Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1

Seed rain and seedling establishment of *Picea glauca* and *Abies balsamea* after partial cutting in plantations and natural stands

Authors and contact information

Laurent Gagné[1]	Université du Québec à Rimouski, Département de biologie, chimie et géographie, Chaire de recherche sur la forêt habitée, 300 Allée des Ursulines, Rimouski (Québec) G5L 3A1 Email: lgagne@crdbsl.org
Luc Sirois	Université du Québec à Rimouski, Département de biologie, chimie et géographie, Chaire de recherche sur la forêt habitée, 300 Allée des Ursulines, Rimouski (Québec) G5L 3A1 | Email: luc_sirois@uqar.ca
Luc Lavoie	Collectif régional de développement du Bas-Saint-Laurent, 186 rue Lavoie, Rimouski (Québec) G5L 5Z1 | Email: llavoie@crdbsl.org

Key-words : balsam fir, white spruce, seedlings, partial cut, plantation, naturals stands, light, seed rain

[1] Corresponding author and current address: Collectif régional de développement du Bas-St-Laurent, 186 rue Lavoie, Rimouski (Québec), Canada G5L 5Z1 | Telephone: 418-724-6440 #253 | Email: lgagne@crdbsl.org

Abstract: This study documents the conditions associated to white spruce and balsam fir regeneration after partial cutting. Measurements were collected 9 to 30 years after partial cutting in 12 natural fir stands and 5 white spruce plantations. We estimated seed input, measured light reaching the undergrowth, recorded seedlings (<150 cm) and their age on 6 different seedling establishment substrates: mineral soil, moss, rotten wood, litterfall, herbaceous and dead wood. Partial cutting generally favours the establishment and growth of seedlings. The number of fir and spruce seedlings is always greater in natural stands than in plantations, a trend likely associated with the reduced abundance of preferential establishment substrate in the latter. White spruce significantly prefers rotten wood while fir settles on all types of substrates that cover at least 10% of the forest floor. There is a strong relationship between light intensity and the median height of spruce seedlings, but this relationship is non-significant for fir. Seedlings of both species can survive at incident light intensities as low as 3%, but an intensity of 15% or more seems to offer the best growth conditions. The conditions for successful forest regeneration proposed in this study should be applied when the goal is to establish a new stand prior to clear cutting or to convert stand structure.

1. Introduction

The promotion of natural regeneration in forests managed through partial cutting offers several silvicultural, economic [40] and ecological [1] benefits. It provides demographic stability within the stand [1-29-37], decreases reforestation costs [30-40] and diversifies stand structure. The rate of seedlings establishment is subject to regulatory factors related to seed trees [47], quality of substrate for germination and early growth [4-51], and light [35]. Therefore, logging operations in a sexually mature forest stand cause profound changes in the conditions for the establishment of regeneration of valued tree species [4].

First, reduced competition in partially cut stands generally provides larger seed trees able to produce large quantities of viable seeds [14-15-18]. In stands composed of fir and spruce, the selection of trees left standing is of great importance, as spruce regeneration is far more challenging than that of fir [4-23-48-51]. In addition, any type of logging operation modifies the diversity and the quality of substrates on which seeds fall and seedlings eventually grow, notably through logging leftovers (crowns, branches, stumps) remaining on the ground [21]. These decaying woody debris [8] constitute one of the preferential substrates for germination, particularly for Norway spruce (*Picea abies* [25]) and white spruce (*Picea glauca* [52]). Finally, partial cutting increases undergrowth incident light enough to ensure better seedling growth [14-40], but this effect vanishes as residual trees grow [11-28]. When severe shaded conditions persist for too long in the undergrowth, tree seedling mortality rates increase [35], as incident radiation of less than 10% would be unfavourable for the growth in height of seedlings of shade-tolerant tree species like balsam fir (*Abies balsamea* [6-35]) and white spruce (*Picea glauca* [36]).

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1

Spruce plantations are relatively novel ecosystems whose regeneration dynamics are not well known. The effect of seed trees, seedling establishment substrates, and light condition on natural regeneration has rarely been studied in spruce plantations undergoing a partial cut regime [22-50]. In addition, these effects have rarely been compared between natural stands and plantations, although natural fir and spruce-dominated stands [13] and spruce plantations [19] are widespread across North America. Therefore, this study aims to verify, for natural stands and plantations, *i*) whether there is a relationship between seed production and seedling density for balsam fir (Abies balsamea) and white spruce (Picea glauca) depending on stand origin, *ii*) whether partial cutting favours the establishment of regeneration, *iii*) whether certain seedbed substrates favour regeneration more than others depending on stand origin, and *iv*) whether light has an effect on seedling growth several years after partial cutting.

2. Material and methods

2.1 Study sites

This study was conducted at the interface of the balsam fir-yellow birch and the balsam fir-white birch bioclimatic domains in Bas-Saint-Laurent, Quebec [58]. A random selection was made among 24 stands of either naturally occurring fir-dominated stands (n=16) or white spruce plantations (n=8) that were recently thinned. A total of 17 sites were selected, of which 12 were found in natural stands and 5 were found in plantations. Stand age ranged from 37 to 104 years old and the time lapse since partial cut ranged from 8 to 23 years for natural stands and from 8 to 30 years for plantations (Table 1). The partial cuts varied in intensity from low to high, with the proportion of stems removed ranging from 14% to 74%. Naturally occurring stands were mostly composed of balsam fir (hereafter referred to as fir) with a proportion of white spruce (hereafter

 doi:10.20944/preprints201808.0515.v1

referred to as spruce) ranging from 10% to 50%; spruce plantations had a proportion of fir ranging from 0% to 10%. All sites had a site index (SI) greater than 9 m at 25 years.

2.2 Measurements and estimations

For each site, we randomly established 2 sampling units (SU) spaced 30 to 150 m apart, each measuring 200 m^2 (20 m x 10 m) with a buffer zone of 5 m around the perimeter. Each SU was divided into 50 subunits of 4 m^2 (2 m x 2 m). All living trees with a DBH >5.1 cm were identified at the species level, measured (DBH) and mapped using azimuth and distance from a corner of the SU (reference point). In the buffer zone, only spruce with a DBH >10 cm were mapped in order to focus on the potential seed trees of this species. The density ($n.m^{-2}$) of fallen fir and spruce seeds within each 4 m^2 subunit was estimated using Greene's (2000) [18] models. The first model estimates the number of seeds annually produced by each seed tree (Q) as such:

$$[1]\ Q = 3067m^{-0.58}B^{0.92}$$

where m is the mass of a spruce (0.002 g) or fir (0.008 g) seed, and B is seed tree's basal area (m^2) at breast height (1.3 m).

The second model estimates the number of seeds/m^2 scattered on the ground as a function of the distance (x) between a given seed tree and the centroid of each subunit:

$$[2]\ Q_{(x)} = aQe^{-0.15xf^{0.82}}$$

where $Q_{(x)}$ defines the number of seeds scattered per m^2 at a distance x of a seed tree, a is set to 0.25, which corresponds to a forest with medium seed production [18], and f represents the seed's final velocity: 0.65 m/s for spruce and 0.86 m/s for fir [18]. Using these two models, for each

 doi:10.20944/preprints201808.0515.v1

seed tree, we calculated the total number of fallen seeds in each 4 m^2 subunit. These values were compared to the number of spruce and fir seedlings counted in each subunit.

In all subunits, we estimated the percentage of cover of each of the six seedbed types: mineral soil, moss, litterfall, herbaceous, rotten wood and deadwood (corresponding to decomposition classes 3 to 5 and 1 to 2, respectively, according to [8]). Then we determined the age and the number of spruce and fir seedlings per substrate type and height category: 1-10 cm, 11-20 cm, 21-30 cm, 31-50 cm, 51-100 cm and 101-150 cm. The age of seedlings <50 cm was estimated using terminal bud scars while annual growth rings were used for seedlings >50 cm. Age allowed us to differentiate seedlings established before versus after partial cut.

