

Communication

Vulnerability of Conifer Regeneration to Spruce Budworm Outbreaks in the Eastern Canadian Boreal Forest

Janie Lavoie ^{1,†}, Miguel Montoro Girona ^{2,3,*} and Hubert Morin ¹

¹ Département des Sciences Fondamentales, Université du Québec à Chicoutimi, 555 boul. de l'Université, Chicoutimi, QC G7H 2B1, Canada; janie.lavoie1@uqac.ca (J.L.); hubert_morin@uqac.ca (H.M.)

² Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC J9X 5E4, Canada

³ Ecology Restoration Group, Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences (SLU), 901 83 Umeå, Sweden

* Correspondence: miguel.montoro@uqat.ca; Tel.: +1-819-762-0971

† Co-first author.

Received: 19 August 2019; Accepted: 27 September 2019; Published: 29 September 2019



Abstract: Spruce budworm (*Choristoneura fumiferana*) is the main defoliator of conifer trees in North American boreal forests, affecting extensive areas and causing marked losses of timber supplies. In 2017, spruce budworm affected more than 7 million ha of Eastern Canadian forest. Defoliation was particularly severe for black spruce (*Picea mariana* (Mill.) B.S.P.), one of the most important commercial trees in Canada. During the last decades, intensive forest exploitation practices have created vast stands of young balsam fir (*Abies balsamea* (L.) Mill.) and black spruce. Most research focused on the impacts of spruce budworm has been on mature stands; its effects on regeneration, however, have been neglected. This study evaluates the impacts of spruce budworm on the defoliation of conifer seedlings (black spruce and balsam fir) in clearcuts. We measured the cumulative and annual defoliation of seedlings within six clearcut black spruce stands in Quebec (Canada) that had experienced severe levels of defoliation due to spruce budworm. For all sampled seedlings, we recorded tree species, height class, and distance to the residual forest. Seedling height and species strongly influenced defoliation level. Small seedlings were less affected by spruce budworm activity. As well, cumulative defoliation for balsam fir was double that of black spruce (21% and 9%, respectively). Distance to residual stands had no significant effect on seedling defoliation. As insect outbreaks in boreal forests are expected to become more severe and frequent in the near future, our results are important for adapting forest management strategies to insect outbreaks in a context of climate change.

Keywords: black spruce; balsam fir; clearcut; edge effect; forest damages; forest dynamics; global change; natural disturbances; sustainable forest management; seedlings

1. Introduction

Natural and anthropic disturbances determine the dynamics, structure, and composition of forests and control the functioning of forested ecosystems [1,2]. In forests with long fire cycles, disturbances such as insect outbreaks and windthrow play major roles in forest landscapes [3–5]. Insect outbreaks must be considered in forestry planning due to the important economic and ecological implications of these disturbances [6,7]. Insect outbreaks affect timber supplies and have a marked impact on overall forest productivity. For this reason, many studies have evaluated the vulnerability of mature trees in boreal forests to this type of disturbance (e.g., References [8–10]). However, there is still a lack of information regarding the impact of insect outbreaks on seedling regeneration. In the last decades, the

greater intensity of harvest practices has increased pressure on boreal forests to respond to the high demand for wood in the international market [11,12]. Between 1990 and 2016, the harvested area in Canada reached 24 million ha, most of this area (86%) being harvested using clearcutting methods [13]. Consequently, a large surface of the North American boreal forest exists at an early development stage; the post-disturbance regeneration phase deserves more attention as it may provide early warning of ecosystem processes degrading [14]. Therefore, assessing the vulnerability of seedlings to insect outbreaks is critical for evaluating the persistence, productivity, and resilience of forest ecosystems, especially in the context of climate change with the expected increase in the frequency and severity of natural disturbances in the boreal biome [1].

Spruce budworm (*Choristoneura fumiferana* (Clem)) (SBW) is the main defoliator of North American boreal forests [15]. Between 1990 and 2016 in the Canadian boreal forest alone, 93 million ha were affected by SBW activity [13,16]; this extent is equivalent to an area that is more than 5× that of the state of Florida (USA). Damage to the forest occurs during the larval budworm stage when this insect consumes annual foliage, thereby reducing the foliar area of conifers that is available for photosynthesis [16]. This lepidopteran has a 10-year cycle and an outbreak frequency of 30–40 years [17]. In the last decades, the severity and frequency of SBW outbreaks have increased and spatial patterns have changed [18,19]. Outbreaks now reach latitudes to the North of previously-observed infestations, possibly because of modified stand structure, species composition, and host species distribution, as well as climate warming [20,21].

SBW outbreaks reflect a complex phenomenon influenced by multiple factors. Tree vulnerability depends on species, stage development, height, spatial location, and regional climatic conditions [22–24]. The most vulnerable species are balsam fir (*Abies balsamea* (L.) Mill.), followed by white spruce (*Picea glauca* (Moench) Voss.) and black spruce (*Picea mariana* (Mill.) BSP) [25]. Balsam fir budburst occurs 14 days earlier than that of black spruce and is synchronized with SBW emergence; this synchrony explains the greater vulnerability of balsam fir to defoliation [26]. Phenological asynchrony between black spruce and the insect improves the resistance of this host to defoliation and provides some protection from severe SBW defoliation [27,28]. SBW not only has an impact on mature trees but also affects the regeneration phase, i.e., seedlings [22]. The nutritional properties of foliage vary between species, but they are influenced mainly by the phase of stage development, directly affecting vulnerability to defoliation due to the differing chemical composition of leaves [29]. The foliage of seedlings has higher concentrations of nitrogen, sugar, and secondary compounds, e.g., tannins, than mature trees. Lower concentrations decrease the nutritional quality of foliage and reduce the suitability for the development of SBW larvae [30]. Similar to mature trees, taller seedlings generally have a larger crown that can intercept larvae; thus height could influence larval density on seedlings [31]. The proximity of seedlings to residual patches and competition related to stand density could also be crucial in the seedling vulnerability to SBW activity, especially within clearcut stands where the sheltering effect provided by mature trees is almost nonexistent [32]. Thus, a better understanding of the vulnerability of conifer regeneration to SBW outbreaks requires that these factors be examined as they may strongly influence seedling defoliation [22,33,34].

To mitigate the projected future impacts of insect disturbance, several studies have examined the effect of SBW outbreak under different silvicultural treatments [35–37]. These studies focused on mature stands; few studies, however, have investigated seedling vulnerability. Although the role of forest overstory composition on seedling defoliation [22,38] and post-outbreak seedling response [39,40] have been evaluated, SBW effects on boreal forest seedlings remain understudied. Thus, as much of the Eastern Canadian forest area previously harvested by clearcutting is affected by SBW activity, a better understanding of the impacts of SBW outbreaks on seedlings in these early-stage stands should be a major priority in forest management strategies.

Here we investigate the vulnerability of conifer regeneration to SBW outbreak within clearcut areas of the Eastern Canadian boreal forest. We aimed to quantify cumulative and annual defoliation levels on seedlings based on (i) conifer species, (ii) seedling height classes, and (iii) distance to the residual forest. We hypothesized that:

- (i) Balsam fir will be more affected by SBW than black spruce due to the phenological synchrony of balsam fir with SBW.
- (ii) Taller seedlings will have a higher level of defoliation due to the sheltering effect provided to smaller seedlings.
- (iii) Defoliation will be more intense as the distance between seedling and residual forest increases because the refugee effect of the mature stand is increasingly limited with distance.

