forests

MDPI

Article

Natural Regeneration Following Partial and Clear-Cut Harvesting in Mature Aspen-Jack Pine Stands in Eastern Canada

Kobra Maleki *, Freddy Nguema Allogo and Benoit Lafleur

Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 445 Boul. de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada; Freddy.NguemaAllogo@uqat.ca (F.N.A.); Benoit.Lafleur@uqat.ca (B.L.)

* Correspondence: kobra.maleki@uqat.ca; Tel.: +1-819-762-0971 (ext. 2462)

Received: 10 June 2020; Accepted: 30 June 2020; Published: 8 July 2020

Abstract: Over the last three decades, the ecological basis for the generalized use of even-aged silviculture in boreal forests has been increasingly challenged. In boreal mixed-wood landscapes, the diminishing proportion of conifers, to the benefit of intolerant hardwoods, has been a primary concern, coupled with the general rarefication of old-growth conifer-dominated stands. In this context, partial cutting, extended rotations and forest renewal techniques that eliminate or reduce regenerating hardwoods have been proposed as means of regaining greater conifer cover. As a result, experimentation and industrial application of various forms of both variable retention and partial harvesting are occurring across the commercial Canadian boreal forest. In this study, we compared the effects of two harvesting intensities, clearcutting and low-intensity partial cutting (removal of 25–31% of tree basal area), on hardwood and conifer regeneration levels 7–19 years following treatments in aspen (*Populus tremuloides*)-dominated stands and verified whether regeneration differences existed between micro-sites on and off machinery trails. The abundance of aspen regeneration increased with percent basal area removal and was positively correlated to the abundance of mature aspen prior to harvesting. The abundance of fir (*Abies balsamea*) regeneration after partial cutting was similar to controls and higher than after clear-cutting and was positively correlated with ground cover of mixed litter (i.e., mixture of needles and leaves) and negatively correlated with ground cover of broadleaf litter. These results suggest that it is possible in boreal mixed-woods to control aspen abundance and promote or maintain conifer regeneration through silvicultural treatments that limit canopy opening and promote mixed forest floor litter.

Keywords: balsam fir; soil disturbance; seedling; sapling abundance; height growth; substrate

1. Introduction

Mixed forests (i.e., forests comprised of a mixture of hardwood and softwood species) are an important ecological and economic component of the Canadian boreal forest [1]. Primary natural disturbances, such as forest fires, and secondary disturbances, such as insect outbreaks, are the main drivers of forest dynamics in the boreal mixed-woods [2–4]. Commercial, mechanized logging has been generally applied in the boreal forest since the 1950s and is also a major disturbance agent in the boreal mixed-woods [5]. Forest ecosystem management recognizes the understanding of natural disturbance dynamics as an important reference for setting regional-level forest composition and age structure objectives and guiding stand-level silvicultural interventions [6].

In the boreal mixed-woods, where species composition and structure change over time through canopy succession, clear-cutting and uneven-aged management (e.g., partial and selection cutting) have been suggested to respectively reinitiate even-aged stands as an analogue to severe fire and mimic canopy succession and gradual stand break-up [7–10]. At the landscape level, a wider use of partial cutting could limit the regeneration of shade-intolerant, pioneer tree species, such as trembling aspen (*Populus tremuloides* Michx) and white birch (*Betula papyrifera* Marsh), as well as that of hardwood shrubs, such as mountain maple (*Acer spicatum* Lambert). Partial cuts could therefore maintain stand structures and compositions, which are key habitat attributes for several plant and animal species in the boreal mixed-woods [11,12], similar to those resulting from natural secondary disturbances, such as insect outbreaks and windthrow [13–15], and alleviate the undesired effect of clear-cutting at the landscape scale. For instance, in many parts of the eastern boreal mixed-wood and continuous coniferous forests, the large-scale use of clear-cutting (in Quebec called cutting with protection of regeneration and soil, CPRS) and relatively short rotations (80–100 years) have led to a decrease in habitat and ecosystem diversity [16] and an increase in the relative proportion of pioneer, shade-intolerant hardwoods, especially trembling aspen [12,17]. As such, the increase in the proportion of the territory dominated by trembling aspen, mainly due to its ability to regenerate by suckering, is indicative of the rejuvenation of the boreal mixed-woods [14,15].

Machinery traffic during harvesting operations can cause direct soil disturbance, especially when undertaken outside of the winter season. This disturbance may result in reduced organic layer thickness, exposed mineral soil, compacted organic and surface mineral soil horizons, and altered soil drainage, all of which can affect forest productivity and natural regeneration dynamics [18,19]. In general, physical disturbance associated with forest harvesting is greatest in and close to trails compared to off-trail areas, which can locally influence the abundance and growth of natural regeneration [19]. For instance, Brais et al. [14] observed more aspen suckering on machinery trails (ca. 5% of partially harvested areas), where some soil physical disturbance and increased light availability occurred. In contrast, the abundance of balsam fir regeneration was lower on trails as a result of machinery traffic and consequent soil disturbance [15], and possibly because of sudden water stress and sun exposure immediately after complete canopy removal for larger seedlings [20].

Furthermore, it is well known that habitat factors, such as types of seed bed and growing substrate, and species traits, such as mode of reproduction and shade tolerance, influence the establishment and growth of natural regeneration [11,21,22]. For instance, regeneration of trembling aspen, a shade-intolerant species, which mainly reproduces locally by suckering, is more abundant following low-retention harvesting [13]. Other boreal species, such as very shade-tolerant balsam fir (*Abies balsamea* [L.] Mill) and moderately tolerant white spruce (*Picea glauca* [Moench] Voss), which reproduce exclusively by seed, are more abundant following high-retention harvesting [13] and more dependent on seedbed and substrate type for establishment. According to Burns and Honkala [23] and Simard et al. [24], exposed mineral soil and needle litter are more favorable seedbeds for balsam fir establishment, whereas white spruce establishment is facilitated by well-decomposed woody debris [24,25].

Management of the boreal mixed-woods through short-rotations and low-retention harvesting (i.e., clear-cutting or clear-cutting with protection of regeneration and soil), only partially reproduces the effects of natural disturbances [26]. Indeed, secondary disturbances, such as insect outbreaks, windthrow and gap dynamics, leave significant vertical and horizontal structure in affected stands, and even within large burned areas, some forested areas may totally or partially escape fire [6]. Low-retention harvesting can therefore limit the restoration of forest productivity by limiting seed sources and altering critical biophysical conditions for the regeneration processes. This may pose several challenges to the sustainable management of the boreal forest, such as rejuvenation and homogenization of forest structure and composition [21,26,27]. To face these challenges, variations of partial cutting have been proposed as complementary treatments to conventional even-aged management regimes that have, at least until recently, focused almost exclusively on clear-cutting. While there has clearly been considerable experimental effort to understand the effects of partial cutting on regeneration dynamics in eastern boreal mixed-wood forests [15,26,28,29], given the variation in cover types, regional climate and natural dynamics, our understanding remains fragmented and partial. Moreover, the stands in the present study were at first viewed as silviculturally inappropriate candidates for uneven-aged silviculture or partial harvesting. In effect, the primary justification for applying partial harvesting in these stands was a forest-level issue of delaying final harvest of a portion of a forest area that originated from a fire in 1923. The intent was to extend the period of mature forest cover in a portion of the area while partially recuperating volume in treated stands, rather than necessarily facilitating a transition to a higher conifer composition.

The objective of this study was to improve our understanding of the mid-term (i.e., 7 to 19 years) effects of partial versus complete harvesting and site disturbance levels within these treatments on the abundance and growth of natural regeneration in trembling aspen—jack pine forests. We first hypothesized that high-retention levels, following partial cutting, would have a positive effect on post-harvest natural seedling abundance of coniferous species as a result of (1) lower harvest-related mortality of advanced regeneration compared to clear-cutting/CPRS [29–31], and (2) recruitment due to the presence of tolerant conifer seed sources in the residual canopy (hypothesis (H) 1). Conversely, we anticipated that low-retention harvesting (i.e., clear-cutting/CPRS) would generally induce higher trembling aspen recruitment [13,14,32] (H2). We also predicted that, because mortality of advanced conifer regeneration would be lower off machinery trails, densities (H3) and mean height (H4) of conifer regeneration would be greater off machinery trails than on trails, at least in partial cuts. In addition, assuming higher soil mechanical disturbance and more open light conditions in machinery trails (than off trails) in both CPRS and PC treatments, we anticipated that post-harvest recruitment (H5) and height growth (H6) of aspen regeneration would be higher on trails.

2. Materials and Methods

2.1. Study Area

This study was conducted in the Abitibi region of western Quebec, Canada, approximately 45 km northwest of Rouyn-Noranda. More specifically, the study area is located within the balsam fir-white birch bioclimatic domain [33], at the Lake Duparquet Research and Teaching Forest (LDRTF) (48°30′ N, 79°20′ W), where partial cutting has been practiced operationally since the late 1990s. The climate is continental and, according to the nearest weather station, for the period 1980–2010, the mean annual temperature is 1.0 °C and the mean annual precipitation is 985 mm, while the growing season lasts about 150 to 160 days [34]. Glaciolacustrine clays cover 55% of the LDRTF territory [9] and represent the main legacy of proglacial lakes Ojibway and Barlow [35], whereas glacial till and organic deposits cover respectively 21% and 20% of the territory [36]. Forests within the study area are characterized by pure and mixed stands composed of boreal coniferous and shade-intolerant deciduous species. More specifically, on mesic sites, trembling aspen, white birch and jack pine dominate early successional stands, whereas late-successional stands are dominated by balsam fir and eastern white cedar, in association with white spruce and persistent white birch [10].