Table 1. Site description in 2009

Origin	**Site**	**Age range of dominant tree** n=6	**Years after partial cut**	**Stem removal**	**BA (m^2/ha)**		**Mean dbh (cm)**		**Stems/ha**	
				%	**spruce**	**fir**	**spruce**	**fir**	**spruce**	**fir**
Natural	1	37-40	10	14.0	–	37	–	15	–	1850
	2	52-65	11	67.7	3	26	20	16	75	1325
	3	51-71	10	45.5	5	38	20	16	150	1800
	4	46-52	9	38.2	4	26	18	15	125	1400
	5	37-52	9	36.9	16	15	15	17	700	775
	6	48-60	9	53.0	2	25	21	16	75	1100
	7	55-74	10	27.9	12	26	20	19	300	875
	8	62-71	9	52.1	5	36	20	14	150	2000
	9	60-85	9	11.6	7	32	19	16	200	1350
	10	60-77	14	73.5	4	26	20	19	75	825
	11	73-104	10	74.0	8	26	25	18	150	975
	12	70-75	23	60.4	7	33	20	18	200	1225
Plantation	13[1]	82	30-15[2]	42.0	30	2	23	6	675	150
	14	57	16–6[2]	52.6	40	–	22	–	950	–
	15	49	8	44.3	34	–	17	–	1475	–
	16	52	19–8[2]	50.0	35	–	22	–	825	–
	17	57	12	65.6	29	–	24	–	650	–

[1] Four SU were carried out in the same plantation
[2]Two partial cuts in plantation; in these cases, only seedlings established after the last partial cut were considered in the analyses.

Photosynthetically active radiation (PAR, µmol photons.m^{-2}.s^{-1}) was measured 60 cm aboveground at the centre of each of the 1700 subunits using a BF-3-type device (Sunshine Sensor; Delta-T Devices BF-3 UM-1.0, Data logger; GP1 v2.1) between 9:00 a.m. and 5:00 p.m. during the months of June, July and August. The light measurement is associated with that of a reference sensor placed in an open environment located less than 500 m away from the sensor located under forest cover in order to calculate percentage of incident light at each measurement location [43].

Finally, natural stand age was assessed by drawing core samples at a height of 30 cm from the ground from three trees randomly selected among the dominant trees in each SU. Plantation age corresponds to the year of reforestation; years when a partial cut occurred in each stand type were traced using information obtained from the state's department of forests' unpublished database.

3. Statistical analyses

3.1 Relationship between the estimated amount of dispersed seeds and the number of seedlings

The relationship between the number of fallen seeds and the number of seedlings of each species was determined using simple linear regression for each stand type. Residue normality was validated using the Shapiro test ($p>0.05$).

3.2 Comparison of density and stocking coefficient of seedlings

For each stand type (natural or plantation), we tested whether partial cutting had a significant effect on the density of seedlings and stocking coefficient for each species. Species, period (before vs after cut) and stand type were considered as fixed variables while site was considered as a random variable. We used generalized linear mixed models (GLMM) to compare seedling density and stocking coefficient between species and between stand types. As the raw data did not have a normal distribution even after transformation, we tested several model distributions: Poisson, zero inflated Poisson, negative binomial and zero inflated negative binomial. Using the Akaike information criterion [57], we determined that the negative binomial model was most parsimonious. When the analysis revealed significant differences between group means, means were compared between periods, between species or between stand types using Tukey's multiple comparison test. Here and in all subsequent analyses where it was required, normality was verified using the Shapiro-Wilk test ($p>0.05$) while homoscedasticity and independence of residuals were verified by visual observation of residuals plotted against predicted values.

3.3 Percentage of seedlings per substrate type

For each species, in each stand, we compared the percentage of total seedlings that established on each substrate type to determine if we could identify preferential substrates for seedling establishment. We used a binomial chi-square to compare percentage of total seedlings established on each substrate with cover of the same substrate. The percentage of the area covered by each type of substrate was compared between plantations and natural stands using a binomial chi-square.

3.4 Relationship between median seedling height and incident light

The relationship between the median height of fir and spruce seedlings that have established after the partial cut and the percentage of light transmitted to the centre of each subunit was estimated using simple linear regression. Residue normality was validated using the Shapiro test ($p>0.05$).

All statistical analyses were performed on R, version 2.15.2, using the "nlme" [44] and "gmodels" [75] libraries.

4. Results

4.1 Relationship between the estimated number of dispersed seeds and the number of seedlings

Our results show that in natural stands there is a close relationship between the estimated number of fallen seeds and the density of fir and spruce seedlings (Fig. 1). The estimated number of dispersed seeds explains 81% and 85% of the variance of fir and spruce seedling density, respectively. For the same amount of seeds, seedling density is 15 to 20 times higher for fir than for spruce. In plantations, the number of fallen seeds explains 51% of the variance of the number of spruce seedlings, but it takes 30 to 40 times as many seeds to reach a spruce seedling density similar to the one measured in natural stands. For fir, the relationship between the number of seeds and seedling density is very weak ($R^2 = 0.04$), and the model is not significant ($p = 0.86$). The estimated number of fir seeds is about 20 times smaller than the estimated number of spruce seeds in plantations, yet the density of fir seedlings is at least 10 times greater than that of spruce seedlings.

 doi:10.20944/preprints201808.0515.v1

4.2 Stocking coefficient and density of seedlings

Partial cuts significantly increase the stocking coefficient (Fig. 2) and the density (Figure 3) of fir seedlings in natural stands, while a significant interaction ($p<0.0001$) between treatment and stand type results in an increase in fir density and stocking coefficient in natural stands and a decrease in plantations. For spruce, partial cuts increase the stocking coefficient and the density of seedlings, especially in natural stands, where both these effects are significant (Fig. 2 and 3). Overall, the stocking coefficient and seedlings density of fir and spruce seedlings are significantly higher in natural stands compared to plantations (Fig. 2), and fir had a significantly higher seedling density than spruce, both in naturally occurring stands and in plantations (Fig. 3).

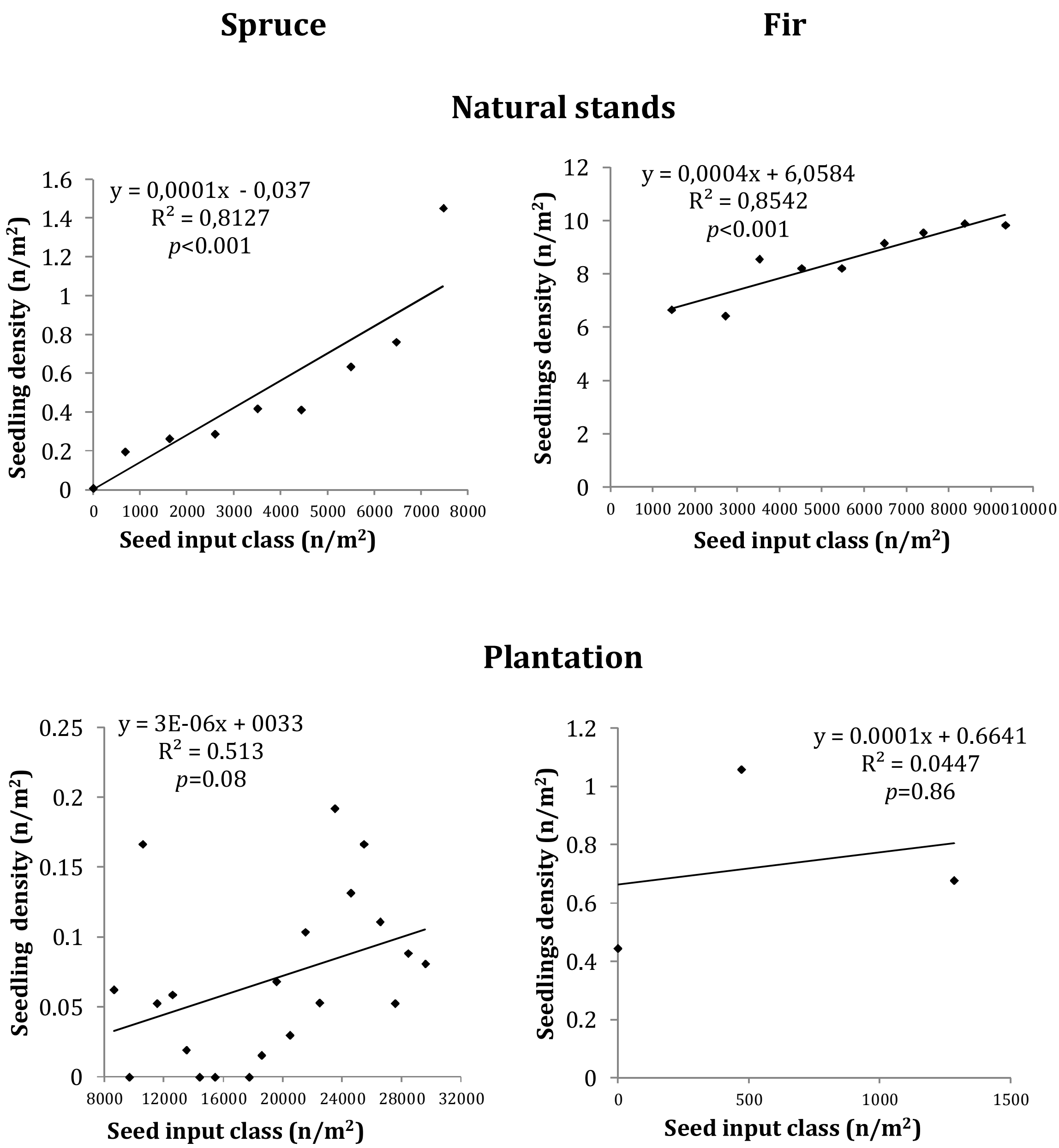


Figure 1. Relationship between spruce and fir seed input and seedling density in natural stands and plantations.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1