2. Materials and Methods

2.1. Study Area

We conducted our study in natural boreal forest stands that had been both clearcut and affected by the current SBW outbreak. Our study region, located North of Lake Saint-Jean, Quebec, Canada (Figure 1) covered 15,438 km² between 48°41′–49°38′ N and 71°38′–72°25′ W in the balsam fir–white birch (*Betula papyrifera* Marsh.) bioclimatic zone [41]. The regional climate is subhumid subpolar, characterized by a short, 100–140-day vegetative season [42]. The annual mean temperature is 2.5 °C, marked by an important seasonal variation [43]. Average annual precipitation is 931 mm with 35% falling as snow [44]. Surficial deposits consist primarily of thick glacial till, and the landscape is generally flat or gently undulating (1% slopes) [45]. The predominant regional soil type is humo-ferric podzol [46]. The main natural disturbance in this forested region is SBW outbreaks. In 2016, SBW severely defoliated 470 km² (3%) of the study area (Figure 1B). Black spruce is the dominant tree species and covers 5046 km² (33%) (Figure 1C) of the study area; this area is considered as a productive forest under intensive management, and clearcutting is the most common silvicultural treatment. Between 1990 and 2003, 725 km² (5%) of the study area was harvested (Figure 1D).

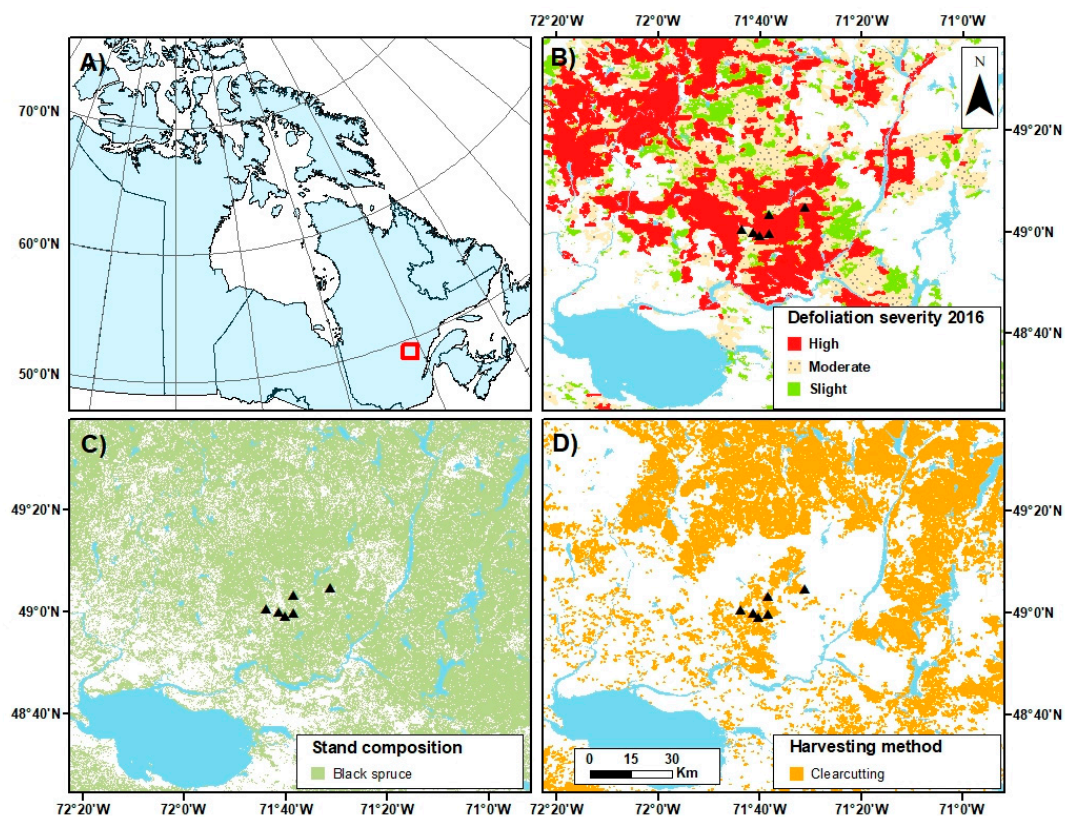


Figure 1. Location of the study area in Canada (A). Disposition of the experimental plots, located North of Lake Saint-Jean, Quebec, Canada in relation to Spruce budworm (SBW) defoliation severity in 2016 (B); species composition, where black spruce stands are represented in green (C), and clearcut areas are in orange (D) [47].

2.2. Site Selection and Experimental Design

Before undertaking our fieldwork, we selected six study sites (Figure 1) based on the criteria of SBW activity, dominant tree species, and forestry practices. For this selection, we relied on the forest inventory data of the Quebec Ministry of Forestry, Wildlife, and Parks [47,48]. We undertook an exhaustive exploration of the study region to ensure the accuracy of our selection criteria and to maximize similarity among the selected study sites. Our specific site criteria were (i) that the site had high level of defoliation by the most recent SBW outbreak, (ii) black spruce dominated the tree assemblage and represented $\geq 75\%$ of the stand basal area, and (iii) the forest within the site had been harvested by clearcutting between 1994 and 2008 (see Table 1), termed clearcutting with protection of advanced regeneration and soils—CPRS in Quebec. We selected sites subjected to clearcutting as it is the most common harvesting approach used in Eastern Canadian boreal forests. CPRS requires harvesting only trees having a diameter at breast height (DBH) of ≥ 9 cm, preserving pre-established seedlings, and minimizing soil disturbance from heavy machinery [49].

Table 1. Plot and seedling characteristics by species, distance and height classes, where the distance classes (R.S., N., I., and D), correspond to residual stand, near, intermediate and distant, respectively.

Plot	Harvesting Date	Species	Number of Seedlings	Distance Classes				Height Classes (cm)				
				R.S.	N	I	D	0 to 50	51 to 100	101 to 150	151 to 200	≥ 200
A	2003	Black spruce	50	17	22	11	0	39	8	3	0	0
		Balsam fir	150	21	65	42	22	75	44	18	4	9
		Total	200	38	87	53	22	114	52	21	4	9
B	2008	Black spruce	76	29	18	19	10	31	22	10	7	6
		Balsam fir	1	1	0	9	0	0	0	0	1	0
		Total	77	30	18	19	10	31	22	10	8	6
C	1994	Black spruce	39	1	3	15	20	25	10	3	1	0
		Balsam fir	29	8	14	3	4	2	12	5	5	5
		Total	68	9	17	18	24	27	22	8	6	5
D	2000	Black spruce	32	6	12	10	4	2	5	8	5	12
		Balsam fir	0	0	0	0	0	0	0	0	0	0
		Total	32	6	12	10	4	2	5	8	5	12
E	1999	Black spruce	40	14	8	11	7	7	17	5	2	9
		Balsam fir	0	0	0	0	0	0	0	0	0	0
		Total	40	14	8	11	7	7	17	5	2	9
F	1999	Black spruce	87	6	28	22	31	18	29	14	17	9
		Balsam fir	1	1	0	0	0	0	0	0	1	0
		Total	88	7	28	22	31	18	29	14	18	9

2.3. Measurements and Data Compilation

At each study site, we plotted out a 100 m² rectangular sampling plot (2 m × 50 m). To account for the edge effect, we set each plot to lie within both the residual stand and clearcut areas (Figure 2). We included the residual stand area to study the effect of insect outbreaks on the patch (including mature trees). The residual stand area was 20 m² (10 m × 2 m). We designed the harvested area (80 m²; 40 m × 2 m) to evaluate the effect of distance from the residual patch on seedling defoliation. We measured all conifer seedlings located within the 100 m² rectangular sampling plot—*n* therefore varied between sites due to the random number of seedlings in each plot. For each seedling, we recorded species, distance from the residual stand, seedling height, and defoliation level. To simplify data analysis, we divided distances into several classes: Residual stand, near (residual stand ≤ 15.0 m), intermediate (15.1 m–30.0 m), and distant (30.1 m–40.0 m). We also divided height into five classes: (1) 0 cm–50 cm, (2) 51 cm–100 cm, (3) 101 cm–150 cm, (4) 151 cm–200 cm, and (5) ≥ 201 cm. We conducted seedling inventories during the summer of 2017, a year after SBW defoliation.