Stand-replacing wildfires and defoliating insect outbreaks are the main natural disturbances of the study region. The fire regime of the past 300 years has been characterized by high-intensity fires that covered vast areas of the study region, particularly in terrain with flat topography [37]. During that period, fire return intervals increased from ~90 years prior to 1850 to 360 years since 1920 (Table 4 in [4]). During the 20th century, three spruce budworm outbreaks were reported in the territory, for the periods 1919–1929, 1930–1950 and 1972–1987 [38,39].

2.2. Study Stand Characteristics and Silvicultural Treatments

The mixed-deciduous stands in this study originated from a fire that occurred in 1923 [37] and were dominated by trembling aspen and generally co-dominated by jack pine (Table 2). At the time of harvesting treatments, 1998–2010, the stands were mature and even-aged with relatively low basal area of spruce and balsam fir in the canopy (Table 2) and had a shrub layer dominated by Mountain maple (*Acer spicatum*) and characteristically sparse conifer regeneration. Jack pine, as a defining species on xeric sites, is an "associated", rather than "defining", mixed-wood species [8] and most commonly found on poor, xeric-mesic fluvio-glacial and till sites, but historically, it has also regenerated after fire in pure and mixed compositions on mesic glacio-lacustrine clay sites in the study area. According to forest mapping, selected stands were established on both glaciolacustrine clay deposits and clayey tills, although granulometric analyses revealed that soil texture of both deposits was classified as clay [40]. All treated stands (except for unharvested control stands), were either partially cut between 1998 and 2010 or totally harvested in winter between 1998 and 2004 (Table 1).

Table 1. Mean basal area (m^2 ha^{-1}) prior to and 7 to 19 years after treatment in 2017, in the boreal mixed-woods of eastern Canada.

Treatment	Harvest Year	Sampling Interval (y)	Stand Basal Area (m^2 ha^{-1})	
			Pre-Harvest	Post-Harvest
Cntrl			40.8	38.0
PC	1998–2010	7–19	45.9	23.2
CPRS	1998–2004	13–19	46.8	4.0

Cntrl: unharvested control; PC: partial cut; CPRS: cutting with protection of regeneration and soil.

The studied sites consisted of unharvested control (Cntrl, 0% basal area (BA) removal), partial cut (PC, 25–31% BA removal) and CPRS (91–92% BA removal). Partial cuts could be considered a form of commercial thinning and CPRS as a variant of clear-cutting in that all merchantable-sized stems (diameter at breast height (DBH) ≥ 9.1 cm) are harvested. All harvesting was done using cut-to-length multifunctional harvesters and forwarders. The French acronym CPRS translates as harvesting with protection of regeneration and soil. Harvesting and forwarding machinery is restricted to parallel trails covering ca. 20–25% of cutover surface and, as a result, regeneration and soils are not directly impacted by machinery between trails.

2.3. Tree and Natural Regeneration Survey

Using 400 m^2 circular sample plots (SP), all sites selected for this study, including controls, had been operationally inventoried prior to harvesting to determine stand composition, DBH of merchantable stems and basal area by species (Table 2). These inventories were done during the summers preceding winter harvesting. Post-treatment data were collected in the summer of 2017; that is, 7 to 19 years after partial cutting treatments and 13 to 19 years after the CPRS treatments. Because of inadequate geolocation of the original SP, post-harvest SP in 2017 were located in the original stands but could not be precisely centered on the original plots, so were randomly installed at least 50 m apart. In order to inventory post-treatment conditions, we used six sites (i.e., replicates) for each treatment (Cntrls, PC and CPRS) and five 400 m^2 SP within each replicate (i.e., 30 per treatment; total of 90 SP). To determine the effect of harvest treatments on the residual tree layer, all merchantable stems were tallied, identified to species, and DBH was noted. In addition, to profile natural regeneration in each SP, we installed one 100 m^2 subplot, in which saplings ($1 < DBH \leq 9.0$ cm) were tallied and identified to species and four 4 m^2 micro-plots to tally seedlings. Note that "advanced regeneration or seedling" refers to a size class (DBH ≤ 1 cm) and that, technically, almost all aspen stems in this size class were of root sucker origin. Results from this sampling protocol are presented in Tables 1–3.

2.4. On and Off Trail Regeneration Survey

A second inventory protocol was used to investigate the effect of local disturbance associated with forest machinery trafficking on the abundance and height growth of natural regeneration. In PC and CPRS treatments, twenty 4 m^2 micro-plots were surveyed in four of the six replicates (total of 160 micro-plots, 80 in and 80 off the machinery trails), whereas 5 micro-plots were surveyed in each Cntrl replicate (total of 30 micro-plots). In these micro-plots, seedlings and aspen suckers (stems ≤ 1 m high and DBH ≤ 1 cm) were identified to species tallied and measured for total height and 3-year annual increment. Finally, in each micro-plot, we visually estimated the percent cover of three soil surface substrate types (broadleaf litter, needle litter and woody debris). Results from this protocol are presented in Tables 4 and 5 and Figures 1 and 2.

2.5. Statistical Analyses

The effects of harvesting treatments on the basal area of residual stands and the abundance of natural regeneration were analysed using mixed-effects analysis of variance (ANOVAs). Harvesting treatment was integrated as a fixed effect, site and plots as random effects and time since harvest as co-variable. Mixed-effects ANOVAs were also used to compare the effects of soil disturbance associated with machinery traffic (i.e., machinery trail position) on the abundance and growth (i.e., total height and 3-year annual increment) of natural regeneration. Location of regeneration (i.e., in or off machinery trails) was used as a fixed effect, site and micro-plots as random effects and time since harvest as a co-variable. In addition, using Pearson correlations, we determined the strength of the relationships between selected habitat factors (i.e., stand composition, organic layer thickness and germination and establishment substrate) and the abundance and growth of natural regeneration.

Variable residuals were tested for normality and homogeneity of variances, and the data were log or square root transformed when necessary. Post-hoc comparisons (Tukey HSD) were made to contrast the levels of the fixed variables, and differences were deemed significant when $p \leq 0.05$. All statistical analyses were conducted using JMP 14.0 [41].

3. Results

3.1. Stand Basal Area Prior to and After Harvesting

Prior to treatment application, all sites were dominated by trembling aspen (≥ 66% of total BA), whereas jack pine, balsam fir and white spruce were the most abundant conifers, with 7–13%, 6–8% and 4–8% of the total stand BA, respectively (Table 2). At this time, there were no significant differences in stand composition among treatments (ANOVA, $p = 0.264$).

As could be expected, after harvesting, total and aspen BA were significantly higher in Cntrl stands than in stands treated with PC and CPRS, and significantly higher in PC stands than in CPRS stands (ANOVA, $p < 0.001$) (Table 2). Relative to Cntrls, total BA values in PC and CPRS treatments were lower by 39% and 89% respectively, and trembling aspen BA was about 43% and 87% lower in PC and CPRS stands, respectively. Balsam fir BA was significantly greater in Cntrl and PC stands than in CPRS stands (ANOVA, $p < 0.001$) (Table 2). Relative to Cntrls, balsam fir BA was lower by 68% (3.8 m^2 ha^{-1}) after PC, and 90% (5.6 m^2 ha^{-1}) after CPRS (ANOVA, $p < 0.001$). Basal area values of white birch and white spruce were greater in Cntrls and PC than in CPRS (ANOVA, $p = 0.008$ and < 0.03, respectively) but not different between Cntrls and PC (Table 2).

Table 2. Mean merchantable stem (DBH ≥ 9.1 cm) basal area (m^2 ha^{-1} ± Standard error) across treatments and species prior to and after treatment in the studied boreal mixed-wood stands. On a given line, values with different letters differ significantly based on Tukey HSD comparisons (α = 0.05).

Species	Treatment			
	Control	**PC**	**CPRS**	***p*-value**
Prior to treatment				
Trembling aspen	31.3 ± 2.1	30.4 ± 2.0	31.7 ± 1.7	0.911
White birch	1.2 ± 2.2	1.8 ± 2.0	1.1 ± 2.0	0.438
Balsam fir	2.6 ± 2.3	2.9 ± 2.2	3.6 ± 4.2	0.598
White spruce	1.6 ± 1.2	2.7 ± 3.3	2.4 ± 2.8	0.685
Black spruce	1.2 ± 1.2	2.5 ± 3.4	1.6 ± 1.2	0.085
Jack pine	2.7 ± 1.4	5.2 ± 4.2	6.1± 4.2	0.735
White cedar	0.2 ± 1.4	0.3 ± 1.5	0.4 ± 1.2	0.454
Total	40.8 ± 2.3	45.9 ± 3.7	46.8 ± 2.0	0.264
After treatment				
Trembling aspen	24.4^{a} ± 1.6	13.8^{b} ± 2.2	3.1^{c} ± 2.4	< 0.001
White birch	1.5^{a} ± 2.0	1.3^{a} ± 1.6	0.2^{b} ± 0.6	0.008
Balsam fir	6.2^{a} ± 4.1	2.4^{a} ± 1.7	0.6^{b} ± 1.5	< 0.001
White spruce	2.3^{a} ± 2.6	3.0^{a} ± 2.6	0.1^{b} ± 0.3	0.030
Black spruce	1.6 ± 3.3	0.2 ± 0.7	0.0 ± 0.0	0.076
Jack pine	1.6 ± 4.2	2.4 ± 4.0	0.0 ± 0.0	0.085
White cedar	0.4 ± 1.4	0.1 ± 0.5	0.0 ± 0.0	0.551
Total	38.0^{a} ± 2.1	23.2^{b} ± 1.4	4.0^{c} ± 0.5	< 0.001

Cntrl: unharvested control; PC: partial cut; CPRS: clear-cut with protection of regeneration and soil.

