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Natural regeneration 18 years after experimental silvicultural treatments in Canadian boreal forests

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ABSTRACT

In Canada, clearcutting is the most widely used silvicultural system in boreal forests despite potential impacts on forest simplification and biodiversity loss. Retaining mature trees is suggested to maintain stand structure and biodiversity, especially for promoting the regeneration of shade-tolerant species. Partial harvesting is considered a promising alternative to the clearcutting system as a means of integrating ecological, economic, and social objectives into silvicultural planning; however, this approach must be developed for use in natural boreal forests. Here, we evaluate the effects of silvicultural treatments on natural regeneration in stands of natural even-aged mature black spruce (*Picea mariana* (Mill.) B.S.P.), 18 years after cutting. In 2003, in the Saguenay and North Shore regions of Quebec, an experimental design of fully randomized blocks was established across six sites, each containing two forest stand types (younger and older stands) and six silvicultural treatments. In 1 512 microplots, we categorized all tree seedlings by species and height class and assessed a dominant seedling for growth-related variables, and microenvironment. We found that 18 years after treatment, mini-strip shelterwood harvesting produced the highest black spruce seedling density (39 765 seedlings/ha). In contrast, clearcutting produced a seedling density that was three times lower than uniform shelterwood harvesting but demonstrated a twofold increase in seedling terminal shoot length growth. Mineral soil, spot scarification, moss cover with *Polytrichum* spp., and distance from residual strips positively correlated with black spruce seedling density. Our study highlights the potential of shelterwood systems as a silvicultural alternative to clearcutting for promoting black spruce regeneration in Canadian boreal forests.

1. Introduction

Despite the global forest area shrinking annually by approximately 10 million ha—the size of South Korea—between 2010 and 2020, the demand for wood products has surged, with industrial roundwood production projected to increase 4 %–8 % by 2030 (FAO, 2024; Zhang et al., 2020). Increased logging to support this demand significantly alters forest ecosystems (Park and Wilson, 2007). Even-aged management based on the clearcut system favors the decline of old-growth forest areas (Martin et al., 2020a,b), the simplification of stand structures (Angelstam, 1998; Bouchard and Pothier, 2011; Raymond et al., 2023), and the loss of biodiversity (Fuller et al., 2004; Kim et al., 2021). Thus, the boreal biome is currently facing challenges stemming from the increasing homogenization and simplification of forest structure across various countries (Puettmann et al., 2015). For instance, in Canada, clearcutting has been the dominant forest management practice across the country. On average, 4000 km^2 of boreal forest is clearcut each year in the country (Girona et al., 2023a; National Forestry Database, 2024). Promoting more diversified forest structures, however, can simultaneously support wood supply needs while enhancing biodiversity and ecosystem services (Girona et al., 2023a; Waldron et al., 2020).

Using partial harvesting as a silvicultural alternative to clearcutting

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can help integrate ecological, economic, and social objectives, while narrowing the gap between natural and managed forests, and hence align with the ecosystem-based management framework (Bose et al., 2014; Gauthier et al., 2023). Although shelterwood systems support ecosystem-based management objectives, achieving successful natural regeneration remains a significant challenge because of factors such as variability in seedling recruitment, competition from understory vegetation, and site-specific conditions (Bose et al., 2023; Lafleur et al., 2010, 2019; Moussaoui et al., 2020). Furthermore, altered fire regimes or increased severity and frequency of extreme droughts because of climate change threaten successful natural regeneration establishment (Boucher et al., 2020; Molina et al., 2022). Thus, the continuous evaluation and refinement of silvicultural treatments are necessary to ensure the efficacy and sustainability of forest management practices adapted to future climate change (Ameray et al., 2024).

MISA (Managing Innovative Silvicultural Alternatives) is a large-scale experiment in the boreal black spruce region of Quebec, Canada, designed to evaluate various silvicultural systems, including novel variants of uniform shelterwood, that differ in their overstory removal and scarification intensities. Earlier results have shown that the uniform shelterwood system is effective in promoting the radial growth of residual trees (Montoro Girona et al., 2016, 2017) with moderate tree mortality by windthrow (Montoro Girona et al., 2019), whereas seed-tree systems promote the establishment of black spruce regeneration over balsam fir (*Abies balsamea*) (L.) Mill (Montoro Girona et al., 2018). However, the factors involved in natural regeneration are not yet fully understood, highlighting the need for long-term ecological monitoring to fully understand and optimize these systems for wider implementation in Canadian boreal forests.

Regeneration success is influenced by a complex interplay of biotic and abiotic factors (Thiffault et al., 2024): belowground intra- and inter-specific competition, interaction with ground-cover species, soil characteristics, disturbances, and light availability, all of which critically affect seedling establishment and growth in boreal forest ecosystems (Bose et al., 2023). For instance, intra- and interspecific competition between seedlings and understory vegetation for light and nutrients has been a major factor affecting post-shelterwood regeneration processes in North American and European forests (Brose and Lear, 1998; Joanisse et al., 2018). In eastern Canadian boreal forests, ericaceous shrubs, such as bog Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron and Judd) and sheep laurel (*Kalmia angustifolia* L.), impede seedling establishment and growth through a combination of mechanisms, including competition for soil nutrients and potential allelopathic interactions (Mallik, 2003). Ground-cover vegetation, such as bryophyte species, also plays a pivotal role in influencing tree regeneration by aiding seed germination by providing and maintaining optimal moisture conditions (Ohlson & Zackrisson, 1992). In a greenhouse experiment, *Sphagnum* spp. ground cover provided an optimal substrate for black spruce germination and early development, although *Sphagnum*-covered substrates eventually inhibited the growth of two-year-old seedlings (Lavoie et al., 2007; Pacé et al., 2018). Soil characteristics also shape the success of natural regeneration in the Canadian boreal forest (Nagati et al., 2020). Black spruce prefers acidic, moist, well-drained soils and is resilient to occasional drought and waterlogged conditions; however, this species also thrives in diverse soil conditions, from rich humus to rocky, shallow soils over bedrock (Viereck and Johnston, 1990). Nonetheless, more intense drought conditions combined with anthropogenic disturbances may significantly alter the composition, structure, and biogeography of forests and produce profound shifts in various ecosystem processes and services (Walker et al., 2015).

Mechanical site preparation by scarification favors successful regeneration by creating favorable microsites for seed germination for light-seeded tree species (Prévost, 1997; Sikström et al., 2020), including black spruce. Seedbed conditions that optimize the survival and growth of conifer seedlings remain poorly understood (Montoro Girona et al., 2023). To elucidate the synergistic effects of scarification and canopy opening on seedling establishment and subsequent growth, there is a pressing need for more comprehensive and long-term studies (Béland et al., 2000; Drössler et al., 2017; Raymond et al., 2000).

Our study aimed to assess the dynamics of natural regeneration and their driving factors in even-aged natural black spruce stands of eastern Canada, 18 years after treatments related to overstory removal and spot scarification. Stands were subjected to five silvicultural systems: three variants of the uniform shelterwood system (close-selection, distant-selection, mini-strip), one seed-tree cutting, and one clearcut. We hypothesized that the shelterwood system offers an optimal balance between light availability and seed sources and that scarification creates adequate seedbeds while controlling competing vegetation for seedling density. Moreover, greater seedling growth can be expected to higher harvest intensities, i.e., seed-tree and clearcut treatments, which enhance light availability in the understory. Relying on these hypotheses, we predicted that (i) the combined application of partial harvesting and scarification would ensure successful conifer regeneration, with higher conifer seedling densities in uniform shelterwood systems than in the clearcut stands; (ii) seedling growth rates would be higher in seed-tree and clearcut systems relative to shelterwood systems; (iii) competitive interactions between black spruce seedlings and the surrounding vegetation would substantially influence black spruce seedling density.

