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Does the type of silvicultural practice influence spruce budworm defoliation of seedlings?

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Abstract. Spruce budworm (*Choristoneura fumiferana* (Clem)) is the main defoliator in the boreal forest of North America, and its outbreaks have major ecological and economic consequences and represent a challenge for forest management. Numerous studies have addressed the effects of this defoliator on mature trees, whereas the effects of spruce budworm on regeneration remain elusive. Furthermore, intensive exploitation practices during the last decades have left a large area of the Canadian boreal forest in an early development stage. In this context, it becomes vital to understand those factors affecting the severity of spruce budworm-related defoliation on regeneration. Here, we determine the defoliation severity of black spruce and balsam fir seedlings in both mature pure black spruce and black spruce–balsam fir stands subjected to two different silvicultural treatments (clear-cutting and partial cutting). Defoliation intensity varied between stand types, silvicultural treatments, species, and height classes. Seedlings in black spruce–balsam fir stands experienced twice the defoliation of those in pure black spruce stands (black spruce seedlings 10% vs. 23%; balsam fir seedlings 29% vs. 47%, respectively). Harvesting methods also influenced seedling defoliation. Under clear-cutting, black spruce seedlings (24%) were three times as defoliated as black spruce seedlings in partial cutting stands (8%), whereas balsam fir seedlings in clear-cutting plots experienced twice the defoliation (42%) of balsam fir seedlings in partial cutting plots (20%). The level of defoliation also increased with seedling height. This study will help silvicultural strategies adapt to the effects of natural disturbance regimes. As the intensity and severity of defoliator outbreaks are expected to increase under climate change, these results will help guide forest management strategies to select harvesting methods that will limit the effects of defoliation on conifer regeneration.

Key words: balsam fir; black spruce; boreal forest; clear-cut; forest damages; global change; insect outbreaks; natural disturbances; partial cuttings; seedlings; silviculture; sustainable forest management.

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Introduction

Natural and anthropogenic disturbances are key elements in forest ecosystem dynamics, structure, and composition (Seidl et al. 2017, Montoro Girona et al. 2018*a*, Labrecque-Foy et al. 2020). Fire, windthrow, and insect outbreak are the most common natural disturbances in the boreal forest (Ulanova 2000, De Grandpré et al. 2018, Ressources naturelles Canada 2018). Although multiple human activities, such as oil and gas extraction and hydroelectric development, affect the boreal forest, the main disturbance remains forest harvesting (Schindler and Lee 2010, Gauthier et al. 2015). The boreal forest covers 14% of the world land area and provides more than 33% of the world's harvested timber; sustainable forest management of this biome is vital (Ressources naturelles Canada 2018). The immediate challenge therefore is to balance forest harvesting, biodiversity conservation, and climate change uncertainties for this biome (Ressources naturelles Canada 2018).

Insect outbreaks and harvesting are major drivers within forest landscapes because of their major ecological consequences. Spruce budworm (*Choristoneura fumiferana* (Clem); SBW) outbreaks represent the most important natural disturbance in terms of affected area—even more than fire—in the eastern North American boreal forest (Blais 1983). In 2019, more than 9 million ha of the boreal forest in Quebec (Canada) was affected by a SBW outbreak (MFFP 2019), an areal extent equivalent to the state of Maine (USA). Forest damage occurs when SBW larvae repeatedly feed on the annual foliage of mature balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss.), and black spruce (*Picea mariana* (Mill.) BSP), which leads to radial growth suppression and tree mortality (Blais 1958, 1962, MacLean 1980). SBW is therefore responsible for marked losses in forest productivity with an important effect on economic activities.

The last decades have been marked by a heightened global demand for wood and wood products. In response, harvesting practices have intensified, and this anthropic pressure on the boreal forest has increased (Jetté et al. 2008, Montoro Girona 2017). Between 1990 and 2016, the harvested area within Canada reached 24 million ha, of which more than 20 million ha (83%) was harvested using clear-cutting methods (National Forestry 2017). Consequently, much of the North American boreal forest currently exists at an early developmental stage. Stand renewal is key to ensuring the persistence of forest ecosystems, and the establishment of regeneration can be compromised by the loss of seed trees owing to high rates of tree mortality.