3.2. Regeneration Abundance 7–19 Years after PC and 13–19 Years after CPRS

Following harvesting, total (seedlings + saplings) regeneration densities per hectare were roughly 16,000, 24,000 and 19,000 in Cntrls, PC and CPRS, respectively (Table 3). In all treatments, broad-leaved regeneration was overwhelmingly composed of trembling aspen and conifer regeneration of balsam fir. Aspen seedlings (primarily root suckers ≤ 1 cm DBH) were significantly more abundant in the PC treatment than in the CPRS treatment and Cntrls (ANOVA, $p < 0.024$) (Table 3), but there was no significant difference in abundance between CPRS and Cntrls (Table 3). Balsam fir seedling density in PC stands was similar to that in Cntrls and significantly greater than following CPRS (ANOVA, $p < 0.001$). Although white spruce seedlings were much less abundant than balsam fir in our sites, they were significantly more abundant in PC treatments than in the CPRS and Cntrls (ANOVA, $p = 0.048$) (Table 3). All other conifer species and white birch had insignificant levels of abundance in the three treatments. After harvesting, PC stands had higher total seedlings density (N ha^{-1}) than Cntrl and CPRS stands, respectively (ANOVA, $p < 0.001$) (Table 3).

Table 3. Mean regeneration density ± N ha^{-1} ± Standard error of seedlings ± ≤ 1 cm DBH and saplings ± 1 < DBH ≤ 9.0 cm across treatments and species 7 to 19 years after treatment in the studied boreal mixed-woods. On a given line, values with different letters differ significantly based on Tukey HSD comparisons ± α = 0.05.

Species	Treatment			
	Control	**PC**	**CPRS**	***p*-Value**
Seedlings				
Trembling aspen	1417^{b} ± 321	5188^{a} ± 884	1667^{b} ± 561	0.024
White birch	42 ± 42	104 ± 61	21 ± 21	0.436
Balsam fir	12,042^{a} ± 2135	13,604^{a} ± 1719	3583^{b} ± 964	< 0.001
White spruce	500^{b} ± 132	1979^{a} ± 596	417^{b} ± 165	0.048
Black spruce	479 ± 209	146 ± 71	312 ± 163	0.678
Jack pine	0 ± 0	0 ± 0	83 ± 83	
White cedar	0 ± 0	63 ± 35	0 ± 0	
Total	14,473^{a} ± 13,268	21,084^{b} ± 19,282	6083^{c} ± 5160	< 0.001
Saplings				
Trembling aspen	173^{c} ± 56	1486^{b} ± 320	10,193^{a} ± 111	< 0.001
White birch	60 ± 20	233 ± 72	533 ± 112	0.225
Balsam fir	1093 ± 175	846 ± 121	1666 ± 711	0.316
White spruce	60 ± 21	103 ± 24	76 ± 32	0.745
Black spruce	53 ± 28	10 ± 7	80 ± 47	0.468
Jack pine	0 ± 0	0 ± 0	53 ± 53	
White cedar	0 ± 0	7 ± 7	0 ± 0	
Total	1439^{b} ± 832	2685^{b} ± 1154	12,601^{a} ± 10,269	< 0.001

Cntrl: unharvested control; PC: partial cut; CPRS: clear-cut with protection of regeneration and soil.

The abundance of trembling aspen saplings (and consequently, total saplings) increased with harvesting intensity, and differences between treatments (CPRS > PC > Cntrls) were significant (ANOVA, $p < 0.001$) (Table 3). There were no significant differences in sapling abundance for any of the other species among harvesting treatments.

3.3. Regeneration Abundance and Growth on and off Machinery Trails

The separate sampling protocol to investigate the effect of location (on versus off machinery trails) on regeneration densities and growth generally confirmed regeneration density comparisons between treatments presented in the previous section (Table 4). Only trembling aspen regeneration in the PC treatment showed a location effect; specifically, in PC sites, regeneration densities were significantly higher on machinery trails than off (Table 4). No other species showed a location effect, although densities of balsam fir were notably, if not significantly, higher off trail than on trail.

Table 4. Mean regeneration density ± N ha^{-1} ± Standard error of seedlings ± ≤ 1 cm DBH on and off machinery trails across treatments and species 7 to 19 years after treatment in the boreal mixed-woods of eastern Canada. On a given line, groups with different letters differ significantly based on Tukey HSD comparisons ± α = 0.05.

Species	Treatment					
	Control	PC-T	PC-OT	CPRS-T	CPRS-OT	*p*-Value
Trembling aspen	2931^{b} ± 635	6667^{a} ± 1280	2073^{b} ± 735	366^{c} ± 316	64^{c} ± 73	< 0.001
White birch	0 ± 0	0 ± 0	0 ± 0	61 ± 71	50 ± 65	0.697
Balsam fir	9083^{a} ± 1028	1710^{b} ± 359	3170^{b} ± 316	119^{c} ± 84	313^{c} ± 190	< 0.001
White spruce	500 ± 446	329 ± 195	366 ± 202	113 ± 110	188 ± 148	0.429
Black spruce	125 ± 107	0 ± 0	0 ± 0	120 ± 120	188 ± 148	0.530
Jack pine	0 ± 0	0 ± 0	0 ± 0	0 ± 0	63 ± 62	
White cedar	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	
Total	12,639^{a} ± 255	8706^{b} ± 224	5609^{b} ± 230	666^{c} ± 220	866^{c} ± 219	< 0.001

Cntrl: unharvested control; PC: partial cut; CPRS: clear-cut with protection of regeneration; T: machinery trails; OT: off machinery trails.

In the medium term (7 to 19 years after PC and 13 to 19 years after CPRS), and taking time since harvesting into account, only trembling aspen regeneration showed significant differences in total height (Figure 1) and recent height growth (Figure 2) between treatments (i.e., CPRS-T and CPRS-OT > PC-T and PC-OT). In both total height and recent height growth, significant differences existed between the three treatments (CPRS > PC > Cntrl) (ANOVA, $p < 0.0003$), although no significant differences existed between on and off trail positions within the two harvesting treatments. Total height and mean annual height growth of other species regenerations did not statistically differ by harvesting intensity or position relative to machinery trail (Figures 1 and 2).

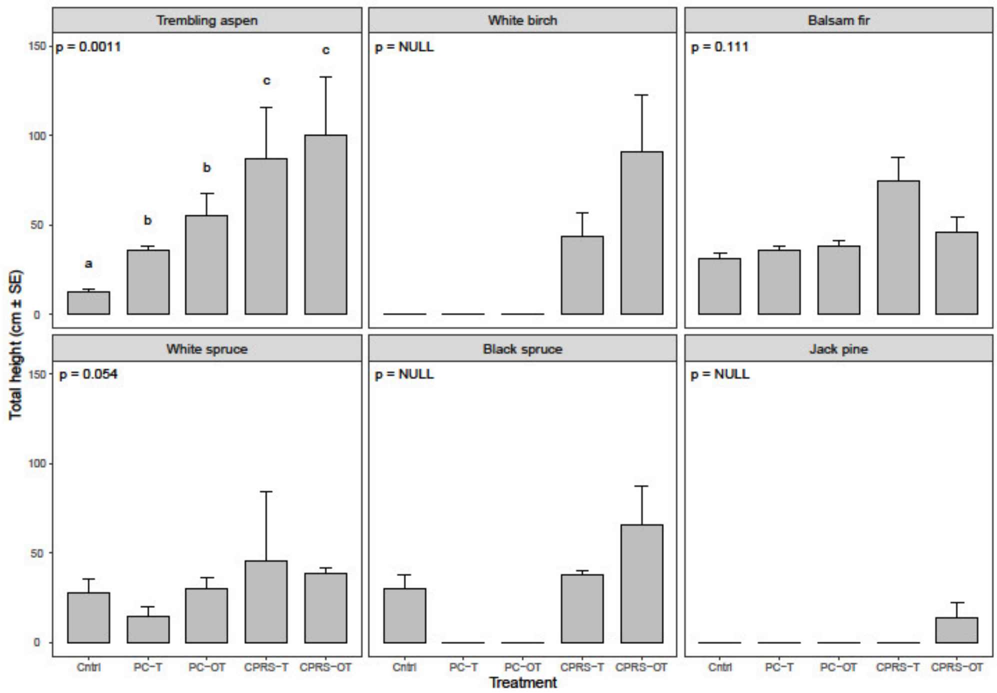

Figure 1. Mean regeneration height (cm ± Standard error) on and off machinery trails (190 micro-plots) across treatments and species 7 to 19 years after treatment in the boreal mixed-woods of eastern Canada. Bars with the same letter are not significantly different at alpha = 0.05, according to the Tukey HSD test. Treatments are Cntrl: unharvested control; PC: partial cut; CPRS: clear-cut with protection of regeneration and positions are T: machinery trails; OT: off machinery trails. See Table 4 for the number of observations.