2. Material and methods

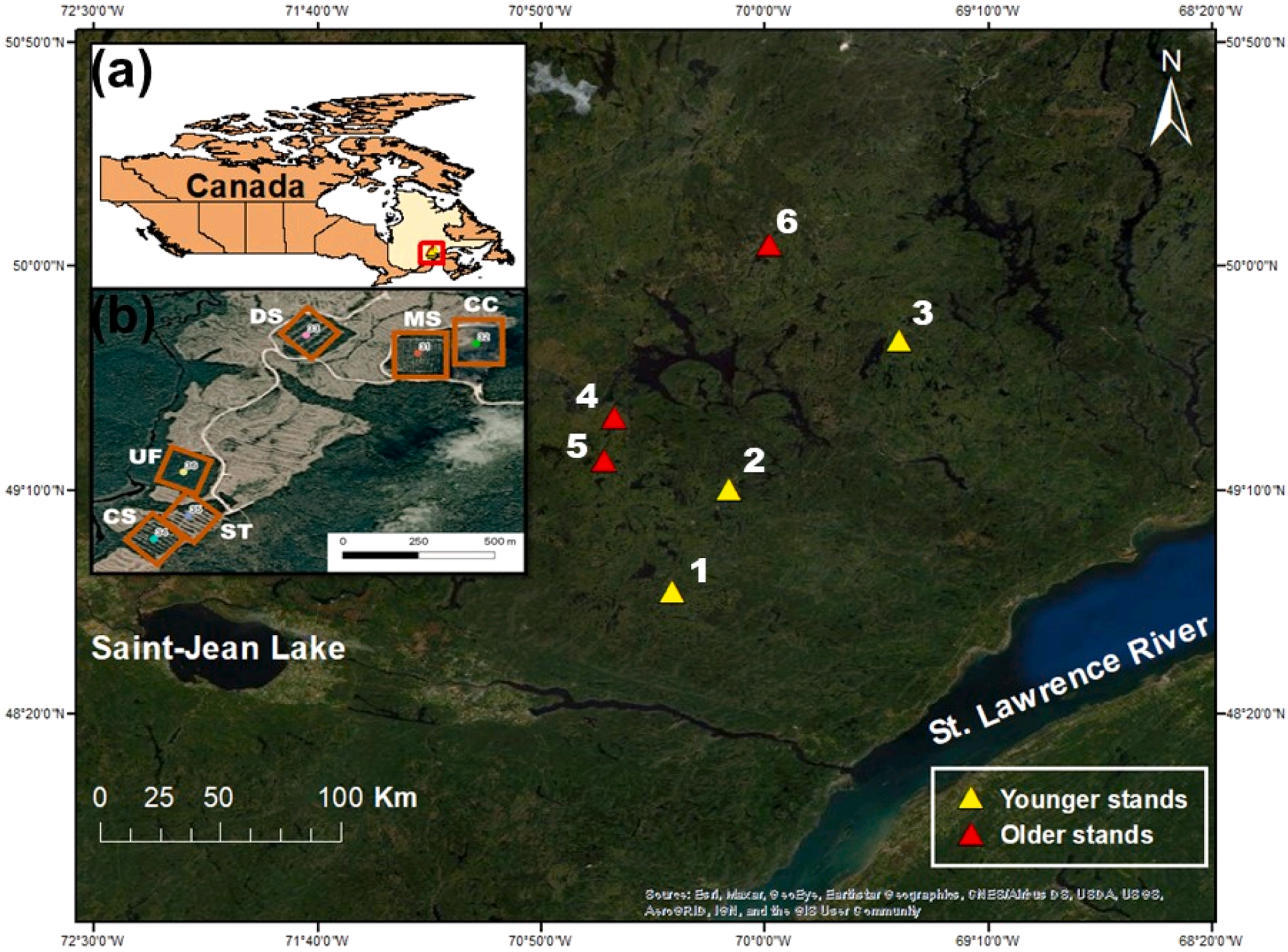
2.1. Study area

The study area comprises natural even-aged black spruce stands located in the northern Saguenay-Lac-Saint-Jean region and North Shore regions of Quebec, Canada (Montoro Girona et al., 2023). The study sites are located within two bioclimatic domains, namely the balsam fir–white birch (*Betula papyrifera* Marsh.) and the black spruce–feathermoss bioclimatic domains (Saucier et al., 2009) (Fig. 1). Regional climate is subhumid continental, with a short growing season of 140 days (Rossi et al., 2011). The annual mean temperature is 2.8 °C and is characterized by cold winters (–15.7 °C) and cool summers (18.4 °C) in the data collection year (2021). Average annual precipitation is 931 mm in the form of snow or rain (Environment and Climate Change Canada, 2015). Surface deposits are mainly composed of thick glacial tills, and rock outcrops are frequent at the top of steep slopes (Robitaille and Saucier, 1998). The predominant soil type is humo-ferric podzol (Montoro Girona et al., 2018). In the experimental sites, the soil texture ranges from sandy clay loam to sandy loam.

2.2. Experimental design

The MISA experiment was structured as two separate fully randomized block designs (Figure S1). One design was implemented in younger even-aged black spruce stands (80–100 years; average density of 2 595 trees/ha), considered to have a low level of advanced regeneration, and the other in older stands (120–150 years; average density of 1 537 trees/ha, considered to have a high level of advanced regeneration. Each design included three blocks, with six silvicultural treatments randomly assigned to 3-hectare units in each block, resulting in 36 experimental units (6 sites × 6 treatments). While this design enables comparisons of treatment effects within each stand type, the stand type itself is not independently replicated across different sites. Therefore, potential site-specific conditions may influence the observed stand type effects, limiting the ability to generalize these effects across broader regions.

Both stand types were homogeneous because of their fire history; this was confirmed through dendrochronological dating of the trees. To study natural regeneration, each experimental unit included one permanent sampling plot (10 × 60 m) with two transects of circular microplots (4 m^2) perpendicular to the main plot (2 transects × 21 microplots × 36 experimental units = 1 512 microplots; Fig. 3).



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Fig. 1. Location of the MISA experimental sites (1–3: younger stands; 4–6: older stands). (a) The northern Saguenay-Saint-Jean-Lake and North Shore regions of Quebec, Canada; (b) Orthophotography depicting the 3 ha experimental units (brown squares) of one block (replicate) as an example. UF, unmanaged forest; MS, mini-strip shelterwood; DS, distant-selection shelterwood; CS, close-selection shelterwood; ST, seed-tree system; CC, clearcut harvesting.

Sampling and measurements were conducted one year before and after harvesting, as well as 10 years (Montoro Girona et al., 2018) and 18 years after harvesting (this study). Prior to cutting, the tree species composition was dominated by black spruce (younger: 95.8 %; older: 96.1 %, total number of stems), with balsam fir (younger: 1.6 %; older: 3.6 %), trembling aspen (*Populus tremuloides* Michx; younger: 2 %; older: 0.2 %), and white birch (younger: 0.5 %; older: 0.1 %) making up the remainder.