With a high harvest volume and low operational costs, clear-cutting represents the most widely applied harvest practice in the Canadian boreal forest. Clear-cutting, however, leads to a simplified stand structure, a decline in habitat diversity, an increase in landscape fragmentation, and a decrease in stand productivity (Fischer and Lindenmayer 2007, Puettmann et al. 2015). Ecosystem-based management has emerged as a novel approach from which partial cutting has been proposed as an alternative harvesting approach within the boreal forest. Partial cutting attempts to reduce differences between natural and managed ecosystems to favor ecosystem integrity, biodiversity conservation, and long-term sustainability (Gauthier et al. 2009, Montoro Girona et al. 2016, Kim et al. 2021). Partial cutting involves harvesting a lower volume of timber, thereby limiting the number and size of openings in the canopy. This practice helps shade-tolerant species, such as black spruce and balsam fir, to establish in the understory (Montoro Girona 2017). The effects of harvesting intensity on radial growth response, tree mortality, and tree regeneration success are well studied (Pamerleau-Couture et al. 2015, Montoro Girona 2017); however, no studies have documented the effects of silvicultural practices on seedling defoliation.

Although SBW prefers mature trees, recent studies confirm that regeneration can experience defoliation in cases where mature trees are severely affected (Cotton-Gagnon et al. 2018, Lavoie et al. 2019). On the other hand, information remains limited regarding the susceptibility and vulnerability of conifer seedlings to SBW and the factors affecting defoliation intensity. This lack of information is present despite regeneration being the main mechanism of stand renewal (Morin and Laprise 1997). Seedling defoliation can be affected by several ecological factors, including tree species, stand type, stand density, height class, and the spatial distribution of seedlings. An improved understanding of the factors that affect the defoliation of regeneration is vital for ensuring the sustainable management of the boreal forest. Under global change scenarios, SBW outbreaks are likely to increase in severity and frequency, thereby affecting tree mortality. Therefore, understanding the effects of SBW on regeneration in North American boreal forests must be a priority (Candau and Fleming 2011, Navarro 2013, Seidl et al. 2017).

Given the lack of research involving the interaction of multiple disturbances, we investigated the effect of harvesting methods on the severity of SBW-related defoliation on conifer regeneration in the eastern Canadian boreal forest. We aimed specifically to measure the defoliation of balsam fir and black spruce seedlings on the basis of stand characteristics, in relation to stand type (pure black spruce stand or black spruce–balsam fir stand), harvesting method (partial cutting or clear-cutting), and seedling characteristics (species, spatial distribution, and height class). We predicted that (1) the higher balsam fir density in black spruce–balsam fir stand increases defoliation of the regeneration; (2) the lower overstory density of the clear-cutting stands heightens seedling defoliation; (3) as the most susceptible and vulnerable species, balsam fir regeneration experiences higher defoliation; (4) seedlings inside the residual strips (within partial cutting plots) or nearer to mature stands (within clear-cutting plots) are subjected to less defoliation because of the protective effect offered by mature trees; and (5) taller seedlings experience more defoliation than smaller seedlings.

Materials and Methods

Study area

We conducted our study in the boreal forest of the North Shore region in Quebec (Canada). The study area extended from 49.9° to 49.7° N and 69.8° to 69.5° W, covering 588 km^2 in the black spruce–feather moss bioclimatic domain (Saucier et al. 1998; Fig. 1). In 2019, the North Shore region was the most SBW-affected region in Quebec in terms of area, having more than 3.6 million ha damaged—this extent was 0.7 million ha greater than the area affected in 2014 (2.9 million ha), a previous year of extensive SBW-related defoliation (Fig. 1B; MFFP 2015, 2019). The study region has been managed intensively over the last decades with 48,493 km^2 of the forest surface harvested, which represents 55% of the area subjected to forestry exploitation in this region. Clear-cutting is the main harvesting method used in these exploited regions (Bureau du forestier en chef 2015; Fig. 1C, D). Regional climate is subhumid subpolar with a short growing season (140 d; Rossi et al. 2011), an annual mean temperature between −2.5° and 1.0°C (Morneau and Landry 2007), and average annual precipitation ranges between 1200 and 1300 mm (MDDELCC 2018). At the sites, the average slope is 8%, surface deposits are mainly thick glacial till, and rocky outcrops are mostly gneiss (Robitaille and Saucier 1998).

Experimental design

We selected 20 sites within an area that was recently affected by SBW. Our selection relied on the forest inventory data of the Quebec Ministry of Forestry, Wildlife, and Parks (Gouvernement du Québec 2016, MFFP 2017) and two main criteria: (1) stand type and (2) harvesting method (Fig. 1). We selected two stand types on the basis of species composition: pure black spruce and black spruce–balsam fir forests. Pure stands contain black spruce covering ≥75% of the basal area. Black spruce–balsam fir stands include black spruce representing at least 50% of the stand basal area and balsam fir, as a codominant species, with at least 25% of the stand basal area (Appendix S1: Fig. S1). The selected harvesting methods were clear-cutting and partial cutting. Within each stand type, we selected five replications for each harvesting method. All study sites had been harvested between 2000 and 2008. We also selected one untreated stand per site as a control plot. Based on the annual reporting of spruce budworm defoliation (aerial surveys), our study area was affected by a severe defoliation from 2014 to 2018 (MFFP 2018). We undertook an exhaustive exploration of the study area before our data collection to verify on the field that the study sites selected with the inventory data were able to ensure the accuracy of our selection criteria.