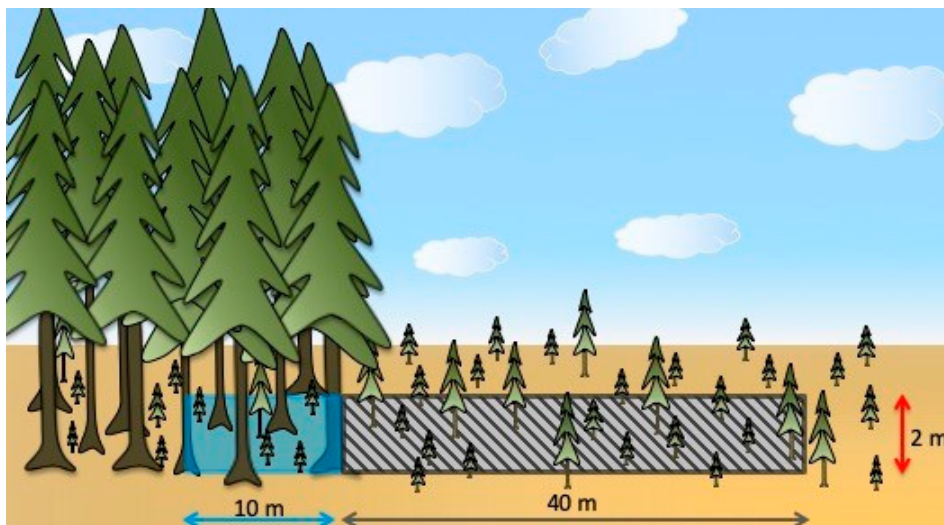


Figure 2. Schematic representation of a sampling plot where the blue rectangle corresponds to the residual stand area (20 m^2), and the grey rectangle represents the harvested area (80 m^2).

To evaluate the vulnerability of conifer regeneration to insect outbreaks, we estimated the cumulative and annual defoliation for each sampled seedling. Cumulative defoliation was estimated as the percentage of defoliated needles over total foliage. The classification followed the Hunter classes [50] (Figure 3). Annual defoliation was estimated on three recent shoots per seedling following the Fettes method [51] (Figure 4). As a complementary measure, to guaranty that the level of stand defoliation was high in the study plots, we noted the cumulative defoliation for randomly selected mature trees within the residual stands (30 per plot) using similar methods as described for the seedlings.

2.4. Data Analysis

We used non-parametric tests due to a data distribution that did not conform to parametric test assumptions. Permutational multivariate analysis of variance (PERMANOVA), based on a Euclidean distance matrix, evaluated the effects of species, height class, and distance on seedling defoliation (cumulative and annual). PERMANOVA was performed using Primer 6 software (Primer-E, Plymouth, UK) [52]. PERMANOVA analyses were run with 9999 permutations. Pairwise tests were applied between species, height, and distance classes when factors were significantly dissimilar ($p < 0.05$) [53]. We then examined the significant pairwise results using Monte Carlo ($p(\text{MC})$) permutation tests [54]. The model included species, position, height class, and their pairwise interactions as fixed effects.

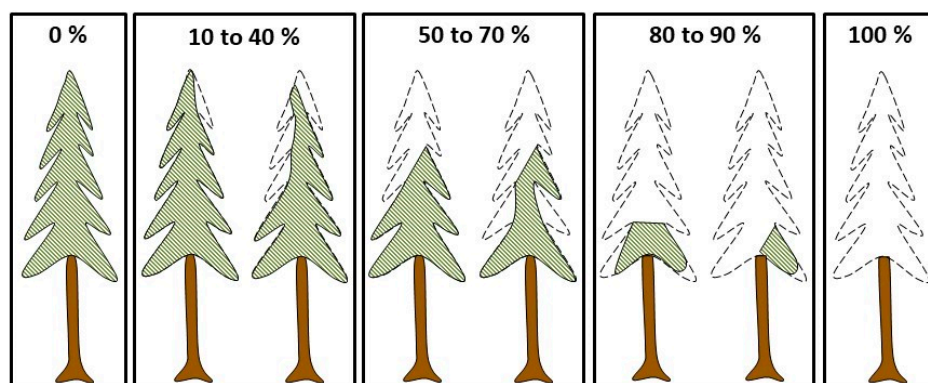


Figure 3. The methodology applied to estimate the level of cumulative defoliation of seedlings and trees. The defoliation scale varies from 0%–100%; green represents healthy or intact foliage, and white represents affected foliage.

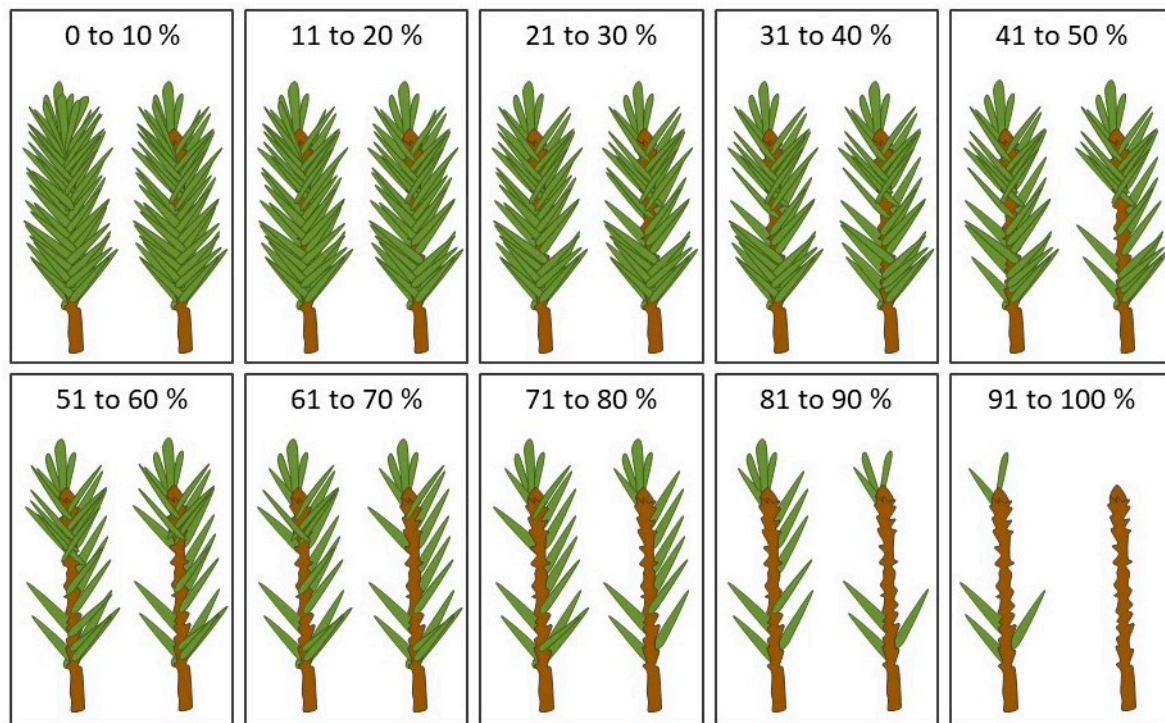


Figure 4. The methodology used to estimate the level of annual defoliation (0%–100%) based on ten defoliation classes for black spruce and balsam fir shoots.

3. Results

3.1. Effect of Height on Seedling Defoliation

PERMANOVA analyses determined significant differences between the cumulative defoliation levels of the height classes (Figure 5A, Table 2). The analysis of the combined species—balsam fir and black spruce seedlings together—revealed a positive correlation between the level of defoliation and height class. Seedlings taller than 200 cm experienced the highest cumulative defoliation (25%) and differed significantly from the other height classes ($p = 0.012$), except for the 151 cm–200 cm height class (mean cumulative defoliation of 20%, $p = 0.316$). The percent defoliation values that we obtained for the ≤ 100 cm height classes (9%–11% mean cumulative defoliation) showed no significant differences ($p = 0.159$). The mean cumulative defoliation of seedlings for the height class 101 cm–150 cm differed from all other height classes (16%, $p = 0.007$), except for the 151 cm–200 cm class ($p = 0.293$). The cumulative defoliation for seedlings ≥ 200 cm in height was greater than other classes ($p = 0.012$), again except for the 151 cm–200 cm class ($p = 0.316$). Species differed in their cumulative defoliation ($p = 0.001$). Balsam fir seedlings were twice as affected as black spruce ($p = 0.001$). However, the cumulative defoliation of black spruce and balsam fir did not differ significantly between height classes (Figure 5B, Table 2).