2.3. *Silvicultural treatments*

Three variants of the uniform shelterwood system differ in their respective spatial and scarification patterns: 1) mini-strips (MS) created narrow corridors (5 m wide skid trails) of 50 % harvested areas with unharvested strips in between, and the highest scarification proportion (average scarified area of 1 296 m^2/ha); 2) distant selection (DS) with the harvester boom created a more spaced and irregular pattern of 50 % tree removal along the 30 m wide skid trails, resulting in the greatest spatial heterogeneity and the lowest scarification proportion (average scarified area of 539 m^2/ha). DS also featured short secondary trails oriented perpendicular to the main skid trails, with each secondary trail spaced 10 m apart; 3) close selection (CS) involved a harvester boom removing trees in a 50 % partial cut up to 20 m on each side of the skid trail (average scarified area of 752 m^2/ha), which resulted in a denser pattern of tree removal than DS (Montoro Girona et al., 2016, 2017) (Fig. 2). The other silvicultural treatments were 4) seed-tree harvesting (ST), where all the merchantable-sized (>9 cm, diameter at breast height) trees were removed, except for a few selected trees (basal area of 10 m^2/ha) for seed production in 15 m cut strips (average scarified area of 848 m^2/ha); 5) clearcutting with the protection of advanced regeneration (CC), which consisted of the complete removal of all merchantable-size trees from the stand without scarification (business as usual); and 6) unmanaged forest (UF), which were control areas without harvesting (Fig. 2) (Montoro Girona et al., 2017; Montoro Girona et al., 2018). The proportion of harvested basal area was 50 % for the three shelterwood systems, 75 % in ST, and 100 % for CC. In 2004, spot scarification was conducted in the seed-tree and shelterwood treatments by creating 2 m^2 rectangular spots with a 10-ton excavator equipped with a 1 m^3 bucket, following a spatial pattern adapted to each treatment (Fig. 2). Overall, partial harvest treatments differ mainly in the spatial distribution of skid trails, residual strips, and scarification spots.

2.4. *Regeneration assessment*

In 2021, we conducted two inventories to study seedling density, growth, and competition between shrubs (e.g., ericaceous species), coniferous (e.g., *A. balsamea*), and deciduous trees (e.g., *B. papyrifera, Salix* spp., *Prunus pensylvanica* L.f., *Sorbus americana* Marshall., *Populus tremuloides*, *Amelanchier* spp., and *Alnus* spp.). The spatial positioning of microplots in relation to harvesting trails was recorded, categorized as

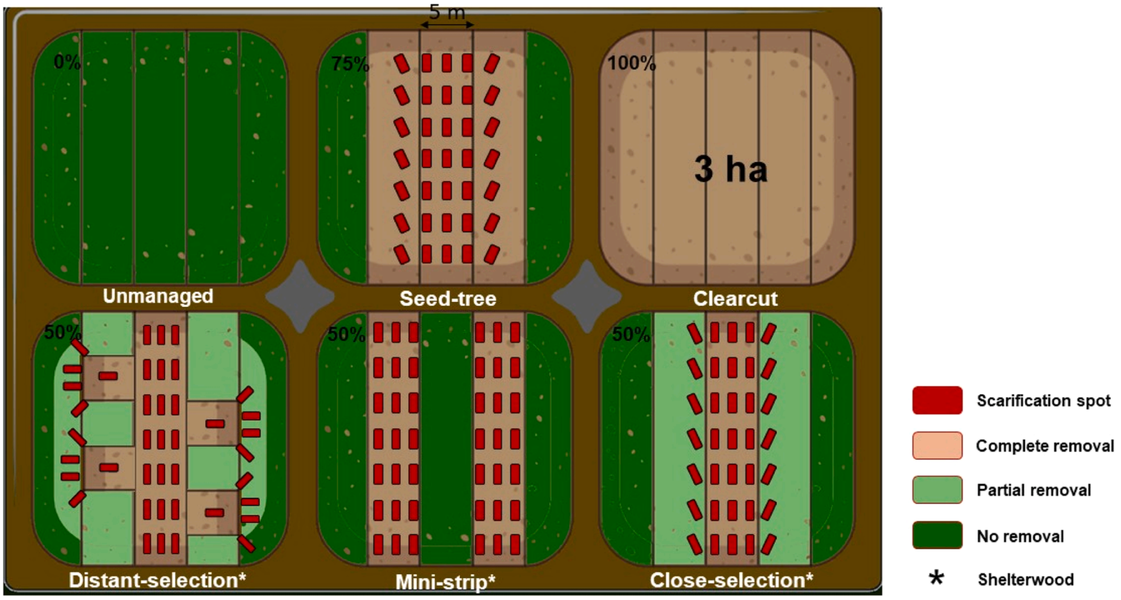


Fig. 2. Spatial patterns of each experimental silvicultural system. The fully harvested areas or skid trails are represented by brown areas, whereas the intact residual strips are shown in dark green. The partially harvested residual strips are depicted in bright green, and red rectangles are used to indicate the scarification spots, each 2 m^2. Scarification was not carried out in the clearcut treatment and unmanaged forests.

strip, edge, or trail. The edge area was defined as the surface within 1.25 m on either side of the trails (Fig. 3). First, all seedlings in each microplot (4 m^2) were counted and categorized by species and height class (A: 0–5 cm; B: 5–30 cm; C: 30 cm to 1 m; D: >1 m with a diameter at breast height (DBH) < 1 cm; E: same height but a DBH of 1–5 cm; F: same height but a DBH of 5–9 cm). Seedling and sapling (height class D, E, F) densities were calculated at the microplot level. We also estimated the percent cover of ericaceous shrubs (*Kalmia angustifolia*, *Rhododendron groenlandicum*). Second, we selected one dominant conifer seedling in each microplot on the basis of growth condition (the largest crown or diameter) (Montoro Girona et al., 2018). For each of the selected seedlings, we measured age (determined by whorl count), diameter, height, terminal shoot length (encompassing three years of growth from 2019 to 2021, measured as the upper internodes of the three most recent annual increments), origin (asexual or sexual), rooting substrate (classified as woody debris, mineral soil, deadwood, and vegetation cover by stratum), and dominant bryophyte species. Five preliminary quality classes were established based on easily measured morphological features commonly associated with survival and growth response (Ruel et al., 1995). We also documented the disturbance types (rut, mound, scarification, windthrow, or intact forest floor) observed in the microplots.

We also assessed the presence and absence of neighboring vegetation groups. The major groups were selected on the basis of their frequency in the microplots; they had to appear in more than 151 of the 1 512 microplots (i.e., >10 %) containing black spruce seedlings. These groups included ericaceous shrubs (Group Ericaceous: *K. angustifolia*, *R. groenlandicum*), conifer seedlings (Group Conifer: *Abies balsamea, Larix laricina* (Du Roi) K. Koch), and deciduous seedlings (Group Deciduous: *Betula papyrifera, Prunus pensylvanica, Salix* sp.). Venn diagrams were used to visualize the number of black spruce seedlings associated with each neighboring group.

2.5. Statistical analysis

To evaluate the effects of silvicultural treatments on conifer seedling and sapling density and competing vegetation cover, we performed an analysis of variance (ANOVA) based on a linear mixed model. Blocks (cluster variable) were considered as a random effect and stand type,

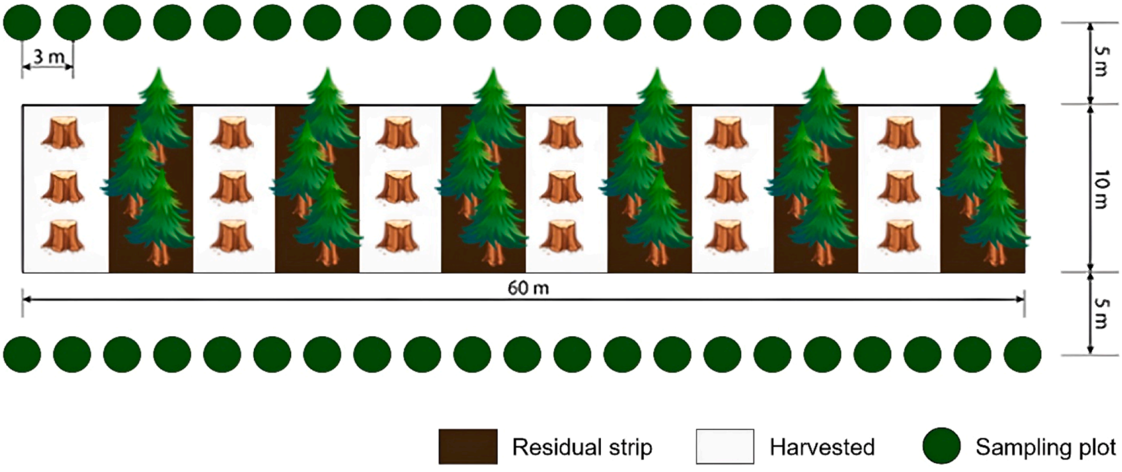


Fig. 3. Illustration of the sampling design for regeneration assessment in a mini-strip, featuring two transects of 4 m^2 circular microplots arranged perpendicularly to the main plot.

silvicultural treatment, and their pairwise interaction, as fixed effects. The mixed effects model accounted for the nested structure of the data, where transects were nested within blocks, and blocks were nested within stand types.