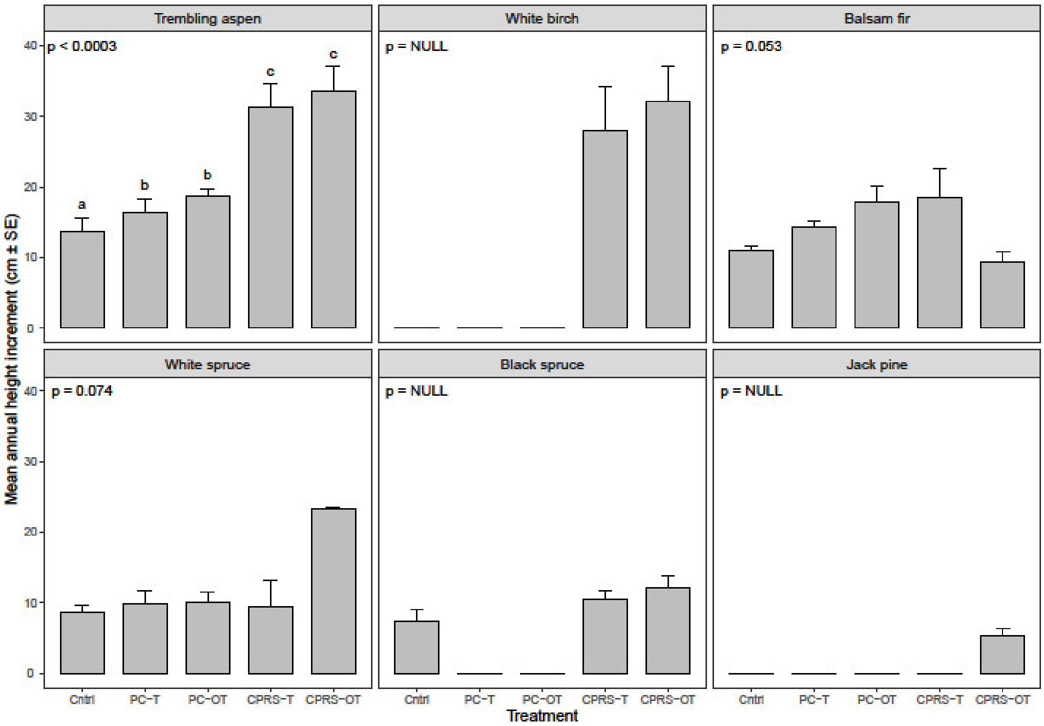

Figure 2. Mean regeneration annual height increment (cm ± Standard error) on and off machinery trails (190 micro-plots) across treatments and species 7 to 19 years after treatment in the boreal mixed-woods of eastern Canada. Bars with the same letter are not significantly different at alpha = 0.05, according to the Tukey HSD test. Treatments are Cntrl: unharvested control; PC: partial cut; CPRS: clear-cut with protection of regeneration and positions are T: machinery trails; OT: off machinery trails. See Table 4 for the number of observations.

3.4. Influence of Basal Area and Ground Cover on Seedling Abundance

Because aspen and balsam fir made up the large majority of broad-leafed and conifer regeneration respectively, we present results mainly for these two species (values for total hardwood and softwood regeneration are virtually identical, respectively). Although significant correlations ($p < 0.05$) were found between seedling abundance and basal area and ground substrates, the Pearson correlation coefficients were relatively low (r ≤ 0.445) (Table 5). Abundance of trembling aspen natural regeneration was negatively correlated to coniferous litter cover and positively correlated to well-decomposed woody debris cover and aspen and fir merchantable basal area prior to harvesting (Table 5). In the case of balsam fir, seedling abundance was negatively correlated to higher deciduous litter cover and aspen basal area following harvesting, and positively correlated with cover of well-decomposed woody debris and coniferous litter and aspen BA prior to harvest (Table 5).

Table 5. Pearson correlation coefficient (*p*-values) between substrate type cover and trembling aspen and balsam fir basal area before and after harvesting, and seedling abundance.

	Well-Decomposed Woody Debris	Deciduous Litter	Coniferous Litter	Basal Area			
				Trembling Aspen		Balsam Fir	
				Pre-Harvest	Post-Harvest	Pre-Harvest	Post-Harvest
Aspen seedling abundance	0.249 (0.018)	0.150 (0.158)	−0.219 (0.038)	0.364 (<0.001)	0.039 (0.717)	0.312 (0.003)	0.136 (0.200)
Fir seedling abundance	0.210 (0.047)	−0.413 (< 0.001)	0.445 (<0.001)	0.327 (0.002)	−0.212 (0.045)	0.007 (0.949)	0.150 (0.157)
Total hardwood abundance	0.252 (0.016)	0.145 (0.174)	−0.216 (0.041)	0.363 (<0.001)	0.039 (0.714)	0.314 (<0.001)	0.135 (0.714)
Total conifer abundance	0.215 (0.042)	−0.215 (0.042)	0.215 (<0.001)	0.036 (0.001)	−0.207 (0.051)	−0.003 (0.978)	0.160 (0.131)

4. Discussion

If favouring conifer recruitment is a primary silvicultural objective, aspen-dominated stands situated on rich sites with limited late-successional conifer species (balsam fir, spruce *spp*.) in the canopy and regeneration layers are not prime candidates for partial cutting [28]. Generally, low levels of advanced conifer regeneration and an aggressive shrub layer (in our case, mainly Mountain maple) that characterize sites like those in this study tend to prevent adequate recruitment and growth of conifer regeneration to successfully allow transition toward a conifer-dominated composition [10,42]. In the spectrum of boreal mixed-wood compositions and dynamics presented by Bergeron et al. [1] (Figure 3), these stands somewhat aptly fall into the "no conifer regeneration" dynamics pattern. As stated in the introduction, the operational partial harvesting of these even-aged stands was primarily intended to delay their final harvest rather than transiting them to conifer-dominated mixed-woods. As such, while reaffirming the "warnings" of MacDonald et al. [28], not all our hypotheses were confirmed.

4.1. Stand Merchantable Basal Area Proportion 7–19 Years after PC and 13–19 Years after CPRS

Post-harvest BA ratio (to total) of merchantable (DBH ≥ 9.1 cm) aspen in 2017 was 26% higher than pre-harvest BA ratio in CPRS sites, whereas the increase was less in PC and Cntrl sites, at about 5%. This could result from the high abundance of aspen in the study sites prior to harvesting, in which CPRSs, through providing heat and full sunlight, favored the vigorous growth of pre-established aspen root suckers and promoted their recruitment to larger DBH size classes [10,14]. Indeed, compared to seedlings and small saplings, large saplings (> 4 m high at harvest), with higher light requirement for survival [43], are likely benefiting more from increased light availability to grow and turn to crop trees [44–46], although they might be more prone to windfall [47]. Tree removal 7–19 years following PCs did not promote the growth of residual aspen trees and regenerations, which led to an increase in commercial aspen BA ratio comparable to Cntrls (i.e., 5%), most likely due to insufficient light and heat supplement into small harvesting openings [13,23], as well as further decrease in light availability induced by crown development of residual trees following PC [45].

Merchantable BA of white birch, balsam fir and white spruce, 7–19 years following harvest, was significantly less in CPRS stands only, whereas PCs could maintain the BA proportion of all species other than aspen comparable to Cntrls. The low abundance of advanced regenerations of those species under aspen canopy [10,48,49], on the one hand, and small PC-gaps that maintain growth dynamics of tree species similar to unharvested sites [1,19,50], on the other hand, might explain these results. In addition, the low BA proportion of these three species might be the outcome of the lower growth rate of birch compared to aspen [10,51,52], as well as approximately 5–10 years delay in the recruitment of slow-growing balsam fir and white spruce, compared to intolerant hardwoods [10,53]. The high competition from herbs and woody shrubs, which massively occupy harvest openings [54], may further limit the growth of small conifers and hardwoods saplings and seedlings [10,42]. Finally, the zero merchantable basal area of black spruce, jack pine and white cedar 13–19 years after CPRS is likely related to very shade-tolerance and slow growth of white cedar (which pre-established stems would still be seedlings or saplings 13–19 years after harvesting), and to the fire-dependent serotinous cones of jack pine and semi-serotinous cones of black spruce [10,55,56]. Since every study site originated from a fire that occurred in 1923 and given the slow growth rate of conifer species relative to birch and aspen, no newly established regeneration of jack pine and very few regeneration of black spruce and white cedar were established at the time of harvest. Besides, due to the competition for light, pre-established seedlings and saplings did not have sufficient time to grow to commercial size (DBH ≥ 9.1 cm).

4.2. Effects of Partial Cutting on Regeneration Abundance of Conifers (H1) and Aspen (H2)

Our first hypothesis concerning the positive effect of partial cutting on conifer abundance, relative to CPRS, was partially validated in that seedling abundance of both balsam fir and white spruce were significantly higher in PCs; however, both causal factors that we assumed to be at play (survival of advanced regeneration and post-treatment recruitment) do not appear to be responsible for the effect. Results showed that densities of conifer (primarily balsam fir) seedlings in PCs, similar to those in Cntrls, were not due to seedling recruitment as a result of higher residual conifer stems in the canopy but rather to higher treatment survival of advanced regeneration relative to the CPRS treatment. This corroborates results presented by Bose et al. [57], who demonstrated that low-intensity partial harvesting tends to maintain natural regeneration dynamics similar to those of unharvested stands. Presence of all other conifer species was negligible in the understory and, given generally low values, we hesitate to emphasize the significance of higher densities of white spruce in the partial cutting treatment relative to both CPRS and Cntrls. Despite relatively high survival of advance fir regeneration in partial cuts, the interim period between harvesting and the post-harvest inventory (7–19 years) was too short to reveal any significant recruitment of fir into the sapling layer. Working in similar stands, Bourgeois et al. [58] observed, in the short-term, a linear height and diameter growth response of balsam fir to canopy opening. Also, in their study, Beaudet et al. [59] modeled variable harvest intensities and spatial configurations and stated that 45–65% uniform partial cuts as well as 30% strip and gap cuts can accelerate the growth responses of shade-tolerant conifers (e.g., balsam fir). This would explain the low recruitment of fir saplings in our partially harvesting stands, where approximately 31% of BA was removed, in a form of commercial thinning.

Concerning our second hypothesis, as expected and reported elsewhere [14,32,60], low-retention harvesting in mixed stands containing trembling aspen generally has the compounded effect of (1) destroying more advanced conifer regeneration and understory vegetation than higher-retention cutting and (2) strongly stimulating suckering of aspen. In this study, similarly low values in "seedling" abundances of aspen in the Cntrls and CPRS are the result of two different dynamics: while the intact aspen-dominated canopies and low understory light levels in Cntrls inhibited root suckering, the short-term dynamics of prolific suckering, high photosynthetic efficiency and fast growth of aspen under full sunlight of the CPRS treatment [3,61] resulted in strong suckering immediately following harvesting. This regeneration process occurred prior to the 13–19-year interval between CPRS treatments and sampling in 2017, but the subsequent effects, that is, low abundance of "seedlings" (DBH < 1 cm) and high recruitment of the initial suckering cohort into the sapling layer are evident. Competition in the shrub and herb layers may also have limited aspen recruitment after the initial pulse of suckering in the CPRS treatment [1,31,62].