Annual defoliation of seedlings differed between height classes when seedlings of both species were combined ($p = 0.001$) (Figure 5C). Each height class differed in terms of mean defoliation ($p = 0.042$), except for seedlings of the 151 cm–200 cm class where the mean defoliation was similar to the 101 cm–150 cm ($p = 0.922$) and ≥ 200 cm classes ($p = 0.068$). Mean values of annual defoliation were 3%, 14%, 25%, 23%, and 33%, arranged in order of height class. However, we observed no differences in defoliation between species for the different height classes (Figure 5D).

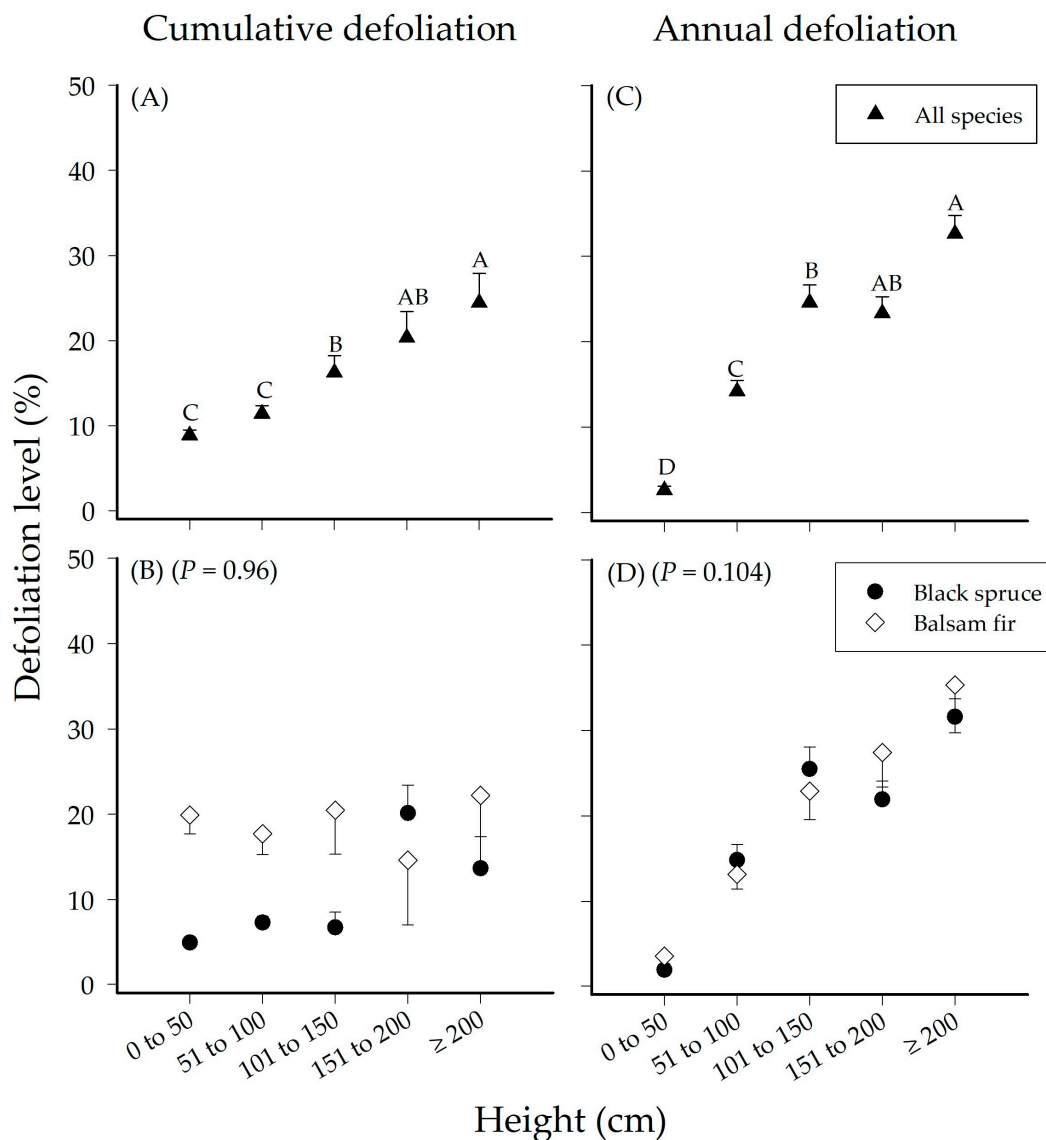


Figure 5. Cumulative defoliation level (%) among height classes (cm) for both seedling species combined (A) and between the conifer species (balsam fir and black spruce) (B). Annual defoliation level (%) among the height classes (cm) for all seedlings (C) and among species (balsam fir and black spruce) (D). Vertical bars show the standard error. Different letters represent significant differences between classes ($p < 0.05$), following $A > B > C$.

Table 2. Results of permutational multivariate analysis of variance (PERMANOVA) for cumulative and annual defoliation between height, species, and height \times species, including degrees of freedom (DF), sum of squares (SS), mean squares (MS), and Monte Carlo permutation test p -values (p (MC)). Values in bold are significant.

	Factors	DF	SS	MS	Pseudo-F	p (MC)
Cumulative Defoliation	Height	4	11061	2765.1	14.553	0.001
	Species	1	8720.2	8720.2	45.895	0.001
	Height \times Species	4	1538.2	384.6	2.024	0.96
	Residual	495	94052	190		
Annual Defoliation	Height	4	1.50×10^5	37559	26.434	0.001
	Species	1	333.4	333.4	0.235	0.849
	Height \times Species	4	9654	2413.5	1.6987	0.104
	Residual	496	7.05×10^5	1420.8		

3.2. Effect of Distance on Seedling Defoliation

For all seedlings, cumulative defoliation varied between 11% and 15% among all distance classes (Figure 6A, Table 3). Distance did not influence the cumulative defoliation rate of seedlings when species were combined, although almost a significant result ($p = 0.054$); however, the effect of distance on cumulative defoliation differed ($p = 0.001$) between balsam fir and black spruce seedlings (Figure 6B). Balsam fir seedlings had higher cumulative defoliation than black spruce for all distance classes. Balsam fir seedlings within the residual stand had similar defoliation values (21%) to the other balsam fir distance classes. The “near” and “distant” balsam fir classes experienced similar defoliation (22% and 27%, respectively), and values were higher than that of the “intermediate” distance ($p = 0.047$). For black spruce, cumulative defoliation varied between 7% and 10% among the distance classes. Annual defoliation of black spruce seedlings was similar for the “near” and “distant” classes; however, these values were higher than the annual defoliation in the “residual stand” and lower than that of the “intermediate” class ($p = 0.036$).