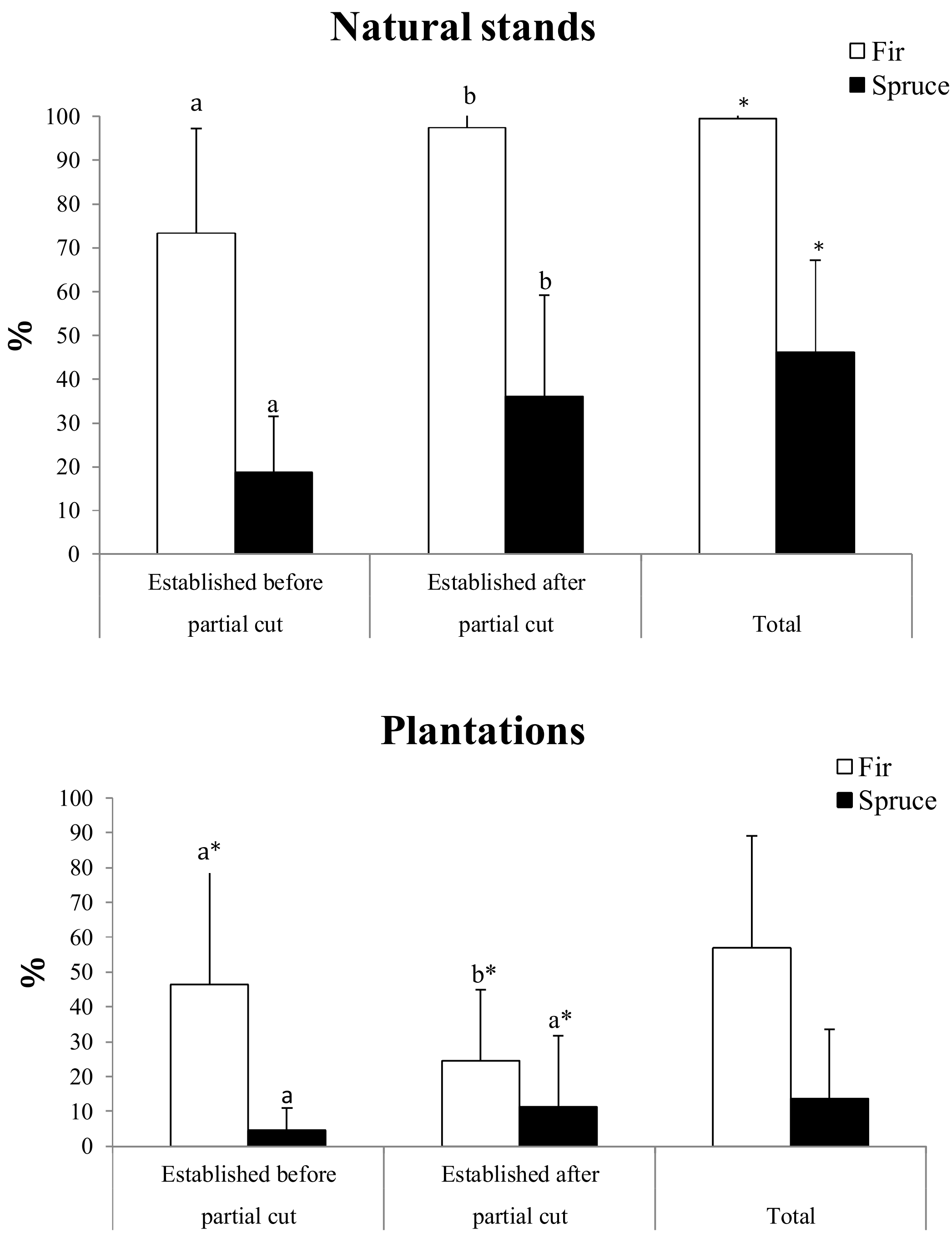
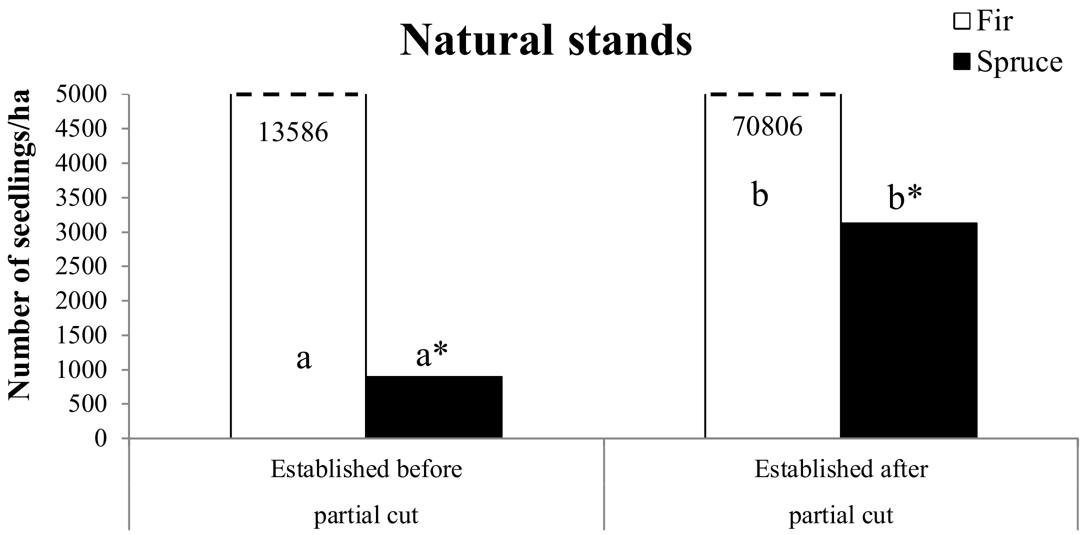


Figure 2. Stocking coefficient (± standard deviation) of fir (white bar) and spruce (black bar) seedlings before and after a partial cut, and total stocking coefficient per species for natural stands and plantations. Lower-case letters indicate a significant difference before and after a partial cut for a given species in a stand type, while asterisks indicate a significant difference between stand types for a given species and period and for total stocking.