That aspen seedling densities were higher in the partial cutting treatment and sapling values intermediate between CPRS and Cntrls demonstrates, as with many other biotic response variables [26], that partial cutting tends to generate effects, which fall between those of unharvested controls and high canopy removal treatments. Partial overstory removal initially creates growing space that provides more resources and thus a less competitive environment than a fully closed canopy [63,64]. These conditions can favor production of aspen suckers, even in small openings [1,53,65], although sucker survival and recruitment into sapling-size may be limited. This suggests, in the marginal understory growing environments of low-intensity partial cuts, a cyclical process of annual aspen suckering, then vigor loss and mortality, unless more favorable growing conditions occur. Sample sizes of other species (jack pine, black spruce, white birch, white cedar) were small, so the discussion focusses on trembling aspen, balsam fir and occasionally white spruce.

Different factors, such as the availability of seed sources, established regeneration prior to harvest and favourable establishment conditions, might influence the regeneration abundance of tree species [10,21,53]. Since tree retention level and spatial configuration of harvesting can control the density and proximity of residual trees within harvested blocks (individual stems and/or patches) and neighboring uncut sites, harvesting can influence the availability of seed sources, distribution and quality of germination substrates and seed dispersal distances [21,27]. Solarik et al. [66] found shorter seed dispersal distances, especially for relatively heavy-seeded conifers, in partial cuts as a result of reduced wind speed under intact stands. Partial overstorey removal in PCs provides more light and nutrients [63,64], in which new seeds can germinate and survive under less competition. Balsam fir had the highest seedling density 7–19 years after treatment. Also, compared to CPRS, fir seedling density was significantly higher in PCs. Our results corroborate those of Prévost and Pothier

[13], who found a very high abundance of coniferous regeneration, especially balsam fir, five years after low-intensity cuts (≤ 50% basal area removal). Balsam fir has shown considerable growth plasticity and adjusts vertical and horizontal (and aerial root) growth allocation as a function of resource availability [58,67]. On the contrary, large openings in CPRSs can induce high recruitment (and competition) of shrubby species, which decrease seed germination and seedling survival of coniferous species [28,42], especially for the slow-growing balsam fir and white spruce [67,68]. Low seed sources and poor seedbed quality (little mineral soil exposure or thin humus layer over mineral soil) could also reduce the generation probability of conifers or enforce more lethal stress for un-germinated seeds [10,27,53]. Moreover, conifers, such as balsam fir and white spruce, may have limited germination due to hydric stress [69]. Although we did not measure soil moisture, we suspect that seedbeds in CPRS were regularly exposed to direct solar radiation, which created drier micro-environmental conditions [13] (compared to Cntrls and PCs), which would reduce seed germination probability.

Furthermore, aspen shoot and leaf blight caused by the pathogen *Venturia macularis*, especially during the wet spring condition [70], might have slowed the growth of young (< 5 years-old) aspen suckers. This pathogen is commonly observed in the study area, especially in young post-harvest stands. In addition, some herbivorous animals such as moose can cause some damages to aspen regenerations as one of their food preferences. Nevertheless, considering the significantly higher sapling density (Table 3), total height and annual height increment of aspen (Figures 1 and 2) in CPRSs than in PCs, we suspect that rapid recruitment of aspen seedlings to saplings layer is the main cause of the absence of seedlings in the regeneration layers in the CPRS treatments. As supported by our results, the parent-tree root system of aspen allows for aspen asexual reproduction (i.e., root suckers) and its fast height growth, resulting in hierarchical superiority to conifers from the early stages of stand developments [21,32]. In agreement with our observation, 10 years after harvesting, Prévost and DeBlois [31] also observed that basal area removal > 65% resulted in aspen regeneration > 200 cm high, whereas conifers' regeneration height was not strongly related to basal area removal percentage and were mostly shorter than 200 cm. Several other studies in the eastern Canadian boreal forests reported that high basal area removal (> 50% basal area) would increase the abundance of natural regeneration of aspen [13,16,22], although lower canopy retention could also favor aspen and shrubs to the detriment of conifer regeneration [13,32,59].

It is worth mentioning that the time necessary for post-fire, aspen-dominated stands to transition toward more mixed-conifer compositions is highly variable [1,21]. The passage of fire generally kills all conifer regeneration in the understory so balsam fir and white spruce recruitment is only possible if nearby cone-bearing trees survive and disperse seed in the ensuing years and decades [1,10]. Moreover, even though fir and spruce may establish from seed at the same time as faster growing intolerant hardwoods, they are generally rapidly overtopped and grow slowly in low-light conditions in developing deciduous stands for a long period of time [10,21].

4.3. Effect of Position Relative to Machinery Trails on Density and Height of Conifers (H3, H4) and Trembling Aspen (H5, H6)

Because we anticipated lower harvest-related mortality of advanced conifer regeneration off machinery trails, we expected that densities would be higher (H3), in which the advanced regeneration would compose a greater part of the conifer regeneration layer, and therefore the mean height of seedlings would be greater (H4) in these positions. This, however, was not the case in this study. No differences in either conifer (balsam fir) density or mean height were observed in off-trail positions compared to trail positions, and in both partial cuts and CPRS. In fact, although not significant, balsam fir regeneration tended to be higher off trails in partial cuts and CPRSs. Working in cut-overs following CPRS harvesting of conifer-dominated stands, Harvey and Brais [19] observed significantly higher densities of primarily pre-established black spruce and balsam fir regeneration between trails, and, on the contrary, high densities of eastern larch that seeded in the disturbed substrate in trails. On machinery trails, harvest-related damages, such as root compaction and bark abrasion [71], soil disturbance [15], sun exposure and consequent water stress [20], as well as greater height of aspen and other grasses than off trails, as discussed later, suggest a higher resources competition that could lead to increased mortality risk of fir regeneration.

Although we anticipated higher aspen seedling density on machinery trails as a result of local soil disturbance and greater canopy opening (H5), this was only validated for partial cuts. Again, because our sampling year, 2017, fell 13 to 19 years post-CPRS, we did not capture the shorter-term regeneration dynamics that consisted of a massive initial pulse of suckering followed by both rapid growth of surviving stems into sapling size and heavy mortality in the interim period [14,57,72]. Since aspen is a shade-intolerant species that generally regenerates locally through root suckering [10], combined effects of overstory removal, which increases light penetration to forest floor [3,61], and soil disturbances [60,73] on machinery trail potentially stimulates aspen suckering. Timber harvesting generally causes soil disturbance and compaction [74,75], and the level of disturbance depends on several factors, such as harvesting season, moisture content of soil, as well as type and weight of machinery and number of machinery passes [76]. Soil compaction due to machinery may reduce soil macro-porosity, aeration and drainage through increasing density and strength among soil particles, which restrict root growth and activities [51], and consequently, aspen regeneration on machinery trails [77,78]. However, in some cases, when the soil texture is fine or the viscosity of soil water is low, soil disturbances might allow for better rutting and alleviate water stress in regenerating aspen suckers through increasing soil water-holding capacity [79]. On machinery trail, machinery possibly favored aspen suckers by (1) destroying competing vegetation, especially shrubs and pre-existing advanced coniferous regeneration [80], (2) increasing soil temperature and nutrient availability [60] and (3) main stem removal and root damage/rutting that triggers suckering [79]. Moreover, in partial cuts, residual trees near machinery trails (i.e., off trails) often have reduced growth and survival probabilities because of limited water uptake capability induced by root damage and impaired root development [76,81,82]. This reduced growth and survival may further stimulate aspen suckering and reduce the shading and competition effect on aspen regeneration from individual trees near the PCs machinery trail borders.

Canopy removal by clear-cutting induces greater height increment of intolerant hardwoods, and more specifically, aspen, compared to unharvested and partial cuts (< 61% basal area removal) [14]. Clear-cutting, like fire, generally creates both physiological (hormonal) and environmental conditions favorable to initiation, growth and survival of aspen suckers, mainly through increased light availability and soil temperature [29,83,84]. When light levels are at least 30% of full sunlight (observed in ≥ 61% basal area cut sites), the majority of aspen regeneration can recruit to 1–2 m height class within two years after harvesting [14], as evident in the CPRS treatment on and off machinery trails (Figure 1). However, contrary to studies reporting lower total height and height growth of aspen on disturbed soils of machinery trails [77,78,85], we did not note any significant effect of positioning (on and off machinery trails) on aspen height and height increment (Figures 1 and 2). This may be due in part to the fact that we limited the size class of stems included in this protocol.

4.4. Influence of Basal Area and Germination Substrates on Seedling Abundance

Pre-harvest basal area of mature aspen trees showed significantly positive correlations with both total hardwoods (and aspen alone) and conifer (balsam fir) seedling abundance. While the positive correlation for aspen was to be expected, the relationship with fir seedling abundance is less clear. The positive influence of pre-harvest aspen basal area on coniferous (balsam fir) seedling abundance may be the result of reduced competition from other understory vegetation, such as grasses, forbs or shrubs [1,68]. That said, high shrub abundance in natural, and presumably silvicultural canopy gaps, can decrease light availability at the forest floor and limit conifer regeneration [43,67,68]. Several studies in the region have shown that conifer regeneration can establish around the same time as aspen establishment, up to 10 years delay following wildfire [3,7,10]; subsequently, balsam fir constantly and abundantly recruits, peaking at around 75 years after stand initiation. Considering the age of stands in this study, relatively high seedling abundance of balsam fir is therefore to be expected.

A small but significant negative relationship between post-harvest aspen basal area and conifer seedling abundance, which was specifically significant for balsam fir, was also detected. Indeed, the post-harvest species composition of the mixed-woods dominated by aspen critically affects softwood regeneration [86]. As discussed earlier, the post-harvest superior abundance of aspen, especially in high-intensity cuts, may restrict conifer establishment and growth through increased competition [30,87].