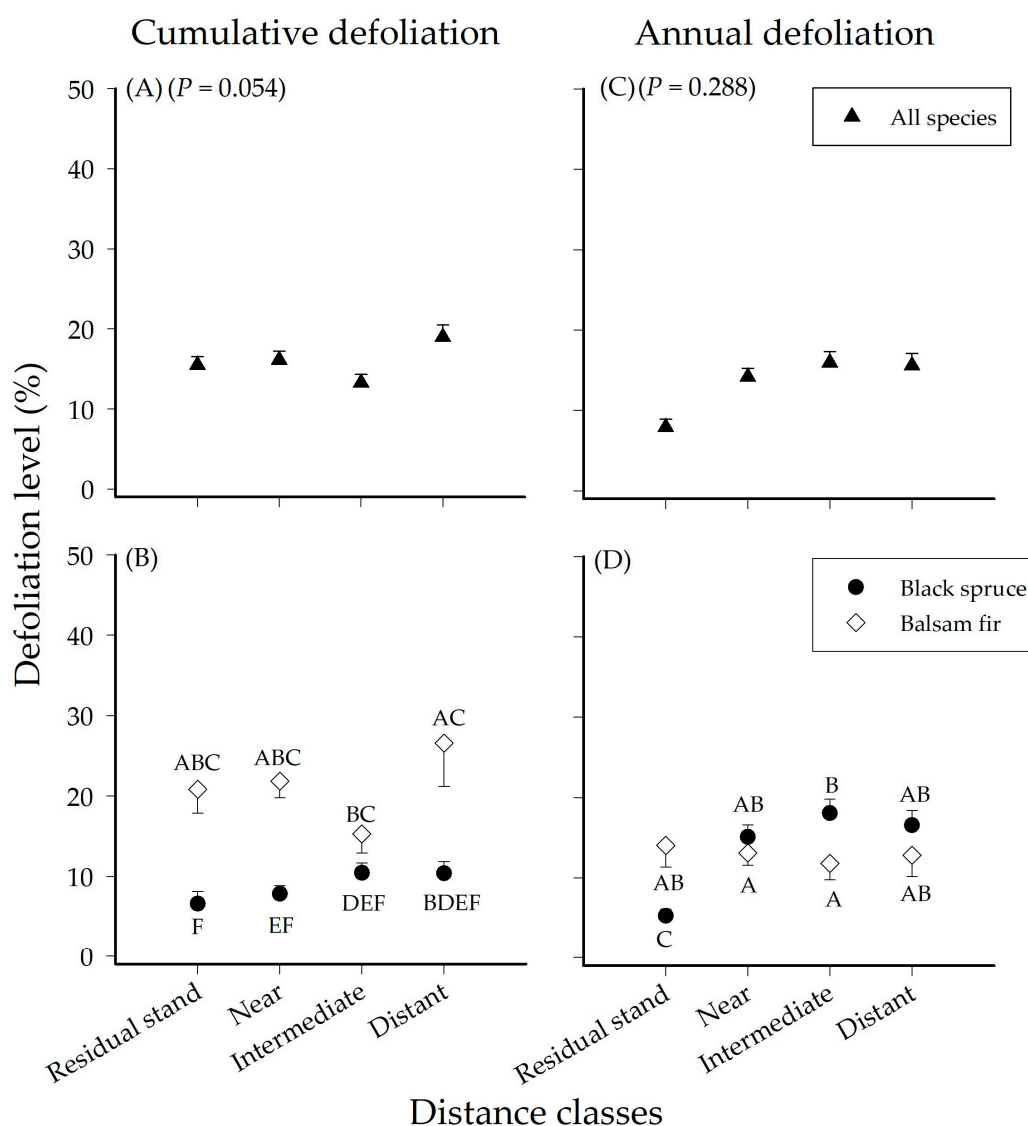


Figure 6. Cumulative defoliation (%) among distance classes for all seedlings combined (A) and among conifer species (balsam fir and black spruce) (B). Annual defoliation (%) among distance classes for all species (C), and among species (balsam fir and black spruce) (D). Vertical bars show the standard error. Different letters represent significant differences between classes ($p < 0.05$), following $A > B > C > D > E > F$.

Table 3. Results of a permutational multivariate analysis of variance (PERMANOVA) for cumulative and annual defoliation among distance, species, and distance × species, including degrees of freedom (DF), sum of squares (SS), mean squares (MS), and Monte Carlo permutation test *p*-values (*p*(MC)). Values in bold are significant.

	Factors	DF	SS	MS	Pseudo- <i>F</i>	<i>p</i> (MC)
Cumulative Defoliation	Distance	3	1586.8	528.95	2.42	0.054
	Species	1	15624	15624	71.52	0.001
	Distance × Species	3	2140.4	713.46	3.27	0.022
	Residual	497	1.09 × 10 ⁵	218.45		
Annual Defoliation	Distance	3	5992.3	1997.4	1.16	0.288
	Species	1	997.9	997.86	0.58	0.573
	Distance × Species	3	10544	3514.5	2.04	0.049
	Residual	498	8.57 × 10 ⁵	1721.9		

Annual defoliation varied little (8%–16%) between the distance classes when all seedlings were combined (Figure 6C). As well, we observed no effect of distance ($p = 0.97$) on the annual defoliation of balsam fir (12%–14%). Black spruce seedlings within the residual stands experienced less defoliation (5%, $p = 0.002$) than the other distance classes (15%–18%). Between-species differences for annual defoliation were not significant ($p = 0.573$) (Figure 6D).

4. Discussion

In recent years, the Eastern Canadian boreal forest has experienced a major SBW outbreak phase, resulting in severe damage to a vast expanse of very productive forest areas. This SBW outbreak has important implications at the ecological (forest dynamics) and economic levels (economic losses). Natural regeneration is a key component of forest management in the boreal biome, given its major role in ensuring the persistence and resilience of forest ecosystems [55,56]. Currently, balsam fir and black spruce stands in the regeneration stage cover a large surface area in Canada due to the strong harvest ratio over the last 20 years. Thus, knowing the impacts of SBW activity on regeneration come to the fore. In this study, we evaluated the cumulative and annual defoliation of conifer seedlings and the factors influencing the vulnerability of conifer regeneration to insect outbreaks, e.g., species, seedling height, and distance from residual forests. We quantified SBW-related defoliation within plots that had undergone clearcutting forestry management. This study was an initial step in improving a methodology for upcoming research regarding the impacts of SBW defoliation on conifer regeneration after silvicultural treatments. Our research, therefore, represents a major contribution in providing a first diagnosis of the vulnerability of conifer seedlings during periods of insect outbreak in clearcut boreal forests.

First, seedling vulnerability differed between balsam fir and black spruce seedlings in terms of cumulative defoliation; balsam fir seedlings were more affected by SBW than black spruce seedlings. These observations confirm our first hypothesis and agree with previous studies (e.g., References [57,58]) that had compared levels of defoliation between species and demonstrated balsam fir's greater vulnerability to SBW activity [25]. The phenological synchrony between balsam fir budburst and the emergence of SBW larvae could explain this heightened vulnerability [59]. Black spruce budburst occurs 10–14 days after balsam fir, and therefore the SBW larvae must feed on older black spruce foliage that is less suitable for larval development [27]. On the other hand, a later black spruce budburst would provide an excellent food supply for later-emerging larvae [26]. Fuentealba et al. [29] highlighted that black spruce foliage had a lower nutritional quality than that of balsam fir. However, this situation could change in the future as climate exerts a strong influence on black spruce phenology [28,60]. As such, the vulnerability of black spruce to SBW could increase as higher springtime temperatures could decrease the gap between black spruce budburst and the emergence of SBW larvae [61]. Consequently, we recommend that regeneration vulnerability to SBW outbreak be accounted for in forest management

strategies, e.g., sites and species selection, when adapting to projected climate change scenarios. Therefore, our study was located in black spruce stands, where balsam fir was the secondary conifer (almost absent in some plots). Even if our results between both species were significantly different, we recommend the development of future research with more replications to better understand the differences between species vulnerability.

Second, the level of defoliation differed depending on conifer seedling height. Thus, the composition of the forest overstory and seedling height influence understory regeneration vulnerability to SBW activity, as observed by Cotton-Gagnon (2018). In agreement with our second hypothesis, defoliation level was positively correlated with seedling height. Similar results were obtained by Nie and MacLean [22] who observed greater defoliation in balsam fir seedlings having a height >30 cm than the smaller seedlings [22]. The relationship between seedling height and defoliation could be explained by the wider crowns that increase larvae density on taller seedlings [62]. SBW larvae fall from the upper to lower branches of mature trees before reaching the understory; thus, overstory vegetation and taller seedlings provide a protector effect for smaller seedlings [38].