 doi:10.20944/preprints201808.0515.v1



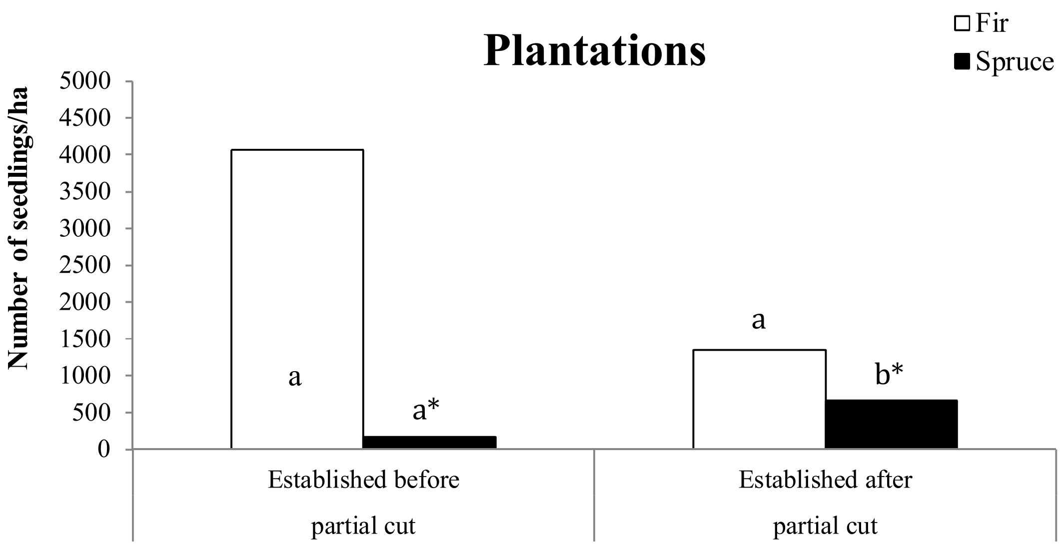


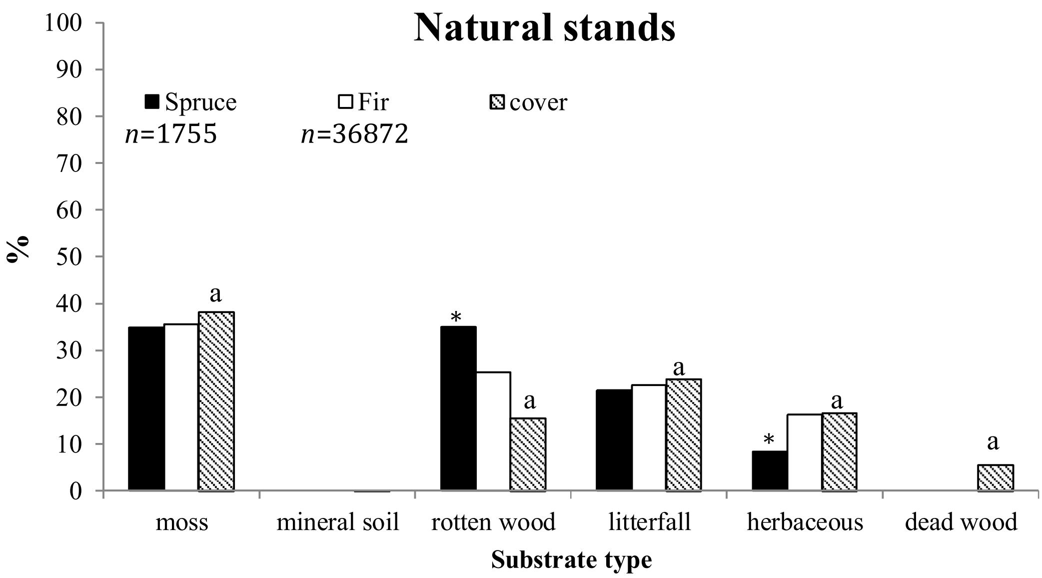
Figure 3. Seedlings density (fir: white bar and spruce: black bar) before and after a partial cut for natural stands and plantations. Lower-case letters indicate a significant difference before vs after a partial cut for a given species in each stand type, while asterisks indicate a significant difference between species for each stand type in a given period.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1

4.3 Percentage of seedlings per substrate type

The ground area covered by the various substrate types differs depending on stand origin. The percentages of area covered by litterfall and deadwood are significantly greater ($p<0.05$) in plantations than in natural stands, and the opposite is true for other substrate types except herbaceous (Fig. 4). In both types of stands, fir and spruce seedlings occur on all substrate types except deadwood; none were found on mineral soil as it was absent during the census (Fig. 4). In natural stands, spruce established more on rotten wood, and spruce established less on herbaceous substrate than expected by chance (Chi-square, $p<0.05$). Approximately 35% of spruce seedlings were found in the 15% stand area covered by rotten wood and 35% of the seedlings were found in the 40% stand area covered by moss (see supplementary Fig. S1A).

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1



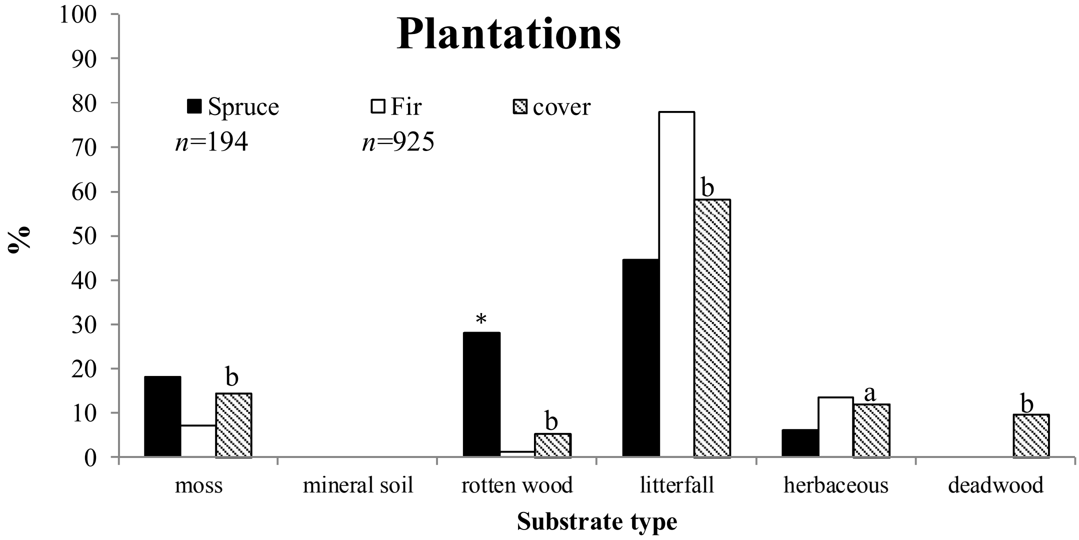


Figure 4. Percentage of total seedlings associated to each substrate type and percentage of cover per substrate for natural stands and plantations. An asterisk indicates a significant difference between a substrate cover and the proportion of seedlings found on this substrate for each species (chi-square-test). Lower-case letters indicate a significant difference in substrate cover between stand types (chi-square test).

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1

In plantations, spruce establishment is markedly associated to rotten wood (Chi-square, $p<0.05$), as this substrate supports 28% of the total number of spruce seedlings while only covering 5% of the available area (Fig. 4 and see supplementary Fig. S1B).

4.4 Relationship between the percentage of incident light, density of seedlings and their height

The proportion of incident light measured at 60 cm from the ground in partially cut stands varied from 3% to 15% of that measured in the open area. The median height of fir and spruce seedlings in the undergrowth is positively influenced by incident light, but while this variable explains 41% of the median height of spruce ($p = 0.018$), this relationship is not significant ($p = 0.14$) for fir (Fig. 5). The relationship between light and the number of seedlings/ha is very weak ($R^2 = 0.04$) but significant ($p<0.05$) for fir and spruce in natural stands and not significant ($p=0.62$) in plantations.