Measurements and data compilation

To ensure a similar level of outbreak severity between both harvesting methods, we evaluated the overall defoliation of mature trees at each site. For these measurements—all sampling

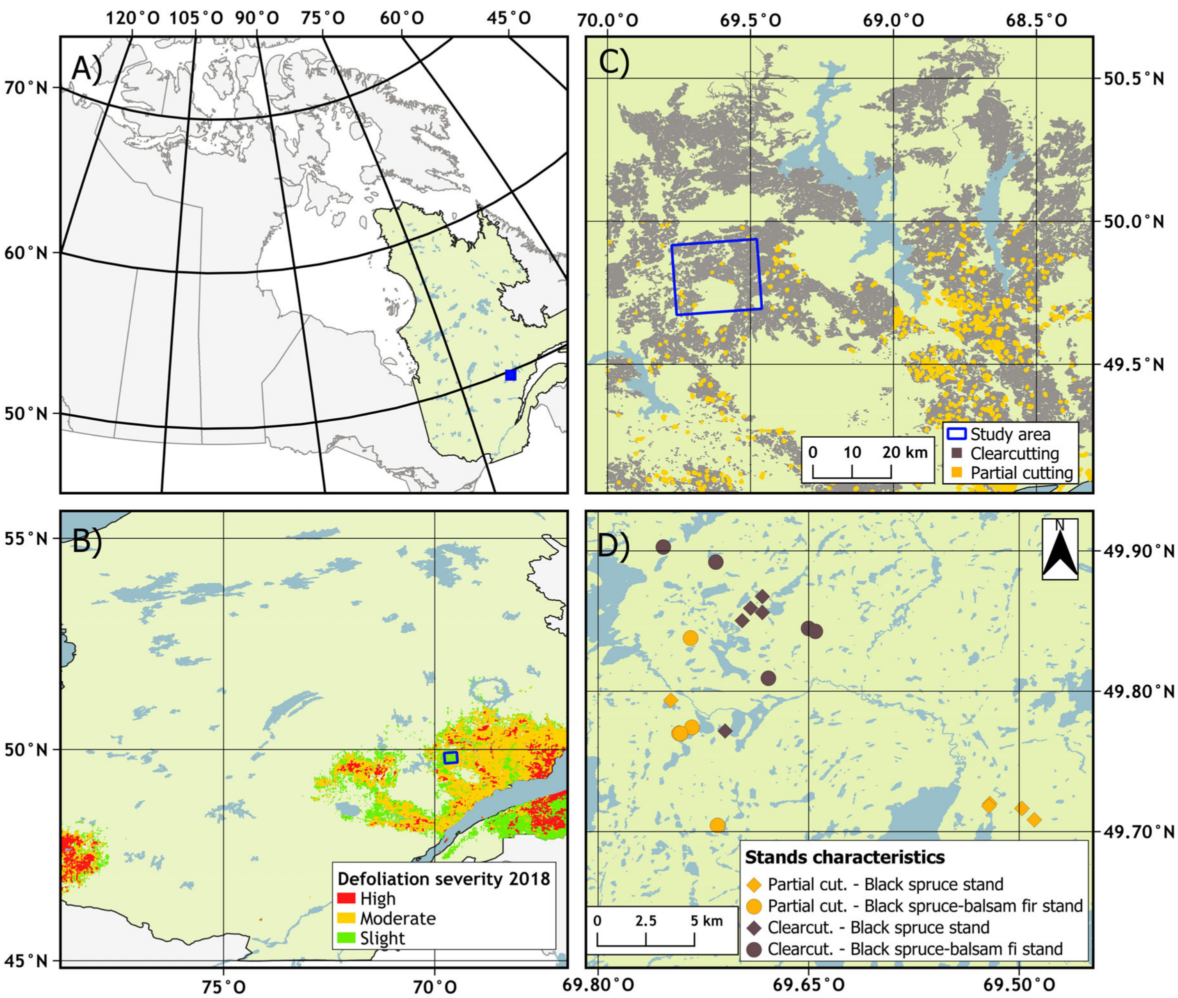

Fig. 1. (A) Study area in the province of Quebec, Canada; (B) SBW defoliation severity in 2018 based on aerial survey data (Gouvernement du Québec 2016) in the North Shore region of Quebec; (C) harvesting methods used in the study area; (D) location of experimental plots. Stands were selected according to stand characteristics; that is, stand type as pure black spruce (diamonds) or black spruce–balsam fir mixed (circles) stands, and harvesting method, that is, clear-cutting (gray) or partial cutting (orange).

occurred in the summer 2018—we randomly selected 30 mature trees and then estimated the percentage of defoliated needles over total foliage.