We also used a multiple linear regression analysis to predict the annual growth (terminal shoot length in the last three years) of black spruce seedlings. Stepwise regression by backward selection was conducted to extract the optimal combination of predictors (sapling density, harvesting intensity, *Polytrichum* spp.? cover, mound, and seedling condition) for the model selection. In addition, we calculated Pearson's correlation coefficients to investigate the relationship between black spruce seedling density/growth and various environmental factors assessed at the microplot level. Principal component analyses (PCA) were performed to investigate the influence of environmental factors affecting seedling density and growth of black spruce and balsam fir. PCA was conducted using the Factoextra package in R, using all the variables assessed at the microplot level. All statistical analyses were performed using R software version 3.6.0 (R Core Development Team, 2024).

3. Results

3.1. Seedling density

We found that the three most regenerated tree species 18 years after silvicultural treatment were black spruce, found in 1 222 microplots (80.8 % detection frequency), balsam fir (464 microplots; 30.7 %), and white birch (318 microplots; 21 %) (Fig. 4). Overall, the dominant species was black spruce, with a density of 28 376 seedlings/ha, followed by balsam fir (8091 seedlings/ha) and white birch (2 066 seedlings/ha). We also found other regenerated tree species, including *Larix laricina,* and deciduous species, such as *Salix* spp., *Prunus pensylvanica*, *Sorbus americana*, *Populus tremuloides*, *Amelanchier* spp., and *Alnus* spp. However, their abundance was insufficient for detailed species-level analysis.

The ANOVA results indicated a significant interaction between stand type and treatment for all three tree species (Table 1). Therefore, the effect of silvicultural treatments on seedling density varied between younger and older stands. For black spruce, mini-strip shelterwood treatment increased seedling density the most, particularly in younger stands ($t = -11.9$, $p < 0.001$), relative to unmanaged forests (Fig. 4). Similarly, other shelterwood variants, i.e., close-selection ($t = -3.9$, $p < 0.001$) and distant-selection ($t = -4.6$, $p < 0.001$), as well as seed-tree harvesting ($t = -3.5$, $p < 0.001$), also significantly enhanced seedling density in younger stands relative to unmanaged forests in older stands. Conversely, seedling density in clearcuts was generally lower than in other treatments, particularly in younger stands. For balsam fir, distant-selection shelterwood increased the seedling density in older stands relative to unmanaged ($t = -5.4$, $p < 0.001$), close-selection ($t = -6.1$, $p < 0.001$), mini-strip ($t = 5.6$, $p < 0.001$), seed-tree ($t = 7.1$, $p < 0.001$), and clearcut treatments ($t = 3.4$, $p < 0.001$). In younger stands, the mini-strip shelterwood treatment significantly increased seedling density relative to unmanaged ($t = -4.9$, $p < 0.001$), close-selection ($t = -5.5$, $p < 0.001$), distant-selection ($t = -6.9$, $p < 0.001$), seed-tree ($t = 5.6$, $p < 0.001$), and clearcut treatments ($t = 7.3$, $p < 0.001$). For white birch, seedling density was more

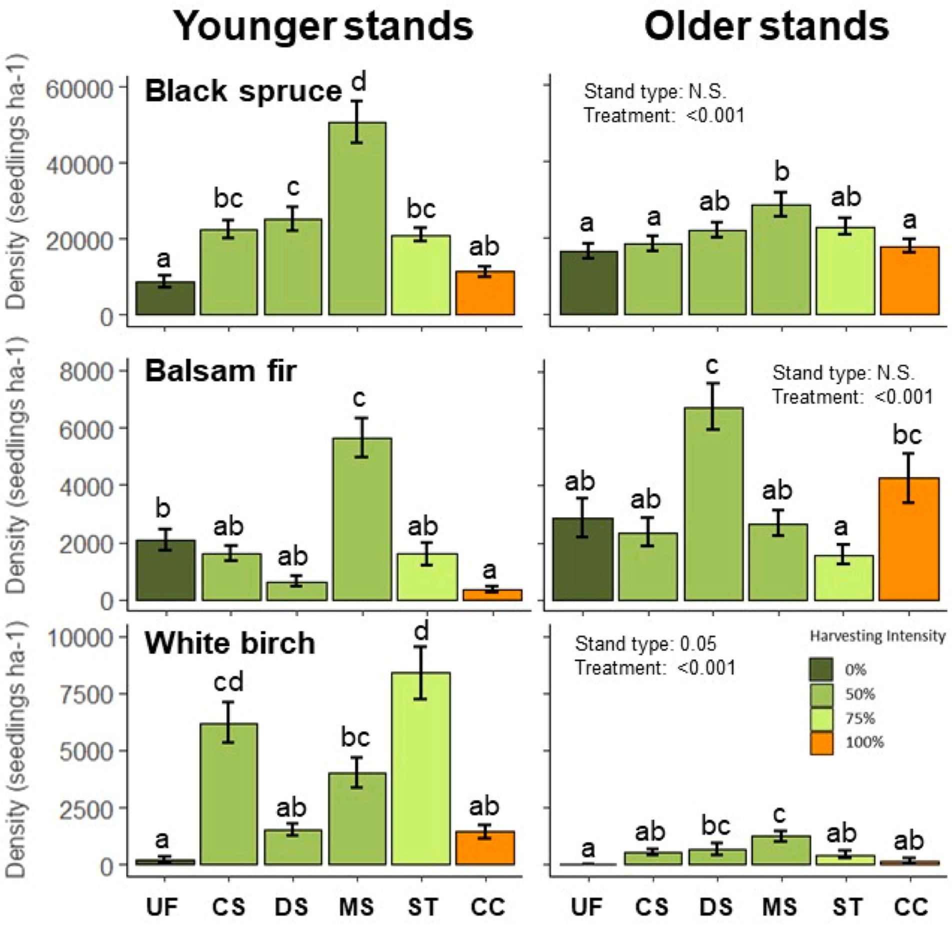


Fig. 4. Seedling density of black spruce, balsam fir, and white birch in younger and older stands, 18 years after silvicultural treatments in black spruce stands. For a given species and stand type, bars with similar letters are not significantly different at α = 0.05. UF, unmanaged forest; CS, close selection; DS, distant selection; MS, mini-strip; ST, seed tree; CC, clearcut.

Table 1

Results from ANOVA with a linear mixed model for the effects of silvicultural treatment and stand type on the seedling density of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*). The analysis included site as a random effect.

		Black spruce		Balsam fir		White birch	
Effect (fixed)	df	*F*	Pr > *F*	*F*	Pr > *F*	*F*	Pr > *F*
Stand type	1	0.08	0.148	1.75	0.26	7.46	0.05
Treatment	5	29.644	**< 0.001**	7.69	**< 0.001**	24.21	**< 0.001**
Stand type × Treatment	5	9.39	**< 0.001**	19.14	**< 0.001**	20.51	**< 0.001**

influenced by stand type ($F = 7.5$, $p = 0.05$) than by conifer species. Seed-tree harvesting significantly improved seedling density relative to the control ($t = -12.1$, $p < 0.001$) and clearcutting ($t = 10.3$, $p < 0.001$) in younger stands but did not produce significant differences with the older unmanaged stands ($t = -0.7$, $p = 0.52$).