 doi:10.20944/preprints201808.0515.v1

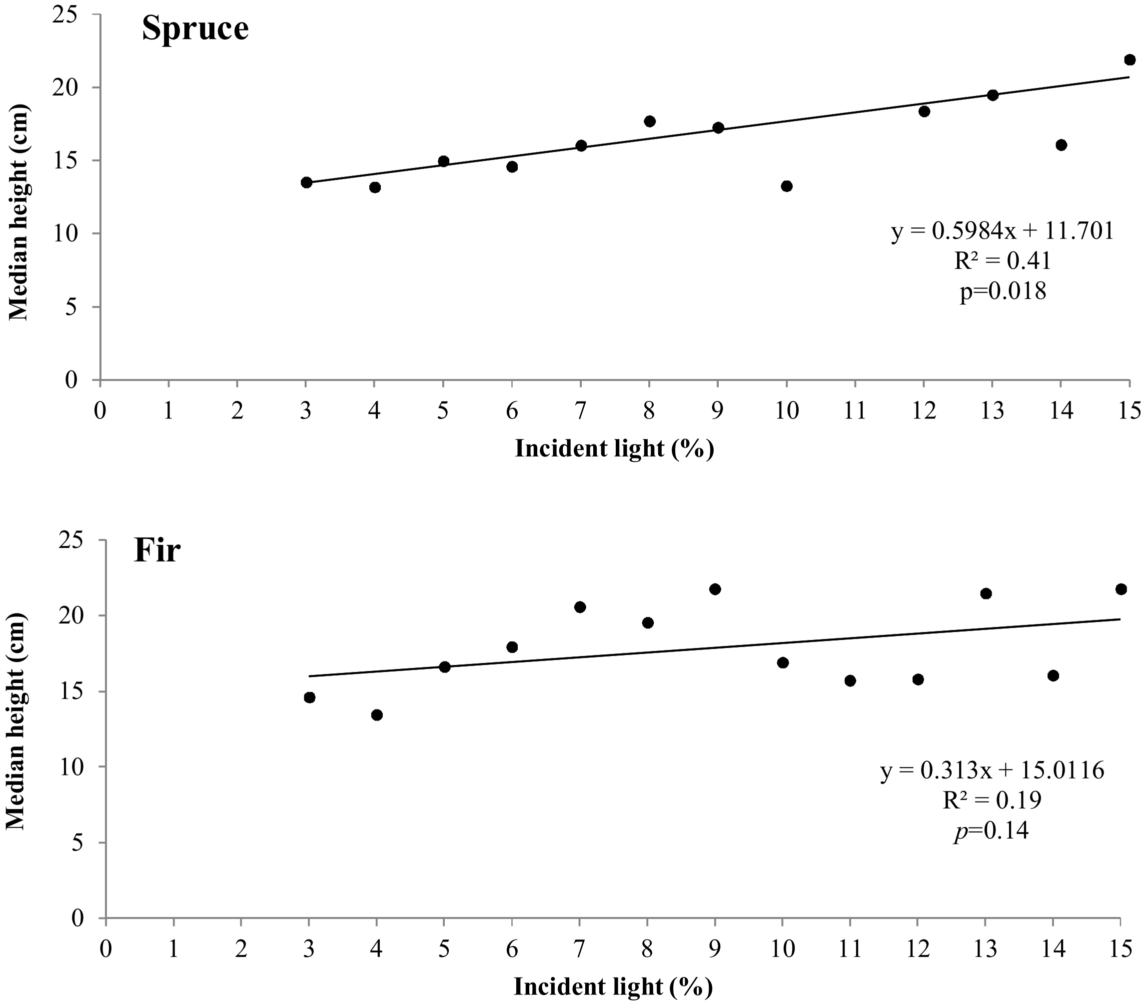


Figure 5. Relationsphip between incident light at 60 cm from the ground and median height for spruce and fir seedlings established after the partial cut in natural stands and plantations combined. n=1420 for fir and n=529 for spruce in total 1700 subunits of 4 m^2.

5. Discussion

This study sheds light on the effects of partial cutting on fir and spruce seedling establishment in natural stands and plantations. Our results show that partial cutting helps with the establishment and growth of seedlings. Fir consistently reach a higher distribution coefficient (80%) than spruce (30%) (Fig. 2). In the northern temperate and boreal forests of eastern Canada mainly composed of fir and spruce species, fir seedlings reach densities greater than 35 000 seedlings/ha while spruce only reach 1000 to 3000 seedlings/ha [23-40-46]. In mixed natural stands found elsewhere in the world, the genus *Abies* is often the one that regenerates most easily when co-occurring with other species [5-24].

Our results indicate that the natural establishment of seedlings is relatively limited in plantations compared to natural stands. This suggests that certain factors favourable to the establishment of regeneration such as substrate type [14-48-51], light [46], stand structure [38] and seed trees [24] might be more limiting in plantations than in natural stands. The plantations examined in this study were established on abandoned agricultural lands that were farmed for decades, which presumably modified soil structure by increasing compaction and decreasing aeration and drainage [2-34-53]. In addition, these years of agricultural activity removed the organic soil horizons and the coarse woody debris that littered the ground [33]. Litterfall composed of conifer needles and twigs is the main ground substrate found in plantations [39]. Although this situation is suitable for fir regeneration, it is quite the opposite for spruce [55]. Rotten wood appears to be the preferred substrate for the establishment of spruce seedlings, as the latter are found on this substrate in a significantly greater proportion than expected by chance based on substrate relative area (Fig. 4 and S1).

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1

The suitability of rotten wood for the establishment of spruce regeneration has been emphasized in several other studies [14-46-48]. Our results indicate that a rotten wood cover greater than 15% promotes adequate spruce regeneration [27], a situation observed in natural stands as opposed to plantations, where rotten wood covers only 5% of the area. A constant supply of woody debris [26] is thus important for the long-term recruitment of rotten wood [7-27-48-52] and the initial survival of spruce seedlings. Rotten wood found on the ground acts as an ecological filter, catching the smaller spruce seeds and letting many of the larger fir seeds make their way the ground [7]. Rotten wood offers ideal germination conditions because this substrate has a better water retention capacity than litterfall [7-9-54]. Spruce and fir establish themselves in greater amount on the litterfall substrate, as the latter covers more than half of the available area (Figure 4). However, both species differ in their ability to survive and grow on this substrate. The very short initial roots produced by spruce rarely manage to get through a thick layer of litterfall as the latter has a coarse porosity and dries up quickly [12-17], inducing a high mortality rate for spruce seedlings [14-31]. Conversely, fir produces longer initial roots [12] able to get through litterfall and reach mineral soil, which makes seedlings less vulnerable to prolonged drought due to its more consistent moisture level [16-45]. This explains why we can usually find more fir seedlings than spruce seedlings on litterfall, especially in plantations (Fig. 4). The herbaceous cover apparently exerts a detrimental effect on spruce establishment, especially in natural stands where this relation is significant (Fig. 4). The slower initial growth of spruce seedlings compared to that of fir [45] would make the former more vulnerable to competitive exclusion by herbs than the latter. Overall, spruce recruitment requires a much greater seed input than fir to reach similar seedling densities [23]. Our results show that the amount of dispersed spruce seeds must be about 45 times greater than that of fir to have an equal number of seedlings of both species in stands in which there is a minimum amount of preferential settling substrate such as rotten wood. These results are similar to estimations for stands dominated by trembling aspen in which white spruce and balsam fir were the companion species [55]. In plantations where the preferential establishment substrate for spruce only reach 5% cover or less, over 250 000 spruce seeds/m^2 would be required to ensure adequate recruitment. Despite the fact that a single white spruce tree that has reached sexual maturity can produce up to 250 000 seeds in mast years [20], such a seed rain is impossible to reach, even in a mature spruce monoculture, where tree density is typically 1200-1500 per ha. Thus, rotten wood availability seems the limiting factor for spruce regeneration in plantations.

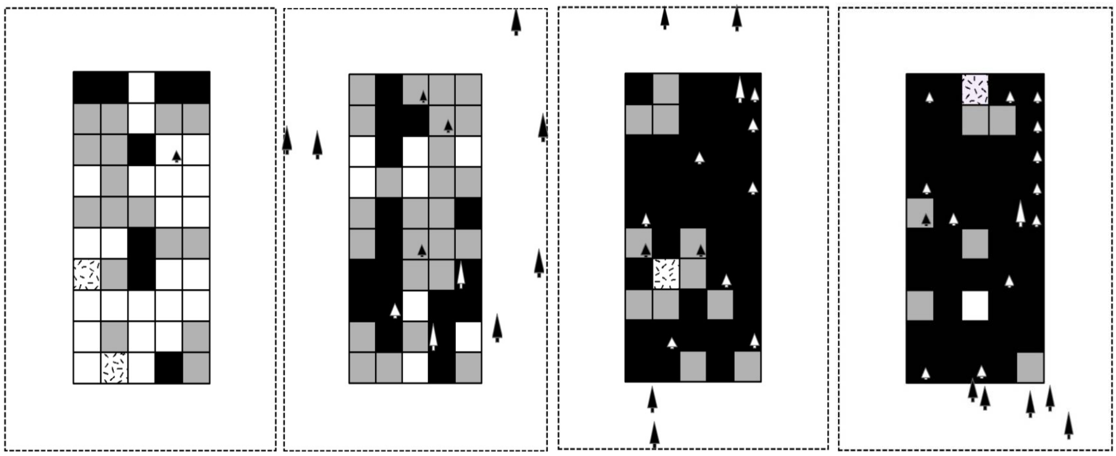
Once seeds have germinated, light is important for seedling survival [10-11-46] and growth [3-42]. According to our results, balsam fir and spruce seedlings can survive and grow in height with light levels as low as 3% [27-42-55], but some argue that an incident light threshold of 15% provides the minimal light requirements for sustained spruce growth [12]. Fir and spruce seedlings that established themselves after partial cutting do not respond in the same manner to gaps in the canopy [32-35]. Fir has a more variable response than spruce, as suggested by the relationship between the percentage of incident light and the median seedling height, which is not significant for fir, as opposed to spruce. This implies that the regeneration of spruce would be favoured by a repeated partial cutting regime that maintains a minimal light level of 15% in the undergrowth [27]. This threshold value could become a criterion for performing partial cuts at the optimal time to promote regeneration.