Stand composition, stand density, and seedling location can also influence defoliation and mortality of regeneration [22,63]. Nie et al. [22] observed that softwood or mixedwood stands favored higher defoliation of balsam fir seedlings. Swaine [63] demonstrated that seedlings protected by a canopy are less susceptible to defoliation than seedlings situated within an open area. Our observations of black spruce seedlings were similar, as seedlings within clearcut areas were twice as defoliated as seedlings within the residual stands. Thus, the open canopy conditions created by clearcutting affected the distribution of species, the type of regeneration [64], and regeneration mortality caused by defoliation. We could not confirm the influence of distance from the residual forest on seedling defoliation. We used a medium-long distance transect (40 m); this distance may be insufficient to identify distance effects on defoliation within open areas. Further research is required to better understand the effect of distance on seedling defoliation using both a longer distance, more plot replications and a greater number of transects within each plot.

Clearcutting is the most widely used harvesting method in Canada [13]. Clearcutting leads to highly fragmented landscapes, declines in habitat diversity, and losses of productivity [65–68]. For this reason, ecosystem-based management proposes partial cuttings as a means of timber harvesting that attempt to (i) preserve the long-term structure and ecological processes responsible for maintaining forest productivity and (ii) ensure ecosystem integrity, biodiversity, and sustainability [55]. Recently, these silvicultural treatments have been adopted within the boreal forest [69,70]. Based on our findings, we consider evaluating the vulnerability of seedlings to SBW outbreaks within partial-cutting sites to be an essential future study requirement. We would hypothesize that, relative to clearcutting, partial cutting would result in lower defoliation of seedlings as the residual stand could protect seedlings from SBW activity.

5. Conclusions

Much effort is being placed on the study of insect outbreaks in the boreal forest to better understand the spatial patterns, future scenarios, insect-climate interactions, and past dynamics of insect outbreaks [71]. Under climate change scenarios, disturbance regimes in boreal forests are expected to be highly affected; for example, scenarios forecast an increase in the frequency and severity of fire, insect outbreaks, and windthrows [1]. Improving our understanding of the variability of natural disturbance cycles at multiple scales will be a major, yet important, challenge in mitigating the effects of climate change on boreal forests and adapting forest management in consequence. Insects outbreaks are a major disturbance agent in forest ecosystems. Tree defoliation affects productivity through reduced growth [72], increases tree mortality [73], decreases ecosystem resilience [74], modifies forest structure and dynamics [75], and heightens the vulnerability of the forest to other disturbances, e.g., windthrow [76]. Most studies focus on mature trees; nonetheless, the vulnerability of seedling regeneration to insect outbreak and the selection of silvicultural practices that minimize the effects of

insect outbreak on stand regeneration remain understudied aspects of forest ecology. Our research demonstrated how species and seedling height were the main factors that explained seedling defoliation levels. SBW affected balsam fir more than black spruce seedlings, and defoliation was greatest for taller seedlings. Although black spruce seedlings within residual stands experienced less defoliation than seedlings in open clearcutting areas, distance from the residual stand did not influence the level of seedling defoliation. These results improve our understanding of the effects of insect outbreaks on conifer regeneration. We suggest that studying the effect of SBW on seedlings should be a priority for the management strategies in Eastern Canadian boreal forests, particularly as boreal forests are expected to undergo marked change due to future warming.

Author Contributions: Conceptualization: M.M.G., H.M. Fieldwork: J.L., M.M.G. Data curation: J.L., M.M.G. Investigation: J.L., M.M.G., H.M. Methodology: M.M.G., J.L. Data analyses: J.L. Project administration: J.L., M.M.G. Resources: H.M. Supervision: H.M., M.M.G. Visualization and edition: J.L., M.M.G. Writing—original draft: J.L., M.M.G. Writing—review: M.M.G., J.L., H.M. Funding: H.M., M.M.G.

Funding: Funding was provided by the Contrat de service de recherche forestière du Ministère des forêts de la faune et des parcs from Québec (Canada) obtained by H.M. and M.M.G.

Acknowledgments: We thank A Bédard and JP Labrecque-Foy for field assistance and F Gionest for logistical help and essential support. We also thank M Cusson for his suggestions, technical advice, and validation of the statistical approach of an earlier version of this manuscript. We also thank MP Fournier for technical advice regarding statistical methods and M Hay for verifying the English of the text.

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

References

- Seidl, R.; Thom, D.; Kautz, M.; Martin-Benito, D.; Peltoniemi, M.; Vacchiano, G.; Wild, J.; Ascoli, D.; Petr, M.; Honkaniemi, J.; et al. Forest disturbances under climate change. *Nat. Clim. Chang.* **2017**, *7*, 395–402. [[CrossRef](#)] [[PubMed](#)]
- Montoro Girona, M.; Navarro, L.; Morin, H. A secret hidden in the sediments: Lepidoptera scales. *Front. Ecol. Evol.* **2018**, *6*, 1–5. [[CrossRef](#)]
- Montoro Girona, M.; Morin, H.; Lussier, J.-M.; Ruel, J.-C. Post-cutting mortality following experimental silvicultural treatments in unmanaged boreal forest stands. *Front. Forests Glob. Chang.* **2019**, *2*, 1–16. [[CrossRef](#)]
- Navarro, L.; Harvey, A.-É.; Ali, A.; Bergeron, Y.; Morin, H. A Holocene landscape dynamic multiproxy reconstruction: How do interactions between fire and insect outbreaks shape an ecosystem over long time scales? *PLoS ONE* **2018**, *15*, e0204316. [[CrossRef](#)]
- Waldron, K.; Ruel, J.-C.; Gauthier, S. The effects of site characteristics on the landscape-level windthrow regime in the North Shore region of Quebec, Canada. *Forestry* **2013**, *86*, 159–171. [[CrossRef](#)]
- De Grandpré, L.; Waldron, K.; Bouchard, M.; Gauthier, S.; Beaudet, M.; Ruel, J.-C.; Hébert, C.; Kneeshaw, D. Incorporating insect and wind disturbances in a natural disturbance-based management framework for the boreal forest. *Forests* **2018**, *9*, 471. [[CrossRef](#)]
- Ulanova, N.G. The effects of windthrow on forests at different spatial scales: A review. *For. Ecol. Manag.* **2000**, *135*, 155–167. [[CrossRef](#)]
- Boulanger, Y.; Gray, D.R.; Cooke, B.J.; De Grandpre, L. Model-specification uncertainty in future forest pest outbreak. *Glob. Chang. Biol.* **2016**, *22*, 1595–1607. [[CrossRef](#)] [[PubMed](#)]
- Alfaro, R.I.; Taylor, S.; Brown, R.G.; Clowater, J.S. Susceptibility of northern British Columbia forest to spruce budworm defoliation. *For. Ecol. Manag.* **2011**, *145*, 181–190. [[CrossRef](#)]
- MacKinnon, W. The Influence of Surrounding Forest Landscape and Stand Conditions on Stand Susceptibility and Vulnerability to Spruce Budworm in New Brunswick. Ph.D. Thesis, University of New Brunswick, Fredericton, NB, Canada, 1992; p. 20.
- Jetté, J.-P.; Vaillancourt, M.-A.; Leduc, A.; Gauthier, S. Les enjeux écologiques de l'aménagement forestier. In *Aménagement Écosystémique en Forêt Boréale*; Presses de l'Université du Québec: Quebec City, QC, Canada, 2008; pp. 1–10.