Our results showed that the abundance of hardwood seedlings increased with an increase in the pre-harvest basal area of balsam fir. On rich, moist sites of the boreal forests, especially in the western mixed-wood forest, aggressive grasses such as bluejoint (*Calamagrostis canadensis*) can expand and take over potential conifer seedbeds within 2–3 years and seriously hamper tree colonization and establishment [62,88]. The high presence of balsam fir, on our 75-year-old stands prior to harvest [10], requiring moisture [3] would probably restrict the invasion of such grasses into canopy gaps created by the mortality of mature aspen trees and be a reason of positive correlation between aspen regeneration abundance and fir basal area.

Germination substrates (e.g., mineral soil exposure, type of litter and quantity and quality of woody debris) play an important role in natural regeneration establishment [89]. Pearson's correlation analyses indicated a significantly positive effect of well-decomposed woody debris on the seedling abundance of both deciduous and coniferous species. In accordance with our result, well-decomposed downed deadwood provides a favorable substrate for seedling recruitment of hardwoods, particularly white birch, and conifers, particularly white cedar and white spruce [7,24,25,90]. Higher seedling establishment on well-decayed wood has been attributed to low resistance to root penetration [91], more stable water availability, thinner moss cover and the raised position compared to the forest floor [92,93].

Regarding litter types, hardwood seedling abundance, especially aspen, was negatively correlated to the ground cover of needle (i.e., coniferous) litter. Decomposition rates are generally lower for coniferous litter than deciduous litter [94]. Lower aspen recruitment on needle litter may be attributed to an insulating effect of conifer litter cover on aspen roots that would reduce suckering [60,95], or simply that aspen root density may be lower under standing conifers. Coniferous litter that rapidly dries out may also reduce aspen suckering [60]. In contrast, coniferous seedling abundance, essentially balsam fir, was positively and negatively correlated to coniferous litter and deciduous litter respectively, results that are supported by Côté and Bélanger [96], Greene et al. [21] and Raymond et al. [89]. Hardwood litter tends to reduce conifer seedling establishment and survivorship by both preventing germinant radicle penetration into the mineral soil and smothering coniferous seedlings [24,93]. Moreover, Clark and Clark [97] and Metcalfe and Grubb [98] reported a negative effect of falling woody branches on the survival of tree regeneration.

5. Conclusions and Silvicultural Implications

The dynamics of forest ecosystems after harvesting are not entirely predictable. The results of this study confirm that the intensity of harvesting in mixed aspen-jack pine stands on rich, mesic sites in the boreal forest influences the relative abundance and growth of the species present. Our results also point to the possibility to limit the regeneration of trembling aspen, through partial cuts, in favor of conifer regeneration, especially balsam fir when already present in the undergrowth. With respect to clear-cuts (CPRSs), partial cuts limit the production, growth and survival of aspen suckers while supporting conifer regeneration establishment and stems' recruitment to upper canopy layers, hence promoting post-treatment softwood recruitment and maintaining mixed-wood stands in the long term.

An ecosystem management approach to managing aspen-dominated mixed-woods should recognize the utility of diversifying silvicultural (harvesting) treatments to match variations in stand conditions and the effects of natural disturbances and succession processes on stand development and forest landscape patterns. Short fire cycles generally pre-empt strong recruitment of late-successional conifers into the canopy layer, so clear-cutting and its variants generally emulate these dynamics as they tend to allow cycling of early successional species. But over longer fire intervals, if fir and spruce seed sources are present, natural processes generally favor the transition to conifer-dominated mixed-woods and this provides at least an ecological justification for applying interventions such as partial cutting and extended rotations to achieve similar ends. Of course, appropriate stand attributes must be present to allow such a transition, and in aspen-jack pine and aspen-dominated mixed-woods, without question, the most important attribute is the presence of a dense layer of advanced conifer regeneration. Without this, especially on rich sites with strong shrub competition, rather than favor conifer recruitment and a transition towards mixed, conifer-dominated compositions, partial cutting followed eventually by a final harvest may simply retard re-initiation of an intolerant hardwood-dominated stand similar to that of our CPRS/clear-cutting treatment. In the current context, economic incentives for partial cutting in aspen-dominated stands are virtually absent, so, from both ecological and economic perspectives, such harvesting practices are best applied where they can be justified on a forest renewal basis. In this context, partial cutting should be part of an overall strategy to maintain a representative proportion of mixed-wood, especially conifer-dominated mixed-wood stands in boreal forest landscapes.

In addition, it would also be important to address the habitat factors that influence the long-term regeneration of coniferous species in aspen-dominated mixed-wood stands. Among these factors, limiting the ground cover of hardwood litter on the soil surface would contribute to increase the abundance of conifer regeneration [21,96]. An interesting approach to managing mixed-wood forests could be to (1) target mixed-wood stands that are most likely to maintain a large portion of conifer species in the canopy, or likely to transit to conifer-dominated mixed-wood stands, and (2) determine an appropriate level of aspen basal area removal, because the more hardwoods are retained in the canopy, the more hardwood litter will be on the forest floor, which means less coniferous regeneration.

Author Contributions: F.N.A. and B.L. designed the study and conducted the analyses. B.L. and K.M. structured and prepared the manuscript. All co-authors reviewed and revised the original draft. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by Mitacs and the Programme Canadien de bourse de la francophonie.

Acknowledgments: We are grateful to Anabelle Gagné for field and lab assistance. The first author acknowledges the support received through the Mitacs accelerate scholarship program and from Norbord Industries, whereas the second author received a scholarship from the Programme Canadien de bourse de la francophonie.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Bergeron, Y.; Chen, H.Y.H.; Kenkel, N.C.; Leduc, A.L.; Macdonald, S.E. Boreal mixedwood stand dynamics: Ecological processes underlying multiple pathways. *For. Chron.* **2014**, *90*, 202–213, doi:10.5558/tfc2014-039.
2. Gauthier, S.; Leduc, A.; Harvey, B.; Bergeron, Y. Les perturbations naturelles et la diversité écosystémique. *Nat. Can.* 2001, *125*, 10–17.
3. Chen, H.Y.H.; Popadiouk, R.V. Dynamics of North American boreal mixedwoods. *Environ. Rev.* **2002**, *10*, 137–166, doi:10.1139/a02-007.
4. Bergeron, Y.; Gauthier, S.; Flannigan, M.; Kafka, V. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* **2004**, *85*, 1916–1932, doi:10.1890/02-0716.
5. Bergeron, Y.; Gauthier, S.; Kafka, V.; Lefort, P.; Lesieur, D. Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry. *Can. J. For. Res.* **2001**, *31*, 384–391, doi:10.1139/x00-178.
6. Bergeron, Y.; Leduc, A.; Harvey, B.; Gauthier, S. Stratégies d'aménagement forestier qui s'inspirent de la dynamique des perturbations naturelles: Considérations à l'échelle du peuplement et de la forêt. *For. Chron.* 1999, *75*, 55–61.
7. Bergeron, Y.; Dubue, M. Succession in the southern part of the Canadian boreal forest. *Vegetatio* **1988**, *79*, 51–63, doi:10.1007/BF00044848.
8. MacDonald, G.B. The case for boreal mixedwood management: An Ontario perspective. *For. Chron.* **1995**, *71*, 725–734, doi:10.5558/tfc71725-6.

9. Bergeron, Y.; Harvey, B. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. *For. Ecol. Manag.* **1997**, *92*, 235–242, doi:10.1016/S0378-1127(96)03924-2.
10. Bergeron, Y. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology* **2000**, *81*, 1500–1516, doi:10.1890/0012-9658(2000)081[1500: SASDIT]2.0.CO;2.
11. Légaré, S.; Bergeron, Y.; Leduc, A.; Paré, D. Comparison of the understory vegetation in boreal forest types of southwest Quebec. *Can. J. Bot.* **2001**, *79*, 1019–1027, doi:10.1139/cjb-79-9-1019.
12. Laquerre, S.; Leduc, A.; Harvey, B.D. Augmentation du couvert en peuplier faux-tremble dans les pessières noires du nord-ouest du Québec après coupe totale. *Écoscience* **2009**, *16*, 483–491, doi:10.2980/16-4-3252.
13. Prévost, M.; Pothier, D. Partial cuts in a trembling aspen—conifer stand: Effects on microenvironmental conditions and regeneration dynamics. *Can. J. For. Res.* **2003**, *33*, 1–15, doi:10.1139/x02-147.
14. Brais, S.; Harvey, B.D.; Bergeron, Y.; Messier, C.; Greene, D.; Belleau, A.; Paré, D. Testing forest ecosystem management in boreal mixedwoods of northwestern Quebec: Initial response of aspen stands to different levels of harvesting. *Can. J. For. Res.* **2004**, *34*, 431–446, doi:10.1139/x03-144.
15. Brais, S.; Work, T.; Robert, É.; O'Connor, C.; Strukelj, M.; Bose, A.; Celentano, D.; Harvey, B. Ecosystem responses to partial harvesting in eastern boreal mixedwood stands. *Forests* **2013**, *4*, 364–385, doi:10.3390/f4020364.
16. Bose, A.K.; Harvey, B.D.; Brais, S. Does partial harvesting promote old-growth attributes of boreal mixedwood trembling aspen (Populus tremuloides Michx.) stands? *For. Ecol. Manag.* **2015**, *353*, 173–186, doi: 10.1016/j.foreco.2015.05.024.
17. Laquerre, S.; Harvey, B.D.; Leduc, A. Spatial analysis of response of trembling aspen patches to clearcutting in black spruce-dominated stands. *For. Chron.* **2011**, *87*, 77–85, doi:10.5558/tfc87077-1.
18. Sims, R.A.; Kershaw, H.M.; Wickware, G.M. *The Autecology of Major Tree Species in the North Central Region of Ontario*; COFRDA report 3302; Canada-Ontario Forest Resource Development Agreement, Canadian Forestry Service: Sault-Ste-Marie, ON, Canada, 1990.
19. Harvey, B.; Brais, S. Effects of mechanized careful logging on natural regeneration and vegetation competition in the southeastern Canadian boreal forest. *Can. J. For. Res.* **2002**, *32*, 653–666, doi:10.1139/x02-006.
20. Parent, S.; Ruel, J.-C. Chronologie de la croissance chez des semis de sapin baumier (Abies balsamea (L.) Mill.) après une coupe à blanc avec protection de la régénération. *For. Chron.* **2002**, *78*, 876–885, doi:10.5558/tfc78876-6.
21. Greene, D.F.; Zasada, J.C.; Sirois, L.; Kneeshaw, D.; Morin, H.; Charron, I.; Simard, M.-J. A review of the regeneration dynamics of North American boreal forest tree species. *Can. J. For. Res.* **1999**, *29*, 824–839, doi:10.1139/x98-112.
22. Pothier, D.; Prévost, M. Photosynthetic light response and growth analysis of competitive regeneration after partial cutting in a boreal mixed stand. *Trees-Struct. Funct.* **2002**, *16*, 365–373, doi:10.1007/s00468-001-0158-y.
23. Burns, R.M.; Honkala, B.H. *Silvics of North America: Volume 2. Hardwoods;* Agriculture Handbook 654; United States Department of Agriculture (USDA), Forest Service: Washigton, DC, USA, 1990.
24. Simard, M.-J.; Bergeron, Y.; Sirois, L. Conifer seedling recruitment in a southeastern Canadian boreal forest: The importance of substrate. *J. Veg. Sci.***1998**, *9*, 575–582, doi:10.2307/3237273.
25. Robert, E.; Brais, S.; Harvey, B.D.; Greene, D. Seedling establishment and survival on decaying logs in boreal mixedwood stands following a mast year. *Can. J. For. Res.* **2012**, *42*, 1446–1455, doi:10.1139/x2012-085.
26. Bose, A.K.; Harvey, B.D.; Brais, S.; Beaudet, M.; Leduc, A. Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: A review. *Forestry* **2014**, *87*, 11–28, doi:10.1093/forestry/cpt047.
27. Asselin, H.; Fortin, M.-J.; Bergeron, Y. Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. *For. Ecol. Manag.* **2001**, *140*, 29–37, doi:10.1016/S0378-1127(00)00273-5.
28. MacDonald, G.B.; Cherry, M.L.; Thompson, D.J. Effect of harvest intensity on development of natural regeneration and shrubs in an Ontario boreal mixedwood stand. *For. Ecol. Manag.* **2004**, *189*, 207–222, doi: 10.1016/j.foreco.2003.08.010.

