birch seedlings was negligible after two years of growth. Such results were not surprising, given that browsing by hare is generally a major factor controlling seedling development only between 3 and 6 years after scarification (Elie et al., 2009).

For all other woody seedlings over 25 cm in height, the percentage of seedlings that were browsed was also relatively low. Browsing damage was mainly incurred by moose rather than by hare. Both species browsed pin cherry and maple species in particular. Beaked hazel was also preferentially browsed by moose, while viburnum was preferentially browsed by hare. The densities of these competing woody species could be regulated by the browsing pressure. This would favour yellow birch growth in the short-term. However, as yellow birch grows taller, it might be more easily browsed by moose and hare in winter. Bédard and DeBlois (2010) reported that ecotones created by such gaps would favour the use of these cuts by hare, given that such openings can generate a greater quantity of browse. Consequently, the development of yellow birch may be impaired, with the proportion of stems of this species being reduced in the future. The harmful effects of combined hare and cervid browsing could hamper the growth of woody plants after the second winter (Lyly et al., 2013). However, irregular shelterwood practices with scarification encourage abundant regeneration of the desired species. For such species, even high browsing pressure should not prevent a sufficient proportion of seedlings from growing and forming the future stand (Elie et al., 2009).

4.4. Snowshoe hare use of irregular shelterwood

We used browse as an index of snowshoe hare use of cuts during summer for two years following treatment, whereas pellets reflected overwinter use two and three years after treatment. The availability of food and cover are crucial to snowshoe hare in winter, the most critical season for this species (Litvaitis et al., 1985; Keith, 1990). In all treatments, average lateral winter cover in our study was \geq 40%, which is the minimum recommended habitat value for hare (Carreker, 1985). Even if the vertical winter cover was lowest in strips and gaps, lateral winter cover and the amount of food that was available did not differ among treatments. This is consistent with our observation that hare pellets were present in every treatment. The positive relationship between overwinter hare use and the quantity of young stems could explain the negative effects of canopy closure on hare use. Similarly, Fuller and Harrison (2013) showed that the aforementioned two variables explained 71% of the variation in microsite use by hares. Indeed, increasing canopy closure restricts the availability of light, which in turn has a negative effect on plant growth (Fuller and Harrison, 2005). This suggests that protection against predation is mainly related to lateral winter cover (Bois et al., 2012). Dense woody vegetation with abundant horizontal cover provides a source of browse as well as cover from predation (Hodges and Sinclair, 2005; Griffin and Mills, 2009).

Although one-year-old seedlings were available to hares at the beginning and end of winter, these seedlings were not tall enough to emerge through the snow cover during most of the winter season. The greater light availability in openings, which allowed better growth of yellow birch seedlings, may explain the positive relationship between the cumulative number of pellets and the distance to gap edges. These results contradict those of Hodson et al. (2010a), who identified hares as being less likely to browse stems that were located relatively far from forest cover, towards the gap centres. In our short-term post-treatment study, the tallest stems available throughout the winter season were mostly located in the centres of openings and would lead to a more intensive use of these areas by hare. Each irregular shelterwood had at least

4000 stems/ha of browse and could be considered as providing optimal snowshoe hare habitat (Guay, 1994). After a few growing seasons, seedlings would exceed winter snow pack depths and serve as a valuable source of nutrients for hares occupying the treated plots.

In the irregular shelterwood treatments, the number of pellets, which was used as an index of hare presence in the study area, was higher in gaps than in strips in both 2012 and 2013. The assessment of herbivore effects on regeneration is sensitive to the period when sampling is being conducted, especially in the case of cyclic species such as hare (Hodson et al., 2010b). The number of pellets declined from 2012 to 2013, suggesting that irregular shelterwood treatments were applied in the decreasing phase of the hare abundance cycle (Assels et al., 2007). Although hare presence in the two years following treatment decreased in the strips and controls, it increased in gaps and uniform irregular shelterwood. Hare seem to favour certain types of irregular shelterwood treatments that could serve as better refuges. As expected, the uniform irregular shelterwood provided good protective cover and distribution of regeneration in the stands. Vertical cover was least optimal in gaps. However, yellow birch, pin cherry and beaked hazel seedlings, as well as the presence of raspberry seedlings, were particularly abundant in gaps. At this stage of regeneration, it is possible that the fast-growing and light-demanding pin cherry could contribute to lateral cover. Indeed, the number of pellets was positively correlated with pin cherry, abundant in gaps. Finally, small circular gaps probably offer fewer opportunities for avian predators to catch hares compared to the long corridors of the strips.

5. Conclusions

All of our irregular shelterwood treatments offered suitable conditions for yellow birch establishment, especially when the soil was disturbed. However, the importance of interspecific competition in irregular shelterwood could affect yellow birch seedling growth in future years and release treatments could be necessary. Uniform irregular shelterwood, which minimized competitor species regeneration in our short-term study, might have the greatest potential for maximizing the development of yellow birch regeneration. From a stand-level perspective, the proportion of stand area treated with the gap pattern following the first harvesting was smaller than that of the other irregular shelterwoods, but gaps had higher yellow birch densities. Thus, this abundant regeneration is more localized than in other irregular shelterwood treatments. In comparison, yellow birch seedling densities were still relatively high but more homogeneously distributed in stands that had been treated by uniform irregular shelterwood. In the long-term, this treatment could encourage lower browsing pressure than in gaps, where all potential browse stems are concentrated. Thus, in the short term, the different irregular shelterwood patterns create favorable conditions for yellow birch establishment, when soil is scarified. However, successful yellow birch seedling establishment depends on seedling survival. Monitoring over a period greater than three years post-harvest would provide valuable information to determine whether initial seedling densities support wood production and provide sufficient available browse for hare and moose.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.06.025>.

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