The sylviculture of fir-spruce dominated forests pose the challenge of spruce regeneration, whereas fir readily regenerates in a larger array of conditions [4-23-48]. In the context of partial cuts, three essential conditions must be met according to our results for spruce to successfully grow from a sprout to a 1.5 m seedling: a rotten wood ground cover of at least 15% combined with other suitable substrate types, a regime of partial cut whose intensity allows the transmission 15% of incident light to the ground, and seed trees that periodically produce between 7 000 to 8 000 seeds per m^2 of soil surface to have an average of 1 spruce seedling per m^2. However, sustained spruce regeneration requires an annual recruitment of a few dozen saplings per hectare [30]. Therefore, it is suggested that a silvicultural regime of repeated partial cuts warrants advanced regeneration in an even-aged management context and may eventually lead to the structural conversion of an even-aged stand to an irregular uneven-aged stand [49]. Such a silvicultural regime would create micro openings in the canopy [32-41], maintaining a minimal level of incident light for optimal seedling growth, while retaining woody debris [14-51] as a preferential seedbed for spruce.

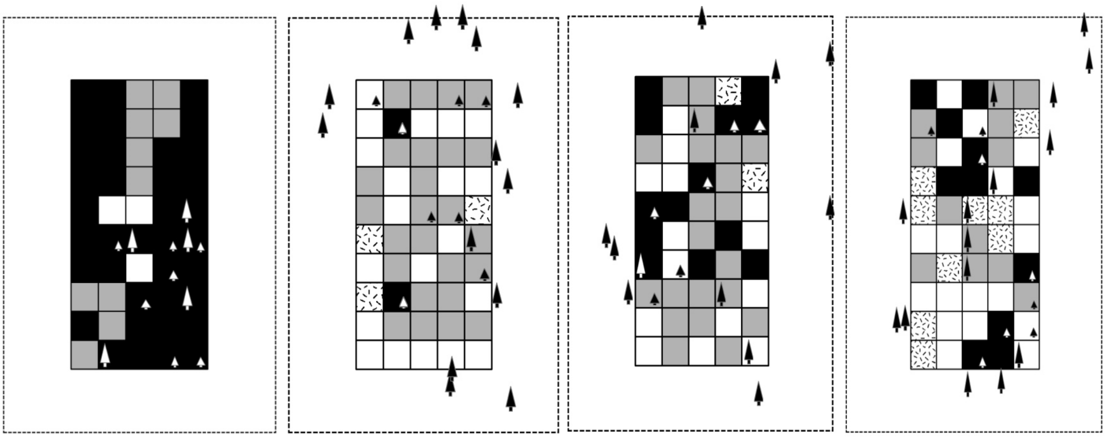
Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1

Supplementary material Fig. S1 A-B

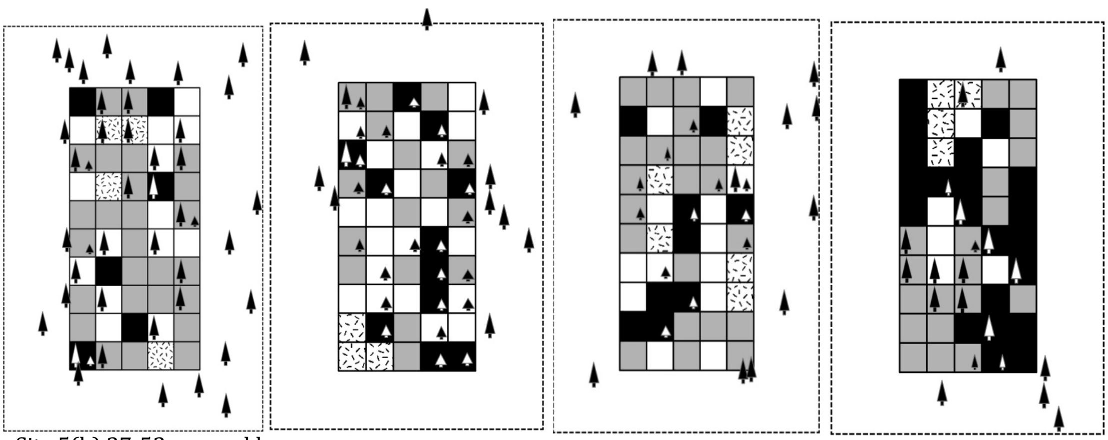
A



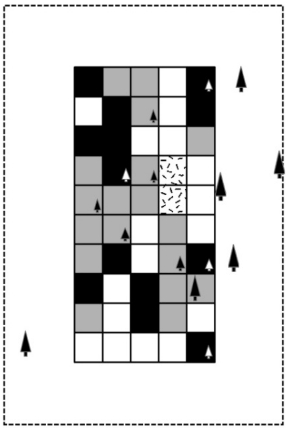
Site 1 37-40 years old | Site 2(a) 52-65 years old | Site 2(b) 52-65 years old | Site 3(a) 51-71 years old

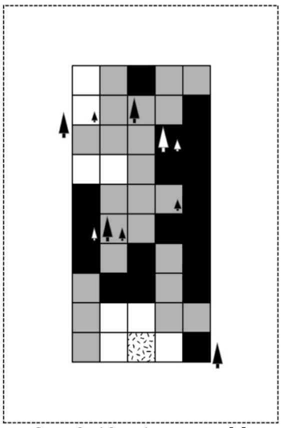


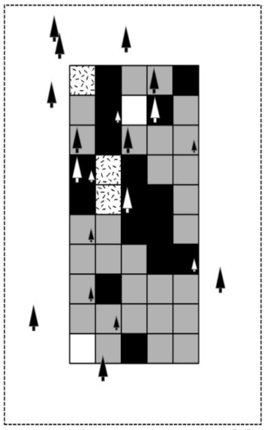
Site 3(b) 51-71 years old | Site 4(a) 46-52 years old | Site 4(b) 46-52 years old | Site 5(a) 37-52 years old

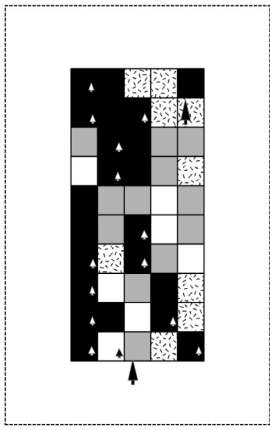


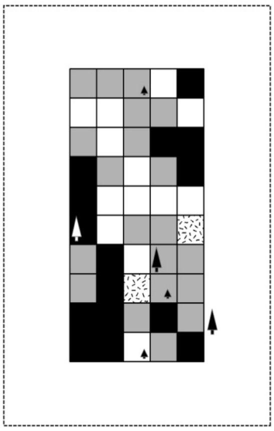
Site 5(b) 37-52 years old | Site 6(a) 48-60 years old | Site 6(b) 48-60 years old | Site 7(a) 55-74 years old

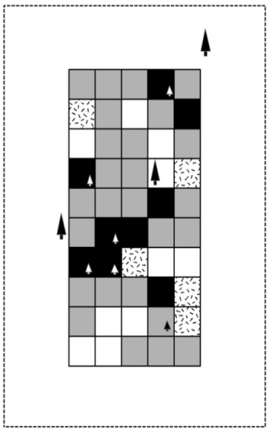

Site 7(b) 55-74 years old

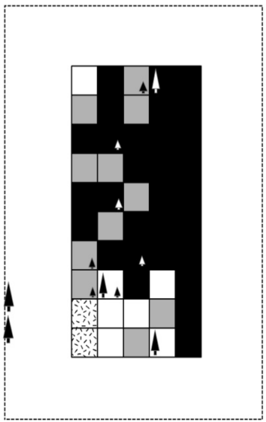

Site 8 62-71 years old

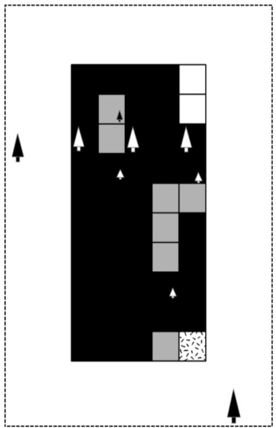

Site 9(a) 60-85 years old

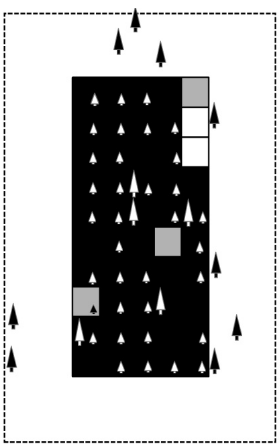

Site 9(b) 60-85 years old

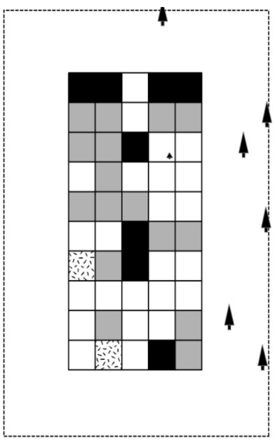

Site 10(a) 60-77 years


Site 10(b) 60-77 years old


Site 11(a) 73-104 years


Site 11(b) 73-104 years old


Site 12(a) 70-75 years old


Site 12(b) 70-75 years old

Symbol legend:
: presence of one or more seed trees (white spruce)
: presence of spruce regeneration, seedlings ≤ 150 cm in height
: limit of 5 m buffer zone around the SU perimeter