29. Prévost, M.; Dumais, D.; Pothier, D. Growth and mortality following partial cutting in a trembling aspen–conifer stand: Results after 10 years. *Can. J. For. Res.* **2010**, *40*, 894–903, doi:10.1139/X10-036.
30. Doucet, R. La Régénération préétablie dans les peuplements forestiers naturels au Québec. *For. Chron.* **1988**, *64*, 116–120, doi:10.5558/tfc64116-2.
31. Prévost, M.; DeBlois, J. Shelterwood cutting to release coniferous advance growth and limit aspen sucker development in a boreal mixedwood stand. *For. Ecol. Manag.* **2014**, *323*, 148–157, doi: 10.1016/j.foreco.2014.03.015.
32. Gradowski, T.; Lieffers, V.J.; Landhäusser, S.M.; Sidders, D.; Volney, J.; Spence, J.R. Regeneration of Populus nine years after variable retention harvest in boreal mixedwood forests. *For. Ecol. Manag.* **2010**, *259*, 383–389, doi: 10.1016/j.foreco.2009.10.033.
33. Saucier, J.P.; Robitaille, A.; Grondin, P.; Bergeron, J.F.; Gosselin, J. *Les Régions Écologiques du Québec MÉRidional*; Ministère des Ressources Naturelles et de la Faune, Direction des Inventaires Forestiers: Quebec, QC, Canada, 2011.
34. Environment Canada. Available online: http://www.climate.weatheroffice.ec.gc.ca (accessed on 28 May 2019).
35. Vincent, J.-S.; Hardy, L. Dynamique et paléogéographie de l'inlandsis laurentidien. *gpq* **1977**, *31*, 357–372, doi:10.7202/1000283ar.
36. Harvey, B.; Leduc, A. *Plan Général D'aménagement-Forêt D'enseignement et de Recherche du lac Duparquet* (*1998–2023*); Groupe de Recherche en Écologie Forestière (UQAM) and Unité de Recherche et de Développement forestier de l'Abitibi-Témiscamingue (UQAT), Quebec, QC, Canada, 1999; p. 153.
37. Dansereau, P.-R.; Bergeron, Y. Fire history in the southern boreal forest of northwestern Quebec. *Can. J. For. Res.* **1993**, *23*, 25–32, doi:10.1139/x93-005.
38. Morin, H.; Laprise, D.; Bergeron, Y. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. *Can. J. For. Res.* **1993**, *23*, 1497–1506, doi:10.1139/x93-189.
39. Campbell, E.M.; David, A. MacLean; Yves Bergeron. The Severity of Budworm-Caused Growth Reductions in Balsam Fir/Spruce Stands Varies with the Hardwood Content of Surrounding Forest Landscapes. *For. Sci.* **2008**, *54*, 195–205, doi:10.1093/forestscience/54.2.195.
40. Soil Classification Working Group. *The Canadian System of Soil Classification*, 3rd ed.; Publ. 1646: Ottawa, ON, Canada, 1998; ISBN o-660-17404-9.
41. SAS. *JMP version 10*; SAS Institute Inc.: Cary, NC, Canada, 2019.
42. Vincent, A.B. Growth habits of mountain maple in the Ontario clay belt. *For. Chron.* **1965**, *41*, 330–344, doi:10.5558/tfc41330-3.
43. Messier, C.; Parent, S.; Bergeron, Y. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *J. Veg. Sci.* **1998**, *9*, 511–520, doi:10.2307/3237266.
44. Pothier, D.; Doucet, R.; Boily, J. The effect of advance regeneration height on future yield of black spruce stands. *Can. J. For. Res.* **1995**, *25*, 536–544, doi:10.1139/x95-061.
45. Man, R.; Kayahara, G.J.; Rice, J.A.; MacDonald, G.B. Eleven-year responses of a boreal mixedwood stand to partial harvesting: Light, vegetation, and regeneration dynamics. *For. Ecol. Manag.* **2008**, *255*, 697–706, doi: 10.1016/j.foreco.2007.09.043.
46. Bose, A.K.; Brais, S.; Harvey, B.D. Trembling aspen (Populus tremuloides Michx.) volume growth in the boreal mixedwood: Effect of partial harvesting, tree social status, and neighborhood competition. *For. Ecol. Manag.* **2014**, *327*, 209–220, doi: 10.1016/j.foreco.2014.05.003.
47. Mitchell, S.J. The windthrow triangle: A relative windthrow hazard assessment procedure for forest managers. *For. Chron.***1995**, *71*, 446–450, doi:10.5558/tfc71446-4.
48. Bouchard, M.; Kneeshaw, D.; Bergeron, Y. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. *For. Ecol. Manag.* **2005**, *204*, 297–313, doi: 10.1016/j.foreco.2004.09.017.
49. Moulinier, J.; Lorenzetti, F.; Bergeron, Y. Effects of a forest tent caterpillar outbreak on the dynamics of mixedwood boreal forests of eastern Canada. *Écoscience* **2013**, *20*, 182–193, doi:10.2980/20-2-3588.
50. Lieffers, V.J.; Messier, C.; Burton, P.J.; Ruel, J.C.; Grover, B.E. *Naturebased Silviculture for Sustaining a Variety of Boreal Forest Values*; Chapter 13; Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L., Eds.; Towards Sustainable Management of the Boreal Forest, NRC Research Press, Canada, 2003; pp. 480–530.
51. Rowe, J.S. Critique of Some Vegetational Concepts as Applied to Forests of Northwestern Alberta. *Can. J. Bot.* **1961**, *39*, 1007–1017, doi:10.1139/b61-086.