12. Montoro Girona, M. À la Recherche de L'aménagement Durable en Forêt Boréale: Croissance, Mortalité et Régénération des Pessières Noires Soumises à Différents Systèmes Sylvicoles. Ph.D. Thesis, Université du Québec à Chicoutimi, Chicoutimi, QC, Canada, 2017; p. 287. [CrossRef]
13. National Forestry. National Forest and Forest Management Statistics. (Last Update 23 February 2017). Available online: http://nfdp.ccfm.org/index_e.php (accessed on 14 November 2018).
14. Gauthier, S.; Bernier, P.; Burton, P.J.; Edwards, J.; Isaac, K.; Isabel, N.; Jayen, K.; Le Goff, H.; Nelson, E.A. Climate change vulnerability and adaptation in the managed Canadian boreal forest. *Environ. Rev.* **2014**, *22*, 256–285. [CrossRef]
15. Ressources Naturelles Canada. La recherche au centre de foresteries des Laurentides de Ressources naturelles Canada « La tordeuse des bourgeons de l'épinette ». In *Spruce Budworm*; Ressources Naturelles Canada: Ottawa, ON, Canada, 2012; pp. 1–16.
16. Ressources Naturelles Canada. Tordeuse des Bourgeons de L'épinette (Fiche D'information). (Last Update 15 August 2016). Available online: <http://www.rncan.gc.ca/forets/feux-insectes-perturbations/principaux-insectes/13404> (accessed on 18 February 2018).
17. Morin, H.; Laprise, D.; Simard, A.A.; Amouch, A. Régime des épidémies de la tordeuse des bourgeons de l'épinette dans l'Est de l'Amérique du Nord. In *Aménagement Écosystémique en Forêt Boréale*; Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., Bergeron, Y., Eds.; Les Presses de l'Université du Québec: Quebec City, QC, Canada, 2008; pp. 165–192.
18. Logan, J.A.; Régnière, J.; Powell, J.A. Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Environ.* **2003**, *1*, 130–137. [CrossRef]
19. Navarro, L.; Morin, H.; Bergeron, Y.; Girona, M.M. Changes in spatiotemporal patterns of 20th century spruce budworm outbreaks in eastern canadian boreal forests. *Front. Plant Sci.* **2018**, *9*, 1905–1920. [CrossRef] [PubMed]
20. Blais, J. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Can. J. For. Res.* **1983**, *13*, 539–547. [CrossRef]
21. Rowe, J.S.; Scotter, G.W. Fire in the boreal forest. *Quat. Res.* **1973**, *3*, 444–464. [CrossRef]
22. Nie, Z.; MacLean, D.; Taylor, A.R. Forest overstory composition and seedling height influence defoliation of understory regeneration by spruce budworm. *For. Ecol. Manag.* **2018**, *409*, 353–360. [CrossRef]
23. Nie, Z.; Maclean, D.A.; Taylor, A.R. Disentangling variables that influence growth response of balsam fir regeneration during a spruce budworm outbreak. *For. Ecol. Manag.* **2019**, *433*, 13–23. [CrossRef]
24. MacKinnon, W.; MacLean, D. Effects of surrounding forest and site conditions on growth reduction of balsam fir and spruce caused by spruce budworm defoliation. *Can. J. For. Res.* **2004**, *34*, 2351–2362. [CrossRef]
25. Hennigar, C.R.; MacLean, D.; Quiring, D.T.; Kershaw, J.A.J. Differences in spruce budworm defoliation among balsam fir and white, red, and black spruce. *For. Sci.* **2008**, *54*, 158–166.
26. Nealis, V.G.; Régnière, J. Insect-host relationships influencing disturbance by the spruce budworm in a boreal mixedwood forest. *Can. J. For. Res.* **2004**, *34*, 1870–1882. [CrossRef]
27. Blais, J. Some relationships of the spruce budworm, *Choristoneura fumiferana* (CLEM.) to black spruce, *Picea mariana* (MOENCH) Voss. *For. Chron.* **1957**, *33*, 364–372. [CrossRef]
28. Pureswaran, D.S.; De Grandpré, L.; Paré, D.; Taylor, A.; Barette, M.; Morin, H.; Régnière, J.; Kneeshaw, D.D. Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. *Ecology* **2015**, *96*, 1480–1491. [CrossRef]
29. Fuentealba, A.; Bauce, É. Carry-over effects of host nutritional quality on performance of spruce budworm progeny. *Bull. Entomol. Res.* **2012**, *102*, 275–284. [CrossRef] [PubMed]
30. Bauce, É.; Crépin, M.; Carisey, N. Spruce budworm growth, development and food utilization on young and old balsam fir trees. *Oecologia* **1994**, *97*, 499–507. [CrossRef] [PubMed]
31. Cotton-Gagnon, A.; Simard, M.; De Grandpré, L.; Kneeshaw, D. Salvage logging during spruce budworm outbreaks increases defoliation of black spruce regeneration. *For. Ecol. Manag.* **2018**, *430*, 421–430. [CrossRef]
32. Bognounou, F.; De Grandpré, L.; Pureswaran, D.S.; Kneeshaw, D. Temporal variation in plant neighborhood effects on the defoliation of primary and secondary hosts by an insect pest. *Ecosphere* **2017**, *8*, 1–15. [CrossRef]
33. Maclean, D.; Piene, H. Spatial and temporal patterns of balsam fir mortality in spaced and unspaced stands caused by spruce budworm defoliation. *Can. J. For. Res.* **1995**, *25*, 902–911. [CrossRef]
34. Piene, H. Spruce budworm defoliation and growth loss in young balsam fir: Defoliation in spaced and unspaced stands and individual tree survival. *Can. J. For. Res.* **1989**, *19*, 1211–1217. [CrossRef]