We then compared seedling density for black spruce, balsam fir, and white birch between younger and older stands. Younger stands showed higher regeneration densities for black spruce (23 238 seedlings/ha) and white birch (3 620 seedlings/ha) than older stands (21 067 seedlings/ha for black spruce, 512 seedlings/ha for white birch). Older stands had a higher balsam fir density (3 411 seedlings/ha) than younger stands (1 981 seedlings/ha).

The silvicultural treatment that promoted the most black spruce regeneration was the mini-strip shelterwood, with 50 751 seedlings/ha in younger stands and 28 780 seedlings/ha in older stands. This treatment also produced the highest balsam fir regeneration in younger stands (5 639 seedlings/ha). However, in older stands, distant-selection harvesting led to the highest balsam fir seedling density (6 767 seedlings/ha). For white birch, the seed-tree treatment was most effective in younger stands (8 375 seedlings/ha), whereas mini-strip harvesting promoted the most regeneration in older stands (1 232 seedlings/ha).

Clearcutting resulted in the lowest seedling densities across treatments and species, particularly in younger stands. For black spruce, clearcutting produced the lowest seedling densities in both stand types (younger: 11 299 seedlings/ha; older: 17 836 seedlings/ha). Similarly, for balsam fir, clearcutting led to the lowest seedling density in younger stands (334 seedlings/ha), although in older stands, clearcutting produced the second-highest balsam fir seedling density. For white birch, clearcutting produced the lowest seedling densities in both younger (1 441 seedlings/ha) and older stands (167 seedlings/ha).

3.2. Conifer seedling growth

Mean annual conifer seedling growth differed in interaction with silvicultural treatments and stand types for both species (Table 2). For black spruce, clearcutting resulted in the highest seedling growth across both younger ($t = -9.8$, $p < 0.001$) and older stands ($t = -9.3$, $p < 0.001$). Seed-tree harvesting produced the second-highest growth in both stand types (younger: $t = -5.7$, $p < 0.001$; older: $t = -5.8$, $p < 0.001$), representing a 224 % increase relative to the control. For balsam fir, seed-tree harvesting led to the greatest seedling growth in younger stands ($t = -4.0$, $p < 0.001$; Table S2.2), although this was not observed in older stands ($t = -0.2$, $p > 0.05$). Conversely, mini-strip harvesting resulted in the highest growth increase in older stands ($t = -2.4$, $p < 0.05$).

Table 2

Results from ANOVA with a linear mixed model for the effects of silvicultural treatments and stand types on mean annual black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) seedling growth between the 16th and 18th growing seasons after harvesting (2019–2021). The analysis included site as a random effect.

		Black spruce		Balsam fir	
Effect (fixed)	df	*F*	Pr > F	*F*	Pr > *F*
Stand type	1	0.16	0.709	0.82	0.26
Treatment	5	45.42	**< 0.001**	5.56	**< 0.001**
Stand type × Treatment	5	8.53	**< 0.001**	3.57	**< 0.01**

For black spruce, the mean annual shoot growth varied from 2.5 to 13.4 cm across both stand types. Most silvicultural treatments (close-selection, distant-selection, seed-tree, clearcut in younger stands and close-selection, seed-tree, clearcut in older stands) resulted in greater annual shoot growth than in the unmanaged conditions (Fig. 5). Clearcutting, in particular, produced the highest annual shoot lengths in both stand types, with growth 426 % higher in younger stands and 257 % higher in older stands than in unmanaged conditions.

For balsam fir, mean annual shoot growth ranged from 4.1 to 12.9 cm across both stand types. All harvesting treatments produced higher annual shoot growth than unmanaged forests, except in older stands harvested through clearcutting, which showed similar values (unmanaged: 4.8 cm; clearcut: 4.9 cm). No clear pattern emerged among the harvesting treatments in either stand type.

The multiple linear regression analysis demonstrated the influence of ecological and management factors on the mean annual growth of black spruce seedlings (Table 3). The significant model ($F = 108.6$; $p < 0.001$) included total sapling density (number of seedlings with more than 1 m in height), harvesting intensity, *Polytrichum* spp. cover, presence of a mound, and quality class as predictors. Total sapling density and harvesting intensity had a positive effect on growth, whereas seedling condition was negatively associated with growth. Although *Polytrichum* spp. cover and the presence of a mound were less significant, they still contributed to the most robust model, which explained approximately 44 % of the variation in annual growth. The model's R^2 was 0.44, with all p-values < 0.05.

3.3. Factors influencing conifer seedling density and growth

The first two dimensions of the PCA explained 36.3 % of the variance in black spruce seedling density (Fig. 6a). Mineral soil (Pearson's $r = 0.24$, $p < 0.001$) as a substrate of the seedling, spot scarification ($r = 0.21$, $p < 0.001$) as a main anthropogenic disturbance in the microplot, moss cover with *Polytrichum* spp. ($r = 0.2$, $p < 0.001$), and distance from the residual strip correlated strongly with black spruce seedling density. The PCA indicated that microplot characteristics associated with spot scarification were positively correlated with black spruce seedling density. For balsam fir, the first two components of the PCA accounted for 41.3 % of the variance in seedling density (Fig. 6b). Organic soil, undisturbed conditions ($r = 0.16$, $p < 0.05$), mound conditions, moss cover with *Ptilium* spp. and *Sphagnum* spp. ($r = 0.17$, $p < 0.05$), and distance from the residual strip were positively correlated with balsam fir seedling density. The PCA revealed that microplot characteristics related to intact and mound conditions were strongly associated with balsam fir regeneration success.

Considering seedling growth response and environmental characteristics, the PCA explained approximately 42 % of the variation for black spruce seedlings and 40 % for balsam fir seedlings, highlighting similar variations from PCA, but different responses between the two conifer species (Figs. 6c, 6d). Black spruce seedling growth was positively correlated with moss cover, particularly with *Ptilium* sp., (Pearson's $r = 0.1$, $p < 0.05$) and negatively correlated with the windthrow disturbance ($r = -0.1$, $p < 0.05$; Fig. 6c). In contrast, windthrow disturbance showed a positive correlation with balsam fir seedling growth ($r = 0.16$, $p < 0.05$), while the undisturbed (intact) microplot