Seedbed substrate legend:
Absence of rotten wood
Presence of rotten wood with 5 to 9% cover
Presence of rotten wood with 10 to 14% cover
Presence of rotten wood with ≥ 15% cover

 doi:10.20944/preprints201808.0515.v1

B

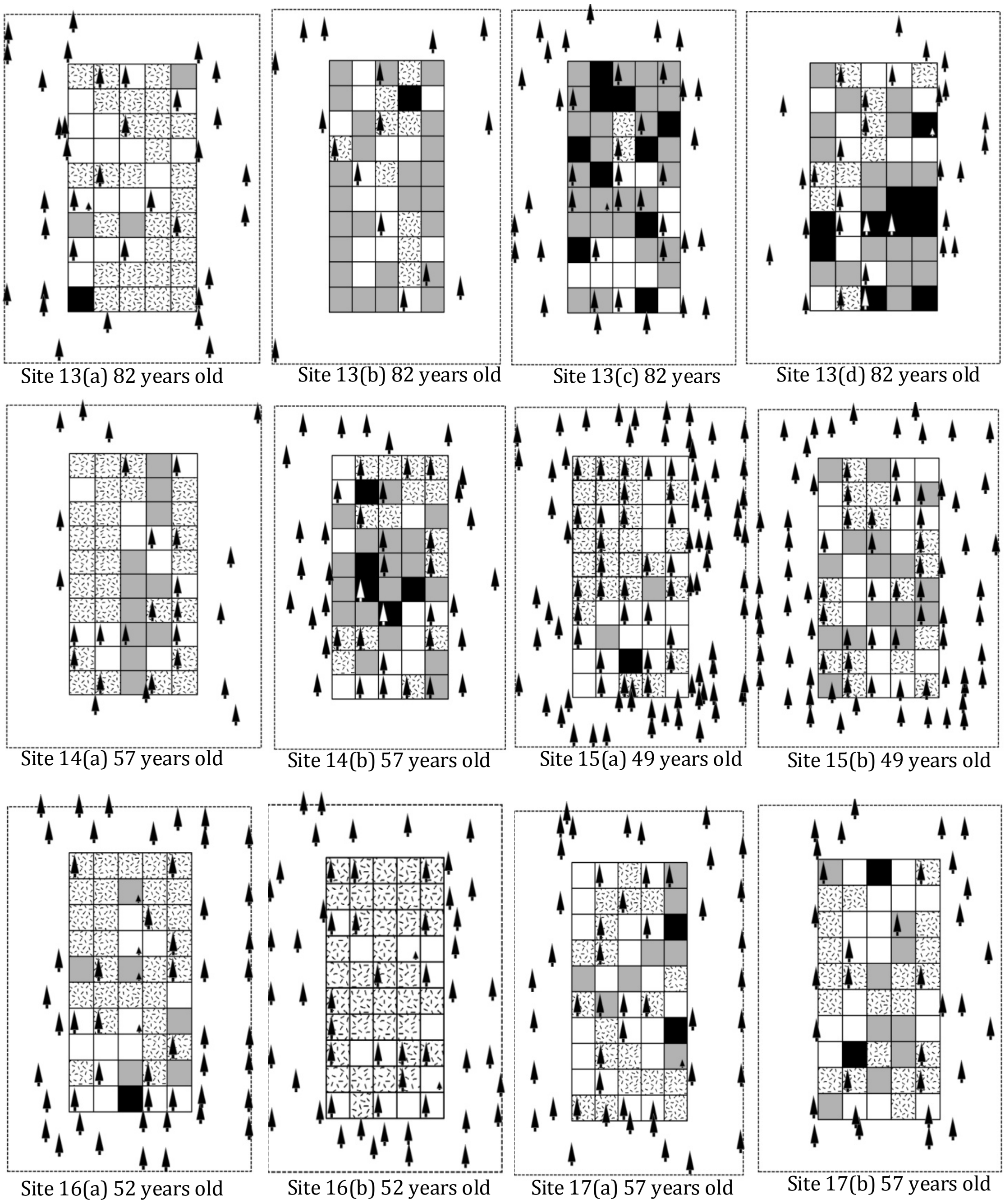


Figure S1. Illustration of the spatial distribution of seed trees, regeneration and the rotten wood seedbed substrate in the 200 m^2 sampling units, and spatial distribution of white spruce seed trees in the buffer zone of (A) natural stands and (B) plantations .

 doi:10.20944/preprints201808.0515.v1

Acknowledgements: Funding for this study was provided by the Chaire de recherche sur la forêt habitée of the Université du Québec à Rimouski, the Conférence Régionale des ÉluEs du Bas-Saint-Laurent and the Ministère des Ressources naturelles et de la faune du Québec. We would like to thank Nicolas Roy, Philippe Roy and for their help with fieldwork and data collection. Special thanks to Dr. Alain Caron for reviewing our statistical analyses.

Authors contributions: L.G., L.S. and L.L. conceived and designed the experiment; L.G. analysed the data, L.S. and L.L. contributed materials and tools, L.G. and L.S. wrote the paper.

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

References

1. Bauhus, J.; Puettmann, K.; Messier, C. Silviculture for old-growth attributes. For. Ecol. Manage. 2009, 258: 525–537.
2. Bizzari, L.E.; Collins, C.D.; Brudvig, L.A.; Damschen, E.I. Historical agriculture and contemporary fire frequency alter soil properties in longleaf pine woodlands. For. Ecol. Manage. 2015, 349: 45-54.
3. Carter, G.A.; Smith, W.K. Influence of shoot structure on light interception and photosynthesis in conifers. Plant Physiol. 1985, 79: 1038-1043.
4. Calogeropoulos, C.; Greene, D.F.; Messier, C.; Brais, S. The effects of harvest intensity and seedbed type on germination and cumulative survivorship of white spruce and balsam fir in northwestern Quebec. Can. J. For. Res. 2004, 34: 1467-1476. doi: 10.1139/X04-036.
5. Cameron, A. Determining the sustainable normal irregular condition: A provisional study on a transformed, irregular mixed species stand in Scotland. Scand. J. For. Res. 2007, 22:13-21.
6. Carswell, F.E.; Doherty, J.E.; Allen, R.B.; Brignall-Theyer, M.E.; Richardson, S.J.; Wiser, S.K. Quantification of the effects of aboveground and belowground competition on growth of seedlings in a conifer–angiosperm forest. Forest Ecology and Management 2012, 269: 188–196.
7. Chećko, E.; Jaroszewicz, B.; Olejniczak, K.; Kwiatkowska-Falińska, A.J. The importance of coarse woody debris for vascular plants in temperate mixed deciduous forests. Can. J. For. Res. 2015, 45: 1154-1163. dx.doi.org/10.1139/cjfr-2014-0473.
8. Christy, E.J.; Mack, R. N. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. Journal of ecology. 1984, 72: 75-91.

9. Cornett, M.W.; Reich, P.B.; Puettmann, K.J.; Frelich, L.E. Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* (Cupressaceae) regeneration. Am. J. Bot. 2000, 87 (12): 1807-1814.
10. Duchesneau, R.; Morin, H. Early seedling demography in balsam fir seedling banks. Can. J. For. Res. 1999, 29:1502-1509.
11. Dumais, D.; Prévost, M. Management for red spruce conservation in Québec: The importance of some physiological and ecological characteristics – A review. The Forestry Chronicle. 2007, 83(3): 378-392
12. Eis, S. Development of white spruce and alpine fir seedlings on cut-over areas in the central interior of British Columbia. The Forestry Chronicle. 1965, 41(4): 419-431.
13. Frank, R.M. *Abies balsamea* (L.) Mill. Balsam fir. *in* Burns, R.M. et Honkola, B.H. Silvics of North America 1990, Vol. 1. Conifers. ISBN-13: 978-0160271458. USDA Forest Service Agriculture Handbook 654 p.
14. Gärtner, S.M.; Lieffers, V.J.; Macdonald, S.E. Ecology and management of natural regeneration of white spruce in the boreal forest. Environmental Reviews 2011, 19:461-478.
15. Greene, D.F.; Johnson, E.A. Estimating the mean annual seed production of trees. Ecology, 1994, 75:642-647.
16. Greene, D.F.; Johnson, E.A. Seed mass and early survivorship of tree species in upland clearings and shelterwood. Can. J. For. Res. 1998, 28: 1307-1316.
17. Greene, D.F.; Zasada, J.C.; Sirois, L.; Kneeshaw, D.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.