52. Caners, R.T.; Kenkel, N.C. Forest stand structure and dynamics at Riding Mountain National Park, Manitoba, Canada. *Community Ecol.* **2003**, *4*, 185–204, doi:10.1556/ComEc.4.2003.2.6.
53. Cumming, S.G.; Schmiegelow, F.K.A.; Burton, P.J. Gap dynamics in boreal aspen stands: Is the forest older than we think? *Ecol. Appl.* **2000**, *10*, 744–759, doi:10.1890/1051-0761(2000)010[0744: GDIBAS]2.0.CO;2.
54. Perala, D.A. Prescribed Burning in an Aspen-Mixed Hardwood Forest. *Can. J. For. Res.* **1974**, *4*, 222–228, doi:10.1139/x74-033.
55. Ilisson, T.; Chen, H.Y.H. The direct regeneration hypothesis in northern forests. *J. Veg. Sci.* **2009**, *20*, 735–744, doi:10.1111/j.1654-1103.2009.01066. x.
56. Kurkowski, T.A.; Mann, D.H.; Rupp, T.S.; Verbyla, D.L. Relative importance of different secondary successional pathways in an Alaskan boreal forest. *Can. J. For. Res.* **2008**, *38*, 1911–1923, doi:10.1139/X08-039.
57. Bose, A.; Nelson, A.S.; Olson, M. Growth and mortality response of forest regeneration to partial harvesting varies by species shade tolerance. *Can. J. For. Res.* **2020**, 0, 0, doi:10.1139/cjfr-2020-0022.
58. Bourgeois, L.; Messier, C.; Brais, S. Mountain maple and balsam fir early response to partial and clear-cut harvesting under aspen stands of northern Quebec. *Can. J. For. Res.* **2004**, *34*, 2049–2059, doi:10.1139/x04-080.
59. Beaudet, M.; Harvey, B.D.; Messier, C.; Coates, K.D.; Poulin, J.; Kneeshaw, D.D.; Brais, S.; Bergeron, Y. Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: A modelling approach. *For. Ecol. Manag.* **2011**, *261*, 84–94, doi: 10.1016/j.foreco.2010.09.033.
60. Frey, B.R.; Lieffers, V.J.; Landhäusser, S.M.; Comeau, P.G.; Greenway, K.J. An analysis of sucker regeneration of trembling aspen. *Can. J. For. Res.* **2003**, *33*, 1169–1179, doi:10.1139/x03-053.
61. Frelich, L.E.; Reich, P.B. Spatial Patterns and Succession in a Minnesota Southern-Boreal Forest. *Ecol. Monogr.* **1995**, *65*, 325–346, doi:10.2307/2937063.
62. Landhäusser, S.M.; Mulak, T.L.; Lieffers, V.J. The effect of roots and litter of Calamagrostis canadensis on root sucker regeneration of Populus tremuloides. *Forestry* **2007**, *80*, 481–488, doi:10.1093/forestry/cpm035.
63. Schneider, R.; Zhang, S.Y.; Swift, D.E.; Bégin, J.; Lussier, J.-M. Predicting selected wood properties of jack pine following commercial thinning. *Can. J. For. Res.* **2008**, *38*, 2030–2043, doi:10.1139/X08-038.
64. Ashton, M.S.; Kelty, M.J. The practice of silviculture. *Applied Forest Ecology*, 10th ed.; Wiley: Hoboken, NJ, USA, 2017; ISBN 9781119270959.
65. Bretfeld, M.; Doerner, J.P.; Franklin, S.B. Radial growth response and vegetative sprouting of aspen following release from competition due to insect-induced conifer mortality. *For. Ecol. Manag.* **2015**, *347*, 96–106, doi: 10.1016/j.foreco.2015.03.006.
66. Solarik, K.A.; Volney, W.J.A.; Lieffers, V.J.; Spence, J.R.; Hamann, A. Factors affecting white spruce and aspen survival after partial harvest. *J. Appl. Ecol.* **2012**, *49*, 145–154, doi:10.1111/j.1365-2664.2011.02089.x.
67. Kneeshaw, D.; Bergeron, Y.; Grandpré, L. de. Early response of Abies balsamea seedlings to artificially created openings. *J. Veg. Sci.* **1998**, *9*, 543–550, doi:10.2307/3237270.
68. Kneeshaw, D.D.; Bergeron, Y. Ecological factors affecting the abondance of advance regeneration in Quebec's southwestern boreal forest. *Can. J. For. Res.* **1996**, *26*, 888–898, doi:10.1139/x26-097.
69. Thomas, P.A.; Wein, R.W. Water availability and the comparative emergence of four conifer species. *Can. J. Bot.* **1985**, *63*, 1740–1746, doi:10.1139/b85-244.
70. Ostry, M.E.; United States. Forest Service. *A Guide to Insect, Disease, and Animal Pests of Poplars*; US Department of Agriculture, Forest Service, USA, **1989**.
71. Thorpe, H.C.; Thomas, S.C.; Caspersen, J.P. Tree mortality following partial harvests is determined by skidding proximity. *Ecol. Appl.* **2008**, *18*, 1652–1663, doi:10.1890/07-1697.1.
72. Bose, A.K.; Harvey, B.D.; Brais, S. Sapling recruitment and mortality dynamics following partial harvesting in aspen-dominated mixedwoods in eastern Canada. *For. Ecol. Manag.* **2014**, *329*, 37–48, doi: 10.1016/j.foreco.2014.06.004.
73. Stone, D.M.; Elioff, J.D. Soil disturbance and aspen regeneration on clay soils: Three case histories. *For. Chron.* **2000**, *76*, 747–752, doi:10.5558/tfc76747-5.
74. Grigal, D.F. Effects of extensive forest management on soil productivity. *For. Ecol. Manag.* **2000**, *138*, 167–185, doi:10.1016/S0378-1127(00)00395-9.
75. Brais, S. Persistence of Soil Compaction and Effects on Seedling Growth in Northwestern Quebec. *Soil Sci. Soc. Am. J.* **2001**, *65*, 1263–1271, doi:10.2136/sssaj2001.6541263x.

76. Puettmann, K.J.; D'Amato, A.W.; Arikian, M.; Zasada, J.C. Spatial impacts of soil disturbance and residual overstory on density and growth of regenerating aspen. *For. Ecol. Manag.* **2008**, *256*, 2110–2120, doi: 10.1016/j.foreco.2008.07.037.
77. Stone, D.M.; Kabzems, R. Aspen development on similar soils in Minnesota and British Columbia after compaction and forest floor removal. *For. Chron.* **2002**, *78*, 886–891, doi:10.5558/tfc78886-6.
78. Mundell, T.L.; Landhäusser, S.M.; Lieffers, V.J. Root carbohydrates and aspen regeneration in relation to season of harvest and machine traffic. *For. Ecol. Manag.* **2008**, *255*, 68–74, doi:10.1016/j.foreco.2007.08.021.
79. Powers, R.F. *On the Sustainable Productivity of Planted Forests;* **1999**, New Forests, 17, 263–306.
80. Man, R.; Rice, J.A.; MacDonald, G.B. Five-year light, vegetation, and regeneration dynamics of boreal mixedwoods following silvicultural treatments to establish productive aspen–spruce mixtures in northeastern Ontario. *Can. J. For. Res.* **2010**, *40*, 1529–1541, doi:10.1139/X10-088.
81. Startsev, A.D.; McNabb, D.H. Skidder traffic effects on water retention, pore-size distribution, and van Genuchten parameters of boreal forest soils. *Soil Sci. Soc. Am. J.* **2001**, *65*, 224–231, doi:10.2136/sssaj2001.651224x.
82. Komatsu, H.; Katayama, A.; Hirose, S.; Kume, A.; Higashi, N.; Ogawa, S.; Otsuki, K. Reduction in soil water availability and tree transpiration in a forest with pedestrian trampling. *Agric. For. Meteorol.* **2007**, *146*, 107–114, doi: 10.1016/j.agrformet.2007.04.014.
83. Steneker, G.A. Factors affecting the suckering of trembling aspen. *For. Chron.***1974**, *50*, 32–34, doi:10.5558/tfc50032-1.
84. Fraver, S.; Wagner, R.G.; Day, M. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. *Can. J. For. Res.* **2002**, *32*, 2094–2105, doi:10.1139/x02-131.
85. Alban, D.H.; Host, G.E.; Elioff, J.D.; Shadis, D.A. *Soil and Vegetation Response to Soil Compaction and Forest Floor Removal after Aspen Harvesting*; Research Paper NC-315. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station, USA, 1994.
86. Greene, D.F.; Kneeshaw, D.D.; Messier, C.; Lieffers, V.; Cormier, D.; Doucet, R.; Coates, K.D.; Groot, A.; Grover, G.; Calogeropoulos, C. Modelling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir). *For. Chron.* **2002**, *78*, 281–295, doi:10.5558/tfc78281-2.
87. Huffman, R.D.; Fajvan, M.A.; Wood, P.B. Effects of residual overstory on aspen development in Minnesota. *Can. J. For. Res.* **1999**, *29*, 284–289, doi:10.1139/x98-202.
88. Landhäusser, S.M.; Lieffers, V.J. Growth of Populus tremuloides in association with Calamagrostis canadensis. *Can. J. For. Res.* **1998**, *28*, 396–401, doi:10.1139/x98-006.
89. Raymond, P.; Ruel, J.-C.; Pineau, M. Effet d'une coupe d'ensemencement et du milieu de germination sur la régénération des sapinières boréales riches de seconde venue du Québec. *For. Chron.* **2000**, *76*, 643–652, doi:10.5558/tfc76643-4.
90. Taylor, A.R.; Chen, H.Y.H. Multiple successional pathways of boreal forest stands in central Canada. *Ecography* **2011**, *34*, 208–219, doi:10.1111/j.1600-0587.2010.06455. x.
91. Narukawa, Y.; Iida, S.; Tanouchi, H.; Abe, S.; Yamamoto, S.-I. State of fallen logs and the occurrence of conifer seedlings and saplings in boreal and subalpine old-growth forests in Japan. *Ecol. Res.* **2003**, *18*, 267–277, doi:10.1046/j.1440-1703.2003.00553. x.
92. Harmon, M.E.; Franklin, J.F. Tree Seedlings on Logs in Picea-Tsuga Forests of Oregon and Washington. *Ecology* **1989**, *70*, 48–59, doi:10.2307/1938411.
93. Simard, M.-J.; Bergeron, Y.; Sirois, L. Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. *Can. J. For. Res.* **2003**, *33*, 672–681, doi:10.1139/X02-204.
94. Berg, B.; McClaugherty, C. Plant litter. *Decomposition, Humus Formation, Carbon Sequestratio*n, 3rd ed.; Springer: Heidelberg, Germany, 2014; ISBN 9783642388200.
95. Lavertu, D.; Mauffette, Y.; Bergeron, Y. Suckering success of aspen (Populus tremuloides Michx.) in relation to stand age and soil disturbance. *J. Veg. Sci.* **1994**, *5*, 561–568.
96. Côté, S.; Bélanger, L. Variations de la régénération préétablie dans les sapinières boréales en fonction de leurs caractéristiques écologiques. *Can. J. For. Res.* **1991**, *21*, 1779–1795, doi:10.1139/x91-246.

97. Clark, D.B.; Clark, D.A. The Role of Physical Damage in the Seedling Mortality Regime of a Neotropical Rain Forest. *Oikos* **1989**, *55*, 225, doi:10.2307/3565426.
98. Metcalfe, D.J.; Grubb, P.J. The responses to shade of seedlings of very small-seeded tree and shrub species from tropical rain forest in Singapore. *Funct. Ecol.* **1997**, *11*, 215–221.