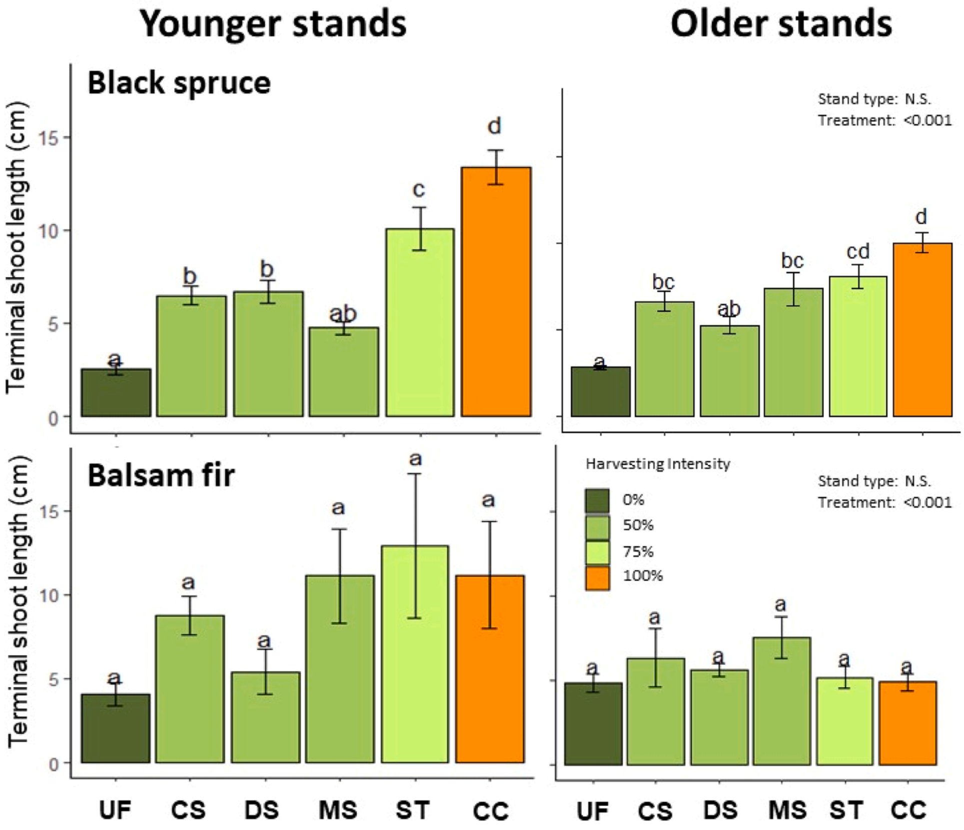


Fig. 5. Mean annual conifer seedling growth between the 16th and 18th growing seasons after harvesting (2019–2021) by silvicultural treatment and stand type. For a given species and stand type, bars with same letters are not significantly different at α = 0.05. UF, unmanaged forest; CS, close selection; DS, distant selection; MS, mini-strip; ST, seed tree; CC, clearcut.

Table 3
Multiple linear regression models for predicting the annual shoot growth of black spruce seedlings on the basis of regeneration.

Predictors	Coefficients	Std. Error	*t* value	Pr(>|*t*|)
(Intercept)	5.574	0.644	8.654	**< 0.001**
Total sapling density	0.706	0.056	12.591	**< 0.001**
Harvesting intensity	0.057	0.006	9.691	**< 0.001**
Polytrichum sp. cover	0.697	0.392	1.78	0.076
Mound	1.016	0.537	1.891	0.059
Quality class	−0.989	0.126	−7.861	**< 0.001**

condition exhibited a negative correlation (r = -0.16, $p < 0.05$; Fig. 6d).

Pleurozium sp. was the most dominant bryophyte covering the soil surface around black spruce seedlings, present in 82 % of the 1512 microplots located in skid trails, 80 % in residual strips, and 79 % at the edge (Table S3). *Sphagnum* spp. and *Gaultheria hispidula* (L.) Muhl. ex Bigelow (creeping snowberry) were also common on the soil surface around black spruce seedlings, regardless of their position (skid trail, residual strip, or edge). In contrast, *Polytrichum* spp. was more dominant in skid trails (34 %) than residual strips (5 %). *Cladina* spp. followed this trend, found in 12 % in skid trails and 4 % of residual strips.

Black spruce was found alongside various neighboring vegetation within 962 of 1 512 microplots (64 %) (Fig. 7). We observed that the highest density of black spruce seedlings, 55 603 per ha, occurred in microplots containing both coniferous and deciduous seedlings. Relative to microplots with only coniferous or only deciduous neighbors, conifer-deciduous vegetation microplots had significantly higher black spruce densities—160 % higher than coniferous-only plots, 150 % higher than deciduous-only plots, and 110 % higher than microplots containing all vegetation. However, black spruce density did not vary significantly with homogeneous species groups. The lowest black spruce seedling density (21 314 seedlings/ha) was found in microplots with *Kalmia*, whereas the highest black spruce seedling density (36 179 seedlings/ha) occurred in microplots with only birch. The presence of *Kalmia* lowered black spruce density by 23 % relative to microplots with only black spruce, whereas the presence of birch increased black spruce density by 31 % compared to black spruce only microplots, demonstrating species-specific effects on black spruce regeneration.

4. Discussion

Our study provides insights into the mid-term response of experimental silvicultural treatments on natural regeneration density and growth in Canadian boreal forests. Our findings highlight the different responses of black spruce, balsam fir, and white birch to treatment and stand type, and elucidate the influence of microplot characteristics on conifer seedling density and growth. Additionally, our research provides a predictive perspective on the future structure and composition of the ecosystem under various management practices.

4.1. Regeneration density

Our regeneration assessment revealed that black spruce was the most dominant species, significantly surpassing balsam fir and white birch in terms of seedling density 18 years post-harvest. The success of black spruce can be attributed to its adaptability to a variety of silvicultural treatments and pre-harvest site conditions, particularly in natural even-aged black spruce–dominated forests. The mini-strip shelterwood treatment, which proved most effective in both younger and older stands, can be credited to the exposure of mineral soil after scarification (Girona et al., 2023c). Specifically, the intermediate shade conditions provided by the residual strips, combined with the reduction of

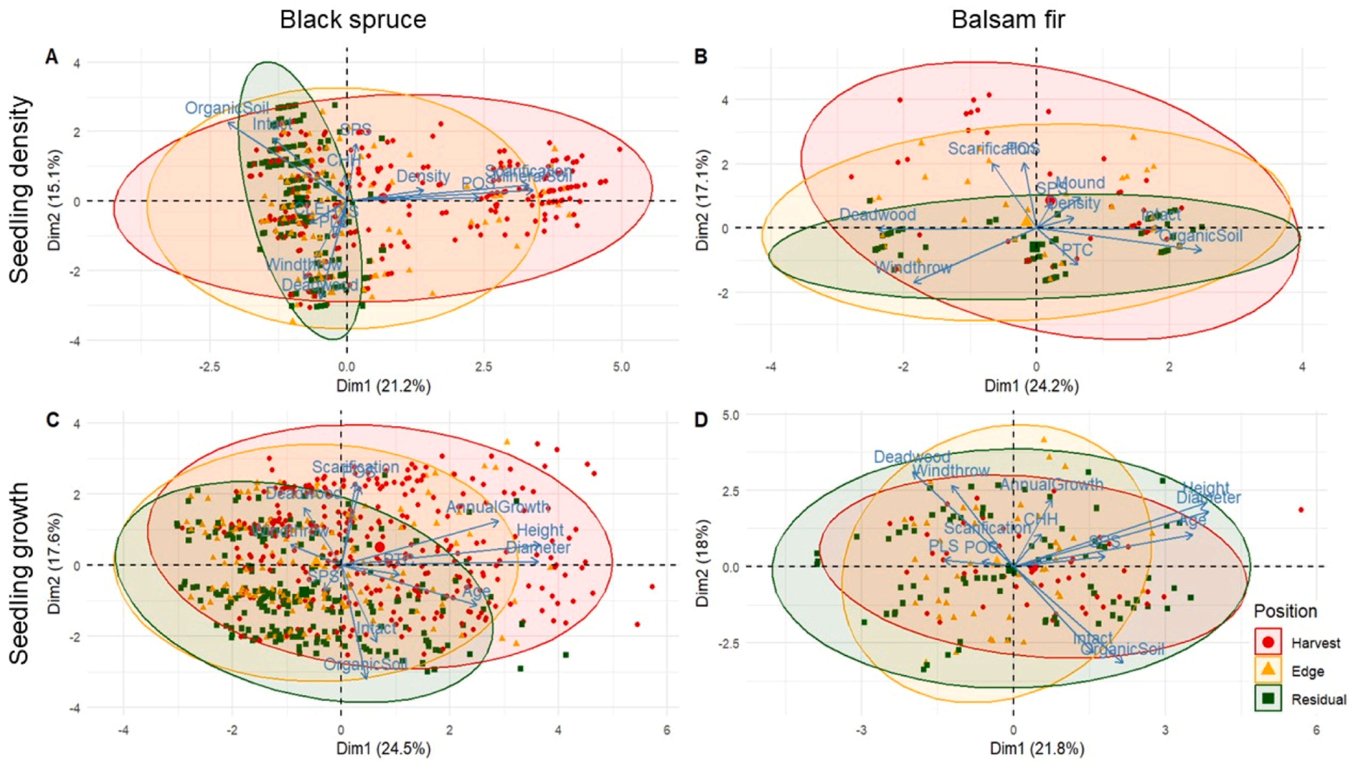


Fig. 6. Principal component analysis (PCA) of microplot environments, seedling density, and annual seedling growth for black spruce and balsam fir regeneration. Each point indicates a microplot (4 m^2). The proportion of the explained variance is indicated for each axis.