18. Greene, D.F. Sexual recruitment of trees in strip cuts in eastern Canada. Can. J. For. Res. 2000, 30: 1256-1263.
19. Groupe d'experts sur la sylviculture intensive de plantations (GESIP), La sylviculture intensive de plantations dans un contexte d'aménagement écosystémique – Rapport du groupe d'experts, sous la direction de M. Barrette et M. Leblanc, Québec, 2013; Gouvernement du Québec ISBN 978-2-550-69378-9 112 p. Numéro de publication : DAEF-0354
20. Hellum, A. K. Grading seed by weight in white spruce. Tree Planters' Notes 1976, 27(l):16-17, 23-24.
21. Hély, C.; Bergeron, Y.; Flannigan. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. 2000, Can. J. For. Res. 30: 674–687.
22. Klopcic, M.; Bončina, A., Recruitment of tree species in mixed selection and irregular shelterwood forest stands. Ann. For. Sci. 2012, 69: 915–925.
23. Kneeshaw, D.D.; and Bergeron, Y. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. 1996, 26: 888-898.
24. Kuehne, C.; Puettmann, K. J. Natural regeneration in thinned Douglas-stands in western Oregon. J. sustainable for. 2008, 27(3): 246-274. doi: 10.1080/10549810802256221.
25. Kuuluvainen, T.; Kalmari, R. Regeneration microsites of Picea abies seedlings in a windthrow area of boreal old-growth forest in southern Finland. Ann. Bot. Fennici 2003, 40: 401-413.
26. Leinonen, K.; Leikola, M.; Peltonen, A.; Räsänen, P.K. Kuusen luontainen uudistuminen Pirkka-Hämeen metsälautakunnassa. Summary : Natural regeneration of Norway spruce

in Pirkka-Häme Forestry Board District, southern Finland. Acta For. Fennica 1989, 209:1-53.

27. Lieffers, V. J.; Stadt, K.J.; Navratil, S. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 1996, 26: 1002-1007.
28. Lieffers, V.J.; Messier, C.; Stadt, K.J.; Gendron, F.; Comeau, P.G. Predicting and managing light in the understrory of boreal forests. Can. J. For. Res. 1999, 29: 796–811.
29. Lundqvist, L. Stand development in uneven-aged sub-alpine *Picea abies* stands after partial harvest estimated from repeated surveys. Forestry, 2004, 77(2):120-129.
30. Lundqvist, L.; Chrimes, D.; Elfving, B.; Mörling, T.; Valinger, E. Stand development after different thinnings in two uneved-aged *Picea abies* forest in Sweden. For. Ecol. Manage. 2007, 238: 141-146.
31. Lundqvist, L.; Nilson, K. Regeneration dynamics in an uneven-aged virgin Norway spruce forest in northern Sweden. Scand. J. For. Res. 2007, 22: 304-309. doi: 10.1080/02827580701479717.
32. Malcolm, D.C.; Mason, W.L.; Clarke, G.C. The transformation of conifer forests in Britain – regeneration gap size and silvicultural systems. For. Ecol. Manag. 2001, 151: 7-23.
33. McLauchlan, K. The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. Ecosystems 2006, 9: 1364–1382.
34. McNabb, D.H.; Startsev, A.D.; Nguyen, H. Soil wetness and traffic level effects on bulk density and air-filled porosity of compacted forest soils. Soil Sci. Soc. Am. J. 2001, 65: 1238–1247.

35. Messier, C.; Doucet, R.; Ruel, J-C.; Claveau, Y.; Kelly, C.; Lechowicz, M.J. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 1999, 29: 812-823.
36. Niensteadt, H.; Zasada, J.C. *Picea glauca* (Moench) Voss. White spruce. *In* Burns, R.M. and Honkola, B.H. Silvics of North America Vol. 1. Conifers. 1990, ISBN-13: 978-0160271458. USDA Forest Service Agriculture Handbook 654 p.
37. Nilson, K.; Lundqvist, L. Effect of stand structure and density on development of natural regeneration in two Picea abies stands in Sweden. Scand. J. For. Res. 2001, 16: 253–259.
38. Noguchi, M.; Okuda, S.; Miyamoto, K.; Itou, T.; Inagaki, Y. Composition, size structure and local variation of naturally regenerated broad-leaved tree species in hinoki cypress plantations: a case study in Shikoku, southwestern Japan. Forestry. 2011, 84(5) : 493-504. doi: 10.1093/foresj/CPR027.
39. Novák, J.; Slodičák, M. Structure and accumulation of litterfall under Norway spruce stands in connection with thinnings. J. For. Sci. 2004, 50 (3):101-108.
40. Olson, M.G.; Meyer, S.R.; Wagner, R.G.; Seymour, R.S. Commercial thinning stimulates natural regeneration in spruce-fir stands. Can. J. For. Res. 2014, 44: 173-181. dx.doi.org/org/10.1139/cjfr-2013-0227.
41. Palik, B.; Mitchell, R.J.; Pecot, S.; Battaglia, M.; Pu, M. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. Ecological Applications. 2003, 13(3): 674-686.
42. Parent, S.; Messier, C. Effets d'un gradient de lumière sur la croissance en hauteur et la morphologie de la cime du sapin baumier régénéré naturellement. Can. J. For. Res. 1995, 25: 878-885.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 30 August 2018 doi:10.20944/preprints201808.0515.v1

43. Paquette, A.; Bouchard, A.; Cogliastro, A. A less restrictive technique for the estimation of understorey light under variable weather conditions. For. Ecol. Manage. 2007, 242: 800-804.
44. Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D. The R Development Core Team, 2010. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-97.
45. Place, I.C.M. The influence of seed-bed conditions on the regeneration of spruce and balsam fir. Canadian Department of Northern Affairs and National Resources, Forestry Branch 1955; Bull. 117.
46. Prévost, M. Effect of cutting intensity on microenvironmental conditions and regeneration dynamics in yellow birch – conifer stands. Can. J. For. Res. 2008, 38 : 317-330. doi :10.1139/X07-168.
47. Rive, A.C. Enhancing natural regeneration of white spruce (*Picea glauca*) via synchronization of a mast year with site manipulations in Abitibi, Quebec. Master degree. Biology department. Concordia university, Montréal, Québec. 2010.
48. 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.
49. Schütz, J.P. Opportunities and strategies of transformation regular forests to irregular forests. For. Ecol. Manag. 2001, 151: 87-94.
50. Schütz, J.P.; Pommerening, A. Can Douglas fir (Pseudotsuga menziesii (Mirb.) Franco.) sustainable grow in complex forest structures? For. Ecol. Manage. 2013, 303:175-183.
51. 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(4) : 575-582.

52. 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.
53. Startsev, A.D.; D.H. McNabb. Effects of compaction on aeration and morphology of boreal forest soils in Alberta, Canada. Can. J. Soil Sci. 2009, 89: 45–56.
54. Waldron, R.M. Factors affecting natural white spruce regeneration on prepared seedbeds at the riding Mountain Forest Experimental Area. Can. Dep. For. Rural Dev. For. Branch Tech. 1966, Note 74.
55. Wang, G.G.; Kemball, K.J. Balsam fir and white spruce seedling recruitment in response to understory release, seedbed type, and litter exclusion in trembling aspen stands. Can. J. For. Res. 2005, 35(3): 667–673. doi:10.1139/x04-212.
56. Warnes, G.R.; Bolker, B.; Lumley, T.; Johnson, R.C. Contributions from Randall C. Johnson are Copyright 2005. SAIC-Frederick, Inc. Funded by the Intramural Research Program, of the NIH, National Cancer Institute and Center for Cancer Research under NCI Contract NO1-CO-12400. gmodels: Various R programming tools for model fitting. R package version 2.15.0. http://CRAN.R-project.org/package=gmodels.
57. Zuur, A.F.; Saveliev A.A.; Ieno E.N. Zero inflated models and generalized linear mixed models with R. Newburgh: Highland Statistics Limited 2012, ISBN: 9780957174108
58. Saucier, J.-P., Robitaille, A., Grondin, P., Bergeron, J.-F. & Gosselin, J. Les régions écologiques du Québec méridional (4e version). 2011, https://mffp.gouv.qc.ca/forets/inventaire/pdf/carte-regions-ecologiques.pdf