35. Sainte-Marie, G.B.; Kneeshaw, D.D.; MacLean, D.A.; Hennigar, C.R. Estimating forest vulnerability to the next spruce budworm outbreak: Will past silvicultural efforts pay dividends? *Can. J. For. Res.* **2015**, *45*, 314–324. [[CrossRef](#)]
36. Baskerville, G. Spruce Budworm: The Answer Is Forest Management: Or Is It. *For. Chron.* **1975**, *51*, 157–160. [[CrossRef](#)]
37. MacLean, D. Forest management strategies to reduce spruce budworm damage in the Fundy Model Forest. *For. Chron.* **1996**, *72*, 399–405. [[CrossRef](#)]
38. Ruel, J.C.; Huot, M. Impacts de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) sur la régénération des sapinières après la coupe à blanc. *For. Chron.* **1993**, *69*, 163–172. [[CrossRef](#)]
39. Krause, C.; Morin, H.; Plourde, P.Y. Juvenile growth of black spruce (*Picea mariana* [Mill.] BSP) stands established during endemic and epidemic attacks by spruce budworm (*Choristoneura fumiferana* [Clemens]) in the boreal forest of Quebec, Canada. *For. Chron.* **2009**, *85*, 267–276. [[CrossRef](#)]
40. Piene, H.; Maclean, D.A.; Landry, M. Spruce budworm defoliation and growth loss in young balsam fir: Relationships between volume growth and foliage weight in spaced and unspaced, defoliated and protected stands. *For. Ecol. Manag.* **2003**, *179*, 37–53. [[CrossRef](#)]
41. Ministère des Ressources Naturelles. *Plan D'aménagement Forestier Intégré Tactique: Unité D'aménagement 024-51*; Secteur des Opération Régionales, Ed.; Ministère des Ressources Naturelles: Quebec City, QC, Canada, 2013; p. 360.
42. Rossi, S.; Morin, H.; Deslauriers, A.; Plourde, P.Y. Predicting xylem phenology in black spruce under climate warming. *Glob. Chang. Biol.* **2011**, *17*, 614–625. [[CrossRef](#)]
43. MDDELCC. Normales Climatiques du Québec 1981–2010: Péribonka. (Last Update 2018). Available online: <http://www.mddelcc.gouv.qc.ca/climat/normales/sommaire.asp?cle=7065960> (accessed on 13 April 2018).
44. Gouvernement du Canada. Canadian Climate Normals 1981–2010 Station Data. (Last Update 11 January 2018). Available online: http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?searchType=stnProv&lstProvince=QC&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=5889&dispBack=0 (accessed on 13 April 2018).
45. Robitaille, A.; Saucier, J.P. *Paysages du Québec méridional*; Les Publications du Québec: Québec, QC, Canada, 1998; p. 213.
46. Raymond, R.; Mailloux, A.; Dubé, A. *Pédologie de la Région du Lac-Saint-Jean*; Ministère de l'Agriculture et de la Colonisation: l'Alimentation, QC, Canada, 1965; p. 159.
47. Gouvernement du Québec. I.G.O.—Données Écoforestières. (Last Update 30 November 2017). Available online: <https://geoegl.msp.gouv.qc.ca/igo/mffpecofor/> (accessed on 27 March 2018).
48. MFFP. *Aires Infestées par la Tordeuse des Bourgeons de L'épinette au Québec en 2016*; Ministère des Forêts, de la Faune et des Parcs: l'Alimentation, QC, Canada, 2016; p. 20.
49. Fenton, N.; Imbeau, L.; Work, T.; Jacobs, J.; Bescond, H.; Drapeau, P.; Bergeron, Y. Lessons learned from 12 years of ecological research on partial cuts in black spruce forests of northwestern Quebec. *For. Chron.* **2013**, *89*, 350–359. [[CrossRef](#)]
50. Hunter, M.L. *Wildlife, Forests, and Forestry: Principales of Managing Forests for Biological Diversity*; Prentice-Hall: Englewood Cliffs, NJ, USA, 1990; p. 370.
51. MacLean, D.; Erdle, T. Development of relationships between spruce budworm defoliation and forest stand increment in New Brunswick. In *Environmental Influences on Tree and Stand Increment*; Solomon, D., Brann, T., Eds.; Maine Agricultural Experiment Station: Durham, NH, USA, 1985; pp. 106–115.
52. Anderson, M.J.; Gorley, R.; Clarke, K. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*; Primer-E Ltd.: Plymouth, UK, 2008; p. 218.
53. Clarke, K.; Gorley, R.; Somerfield, P.; Warwick, R. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, 3rd ed.; Primer-E Ltd.: Plymouth, UK, 2014; p. 262.
54. Triola, M.; Triola, M. *Biostatistique Pour Les Sciences de la Vie et de la Santé*; Pearson: Montreuil, France, 2012; p. 367.
55. Gauthier, S.; Vaillancourt, M.-A.; Leduc, A.; Kneeshaw, D.; Drapeau, P.; De Grandpré, L.; Claveau, Y.; Paré, D. *Ecosystem Management in the Boreal Forest*; Presses de l'Université du Québec: Quebec City, QC, Canada, 2009; p. 570.
56. Prévost, M.; Raymond, P.; Lussier, J.-M. Regeneration dynamics after patch cutting and scarification in yellow birch—Conifer stands. *Can. J. For. Res.* **2010**, *40*, 357–369. [[CrossRef](#)]

57. Fuentealba, A.; Bauce, É. Interspecific variation in resistance of two host tree species to spruce budworm. *Acta Oecol.* **2016**, *70*, 10–20. [[CrossRef](#)]
58. Nealis, V.G. Comparative ecology of conifer-feeding spruce budworms (Lepidoptera: Tortricidae). *Can. Entomol.* **2016**, *148*, S33–S57. [[CrossRef](#)]
59. Chabot, M.; Boulet, B.; Morneau, L. La tordeuse des bourgeons de l'épinette. In *Le Guide Sylvicole du Québec: Les Fondements Biologiques de la Sylviculture. Tome 1*; Les Publications du Québec: Québec, QC, Canada, 2013; pp. 400–413.
60. Fuentealba, A.; Pureswaran, D.S.; Bauce, É.; Despland, E. How does synchrony with host plant affect the performance of an outbreaking insect defoliator? *Oecologia* **2017**, *184*, 847–857. [[CrossRef](#)]
61. Bronson, D.R.; Gower, S.T.; Tanner, M.; Van Herk, I. Effect of ecosystem warming on boreal black spruce bud burst and shoot growth. *Glob. Chang. Biol.* **2009**, *15*, 1534–1543. [[CrossRef](#)]
62. Cotton-Gagnon, A. Effets de Facteurs Naturels et de la Coupe de Récupération sur la Défoliation de la Régénération Préétablie Pendant une Épidémie de la Tordeuse des Bourgeons de L'épinette. Master's Thesis, Université Laval, Quebec City, QC, Canada, 2017; p. 50.
63. Swaine, J.M. The relation of insect activities to forest development as exemplified in the forest of eastern North America. *For. Chron.* **1933**, *9*, 9–32. [[CrossRef](#)]
64. Montoro Girona, M.; Lussier, J.-M.; Morin, H.; Thiffault, N. Conifer regeneration after experimental shelterwood and seed-tree treatments in boreal forests: Finding silvicultural alternatives. *Front. Plant Sci.* **2018**, *9*, 1145–1159. [[CrossRef](#)] [[PubMed](#)]
65. Rosenvald, R.; Löhmus, A. For what, when, and where is green-tree retention better than clear-cutting? A review of the biodiversity aspects. *For. Ecol. Manag.* **2008**, *255*, 1–15. [[CrossRef](#)]
66. Fischer, J.; Lindenmayer, D. Landscape modification and habitat fragmentation: A synthesis. *Glob. Ecol. Biogeogr.* **2007**, *16*, 265–280. [[CrossRef](#)]
67. Puettmann, K.J.; Wilson, S.M.; Baker, S.C.; Donoso, P.J.; Drössler, L.; Amente, G.; Harvey, B.D.; Knoke, T.; Lu, Y.; Nocentini, S.; et al. Silvicultural alternatives to conventional even-aged forest management—What limits global adoption? *For. Ecosyst.* **2015**, *2*, 1–16. [[CrossRef](#)]
68. Groot, A.; Lussier, J.-M.; Mitchell, A.K.; MacIsaac, D.A. A silvicultural systems perspective on changing Canadian forestry practices. *For. Chron.* **2005**, *81*, 50–56. [[CrossRef](#)]
69. Montoro Girona, M.; Morin, H.; Lussier, J.-M.; Walsh, D. Radial growth response of black spruce stands ten years after experimental shelterwoods and seed-tree cuttings in boreal forest. *Forests* **2016**, *7*, 240. [[CrossRef](#)]
70. Montoro Girona, M.; Rossi, S.; Lussier, J.-M.; Walsh, D.; Morin, H. Understanding tree growth responses after partial cuttings: A new approach. *PLoS ONE* **2017**, *12*, e0172653. [[CrossRef](#)]
71. Zhang, X.; Lei, Y.; Ma, Z.; Kneeshaw, D.; Peng, C. Insect-induced tree mortality of boreal forests in eastern Canada under a changing climate. *Ecol. Evol.* **2014**, *4*, 2384–2394. [[CrossRef](#)] [[PubMed](#)]
72. Blais, J.R. The vulnerability of balsam fir to spruce budworm attack in northwestern Ontario, with special reference to the physiological age of tree. *For. Chron.* **1958**, *34*, 405–422. [[CrossRef](#)]
73. Bergeron, Y.; Leduc, A.; Morin, H.; Joyal, C. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Can. J. For. Res.* **1995**, *25*, 1375–1384. [[CrossRef](#)]
74. Johnstone, J.F.; Allen, C.D.; Franklin, J.F.; Frelich, L.E.; Harvey, B.J.; Higuera, P.E.; Mack, M.C.; Meentemeyer, R.K.; Metz, M.R.; Perry, G.L.W.; et al. Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* **2016**, *14*, 369–378. [[CrossRef](#)]
75. Bouchard, M.; Kneeshaw, D.; Messier, C. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. *Can. J. For. Res.* **2007**, *37*, 763–772. [[CrossRef](#)]
76. Taylor, S.L.; MacLean, D.A. Legacy of insect defoliators: Increased wind-related mortality two decades after a spruce budworm outbreak. *For. Sci.* **2008**, *55*, 256–267.