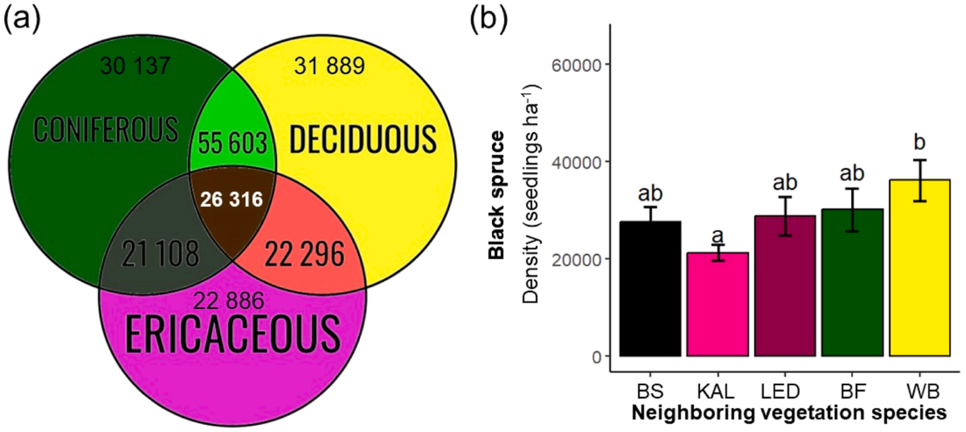


Fig. 7. Black spruce seedling density in relation to different neighboring vegetation groups. (a) Venn diagram for black spruce seedling density in association with three vegetation groups, separate and combined. (b) Black spruce seedling density in association with the most regenerated single species in this study. The major neighboring vegetation groups include ericaceous shrubs (*Kalmia angustifolia, Rhododendron groenlandicum*), conifer seedlings (*Abies balsamea, Larix laricina*), deciduous seedlings (*Betula papyrifera, Prunus pensylvanica, Salix* sp.). BS, black spruce; KAL, *Kalmia*; RHO, *Rhododendron*; BF, balsam fir; WB, white birch.

competitive vegetation in scarified areas, created favorable conditions for black spruce seedling establishment. This led to higher seedling densities than the other treatments, highlighting the advantages of the mini-strip shelterwood method in promoting black spruce regeneration. These findings align with previous research showing that increased scarification positively affects conifer seedling establishment (Johansson et al., 2005). The significant interaction between stand type and silvicultural treatment for black spruce density suggests that younger stands benefit more from shelterwood systems. Younger stands may have more favorable pre-harvest conditions, such as higher stand density and thinner organic layers, which improve post-harvest seedling recruitment (Moussaoui et al., 2020).

Balsam fir performed better in the distant-selection shelterwood treatment in older stands, likely because of its rapid and vigorous growth response to larger canopy openings, in contrast to black spruce (Martin et al., 2020a,b). This aligns with balsam fir's shade tolerance and preference for moist, protected environments (Lavoie et al., 2021). The ecological success of balsam fir is closely tied to its ability to thrive in shaded conditions and its tolerance to cold climates, making it a dominant species in boreal forests, where it often coexists with other conifers. Balsam fir seeds also require a chilling period of 28 –60 days (cold stratification) to overcome dormancy and begin germination (Bonner and Karrfalt, 2008), which could affect their natural regeneration outcomes following silvicultural treatments.

White birch exhibited a stronger response to stand type than other species, with seed-tree harvesting significantly increasing its density in younger stands. This finding aligns with previous research showing that canopy openings enhance birch germination and survival, emphasizing the reliance of white birch on increased light for regeneration (Shields et al., 2007). However, successful regeneration requires not only canopy openings but also an adequate level of residual trees to reduce seedling competition and prevent excessively dry soil conditions. This delicate balance shows the important interactions between light availability, soil moisture, and competition in the regeneration of white birch (Messier et al., 1999).

In our study, clearcutting with the protection of advanced regeneration resulted in the lowest seedling densities across all species and stand types, particularly in younger stands. The high disturbance levels associated with clearcutting create harsh environmental conditions, characterized by intense light, temperature fluctuations, and reduced soil moisture; these conditions inhibit seedling establishment, especially for shade-tolerant species (Kim et al., 2021; Kohout et al., 2018; Roy et al., 2000). In some cases, clearcutting may fail to ensure stand renewal, as indicated by the lower seedling densities and more competitive species observed in our study blocks relative to the controls. This outcome aligns with previous studies that highlight the potential negative impacts of clearcutting on forest ecosystems, including soil erosion, nutrient depletion, and reduced microbial community stability (Kim et al., 2021; Laudon et al., 2011). Over the long-term, clearcutting may increase ecosystem vulnerability to further disturbances, particularly spruce budworm outbreaks exacerbated by climate change (Aakala et al., 2023; Girona et al., 2023b; Montoro Girona et al., 2019; Subedi et al., 2023).

4.2. Seedling growth

Our findings demonstrated the significant impact of silvicultural treatments on the annual growth of conifer seedlings in mid-term post-harvest stands, particularly in terms of terminal shoot length in black spruce and balsam fir. The observed growth patterns were inversely related to seedling density, suggesting that intraspecific competition plays a critical role. Densely populated black spruce seedlings compete for limited resources such as soil nutrients, water, and light (Ammer, 2016). In our study, the higher seedling growth rates in clearcut and seed-tree harvesting treatments may be attributed to larger canopy openings and reduced intraspecific competition. For black spruce seedlings, the number of saplings greater than 1 m in height was a stronger predictor of annual growth than total seedling number; therefore, light availability strongly influences growth. This pattern aligns with previous research showing that increased light availability enhances seedling growth in shade-tolerant species, similar to the response seen in shade-intolerant species (Bebre et al., 2021). These findings underscore the importance of intraspecific competition and light availability as key factors influencing the annual growth of conifer seedlings in these stands. (Marty et al., 2023).

The interaction between stand type and silvicultural treatment further highlights the complexity of forest regeneration processes (Thiffault et al., 2024). For black spruce, the pronounced differences between younger and older stands suggest that the timing and context of harvesting play crucial roles in determining regeneration success (Girona et al., 2023a). Although clearcutting was beneficial in terms of seedling growth across both stand types, the variability in response to other treatments, such as seed-tree and mini-strip harvesting, indicates that stand age and structure are key factors to consider in silvicultural planning. This is particularly relevant for balsam fir, where younger stands responded more favorably to seed-tree harvesting, whereas older stands showed improved growth under mini-strip harvesting (Montoro Girona et al., 2018). The absence of a clear trend among treatments in older balsam fir stands may reflect the species' ecological characteristics, including its shade tolerance and sensitivity to disturbances, such as spruce budworm outbreak and windthrow (Guimond et al., 2024; Lavoie et al., 2021).

Although the influence of *Polytrichum* spp. and mound presence was less pronounced, their inclusion in the optimal model suggests that microsite conditions remain significant in shaping growth outcomes, particularly in environments where soil moisture and temperature are critical limiting factors. Previous research has shown that black spruce height growth tends to be greater on substrates comprising feathermosses and fibrous material, highlighting the importance of bryophyte substrates in influencing black spruce seedling growth (Lavoie et al., 2007). In our study, feathermosses were prevalent across most silvicultural treatments, making it difficult to detect distinct effects attributable to their presence. Although black spruce seedlings were abundant on mineral soil substrate, their growth preference can vary. In some field experiments, black spruce has shown faster height growth on soils covered with moss or a thin organic layer rather than on bare mineral soil (Fleming and Mossa, 1995). Additionally, these microsite conditions can be influenced by understory vegetation, such as ericaceous shrubs, which reduce seedling density and potentially stunt black spruce growth (Martin and Mallik, 2016).

The observed effects may also be attributed to scarification associated with seed-tree and shelterwood harvesting. Although scarification facilitates conifer seedling establishment by exposing mineral soil, it does not necessarily promote seedling growth because of increased nutrient leaching and the promotion of competitive deciduous species such as white birch (Saursaunet et al., 2018). Moreover, the initial benefits of scarification for seedling establishment can be counteracted by its negative effects on subsequent growth and root development.

Intraspecific competition in black spruce can vary with growth stage. Previous research has demonstrated that the size of neighboring trees is the primary factor influencing competition between black spruce and tamarack, regardless of whether the competition was intra- or interspecific (Roy Proulx et al., 2023). This finding underscores the need for further investigation to confirm this effect.

Additionally, these forest stands may require subsequent phases of structural development, which could significantly influence seedling growth. For example, spatial heterogeneity may create a mosaic of growth rates and stand structures, with some areas rapidly developing into closed-canopy forests, whereas others remain in early successional stages for extended periods (Kanjevac et al., 2023). The long-term trajectory of these stands will depend on the interplay of microsite conditions, ongoing competition, and potential disturbances such as insect outbreaks and windthrow (Peterson and Leach, 2008). Thus, continued monitoring is essential to fully understand the natural regeneration dynamics, as shade-tolerant species typically have a slower growth response to silvicultural treatments, and black spruce forests can take up to 200 years to reach maturity (Frelich et al., 2018).

4.3. Factors influencing natural regeneration dynamics in boreal forests

Understanding the driving factors in natural regeneration dynamics after silvicultural treatments is essential for preserving ecosystem resilience, biodiversity, and the long-term sustainability of forest landscapes (Martin et al., 2020b). Our analyses revealed that proximity to skid trails significantly affected the regeneration process of conifer species through scarification and canopy opening. This was reflected in a consistent set of environmental factors influencing the presence of sexual seedlings along trails (in areas such as ruts, mounds, and highly disturbed material) and at the edges (involving windthrow and woody debris) and that of vegetative seedlings (through layering) in residual strips (in relation to bryophyte cover and intact microplots). The strong correlation between the mineral soil, spot scarification, and moss cover, e.g., *Polytrichum* spp., with black spruce seedling density highlights the importance of soil disturbance in creating favorable seedbeds for this species and suggests that appropriate site preparation can enhance conifer regeneration (Béland et al., 2000; Lafleur et al., 2011).

Polytrichum spp. is known for their remarkable hydrophilic properties—retaining up to 646 % of their dry weight in water—potentially creating favorable microsites for black spruce seedling establishment in moisture-limited sites, such as these scarified areas (Coelho et al., 2023).

However, the prevalence of *Polytrichum* spp. may also indicate environmental degradation caused by clearcutting practices, as well as the influence of population biology and reproductive strategies (Bao, 2005). Our study demonstrated differing responses between black spruce and balsam fir to environmental conditions. Whereas black spruce regeneration was strongly correlated with mineral soil and negatively correlated with windthrow conditions, these factors did not significantly affect balsam fir seedling growth. For balsam fir, undisturbed soil conditions and mound formations were beneficial; thus microsite stability and moisture retention are critical for its regeneration (Olesinski et al., 2011). This differential response to environmental conditions can be attributed to the contrasting ecological traits of black spruce and balsam fir, with black spruce being more cold-tolerant and better adapted to poorly drained soils, whereas balsam fir exhibits greater shade tolerance but requires more stable and well-drained microsites for successful regeneration (Messaoud et al., 2019).

Our study shows that the presence of specific vegetation types, such as deciduous trees and *Kalmia*, can significantly affect black spruce regeneration, highlighting the need to manage understory vegetation when implementing shelterwood systems (Thiffault et al., 2013; Walker and Mallik, 2009). The more favorable interaction of deciduous species relative to that of conifers can be explained by black spruce seedlings benefiting from increased light exposure and better access to nutrients and water when deciduous species are leafless in the spring and fall in eastern Canada. Moreover, some deciduous species, like aspen, can enhance soil fertility through the decomposition of their fallen leaf litter (Oboite and Comeau, 2019).

In contrast, *Kalmia* significantly reduced black spruce regeneration in our study, potentially altering future stand dominance. In Newfoundland (Canada), *Kalmia*-dominated heathlands have been shown to decrease the black spruce recruitment rate, with a high proportion of recruited seedlings exhibiting stunt growth (Martin and Mallik, 2016). It is hypothesized that the ectomycorrhizal inoculation of black spruce seedlings could be crucial for their success in *Kalmia* heaths, as stunted growth may be linked to ericoid mycorrhizal fungi (Yamasaki et al., 1998). Further research is needed to better understand how site preparation and management strategies can promote successful black spruce regeneration in the presence of *Kalmia* in boreal stands.

4.4. Implications for boreal forest management

Partial harvesting could serve as a next-generation forest management strategy in the Canadian boreal forest. This approach can help balance ecological and economic objectives by preserving key habitat features, reducing soil disturbance, and supporting the recruitment of both shade-tolerant and shade-intolerant species (Moussaoui et al., 2020). Our findings have significant implications for forest management practices aimed at enhancing conifer regeneration. High regeneration densities, particularly for shade-tolerant species like black spruce, improve the likelihood of stand success and reduce the need for costly and time-consuming artificial regeneration measures, such as site preparation and planting (Gonçalves & Fonseca, 2023).

The species composition (e.g., black spruce, balsam fir, white birch) and detection frequencies across silvicultural treatments and stand types in this study offer valuable insights into future stand development trajectories. These findings can inform management decisions related to vegetation control, thinning interventions, and the necessity of supplemental planting to optimize stand regeneration and long-term forest management sustainability. Accordingly, silvicultural treatments should be tailored to the ecological requirements of target species and stand conditions (Girona et al., 2023b; D'Amato et al., 2023). For example, mini-strip shelterwood and distant-selection harvesting can be strategically applied to promote black spruce and balsam fir regeneration in younger and older stands, respectively, ranging from 80 to 150 years old. In our study, partial harvesting was particularly effective for black spruce, but its applicability may also extend to other conifer species (Bose et al., 2023).

Conversely, clearcutting can create nutrient-deficient soil conditions detrimental to seedling establishment (Kim et al., 2021; Kohout et al., 2018; Sharma et al., 2016). Although clearcutting can sometimes promote early seedling growth by reducing seedling density and minimizing intraspecific competition, its effects vary among stand types and species. Without regeneration-assisting treatments, clearcutting can also extend recovery times (Barrette et al., 2022). This variability suggests that a one-size-fits-all approach to silvicultural treatment is inappropriate. Treatments must be carefully balanced with long-term objectives, such as preserving species diversity and maintaining forest structural complexity.

Continuous long-term monitoring is essential to understanding forest succession, assessing the ongoing effects of these treatments, and adapting strategies as needed to ensure sustainable forest regeneration following partial harvesting.

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CRediT authorship contribution statement

Kim Sanghyun: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bergeron Yves:** Writing – review & editing, Validation, Supervision, Funding acquisition. **Raymond Patricia:** Writing – review & editing, Validation, Supervision, Funding acquisition. **Thiffault Nelson:** Writing – review & editing, Validation, Funding acquisition. **Montoro Girona Miguel:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Miguel Montoro Girona reports financial support was provided by Natural Sciences and Engineering Research Council of Canada. Miguel Montoro Girona reports was provided by Ministry of Natural Resources and Forests. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122655.

Data availability

Data will be made available on request.

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