We undertook an inventory of seedlings after the seasonal SBW defoliation of 2018. We established a 20-m^2 rectangular control plot (10 × 2 m) in each untreated stand (Fig. 2). Within clear-cutting sites, we set up two 60-m^2 rectangular plots (30 × 2 m) within the harvested area. In partial cutting stands, we established a 60-m^2 rectangular plot (30 × 2 m) in the harvested area for each study site.

We measured each conifer seedling located within the established plots during summer 2018 (after the seasonal SBW defoliation). We recorded species, height, and the existing cumulative defoliation (Table 1). Cumulative defoliation, as a measure of the severity of SBW-related defoliation, was evaluated as the percentage of defoliated needles over total foliage (Fig. 3; MFFP 2014, FPInnovations 2015). To evaluate the defoliation, we used the actual percentage of defoliation to be accurate. Fig. 3 is a representation to visualize defoliation level and was adapted from Lavoie et al. (2019).

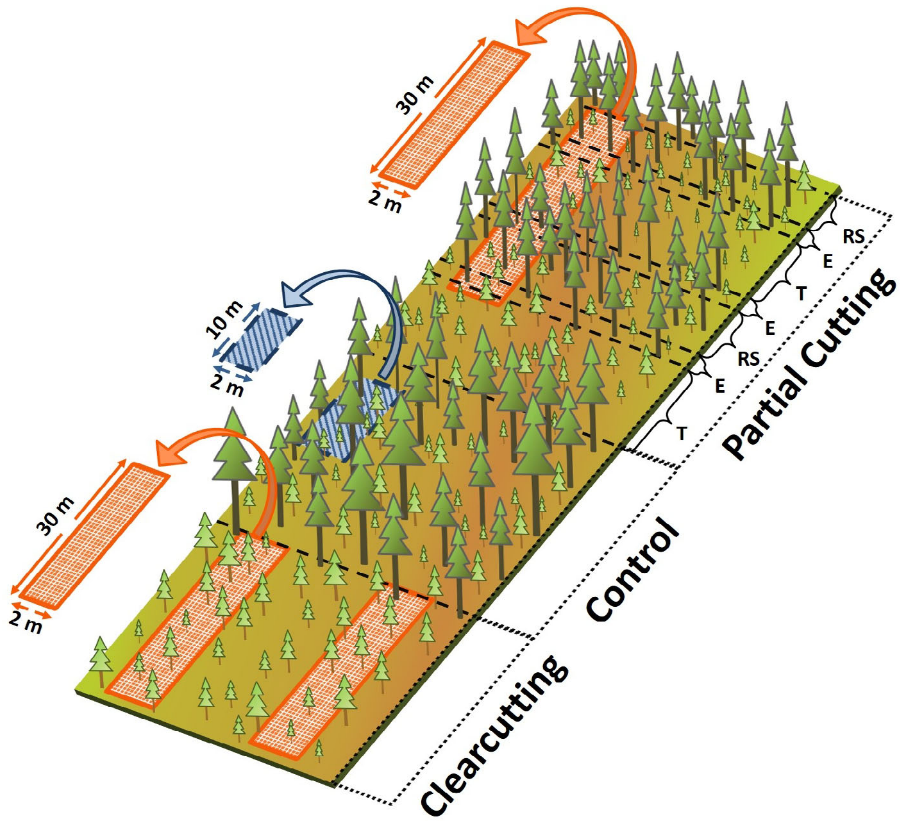

Fig. 2. Schematic representation of a sampling plot in clear-cutting, control, and partial cutting stands. Positions are defined as T, trail; E, edge; and RS, residual strip. The blue and orange rectangles represent the sampling plot in the control (20 m^2) and the cutting (60 m^2) areas, respectively.

We divided height measurements into five classes: (1) 0–14.9 cm, (2) 15–29.9 cm, (3) 30–44.9 cm, (4) 45–100 cm, and (5) ≥101 cm.

We also recorded the spatial location of each seedling (Table 1). For all seedlings within the clear-cutting plots, we measured the distance between the seedling and the mature stand. We defined distance categories in the clear-cutting plots as near (residual stand ≤10 m distance from seedling to stand), intermediate (10.1–20.0 m), and distant (20.1–30.0 m). To represent the spatial heterogeneity of partial cutting stands, we sampled seedlings from the locations identified as trail (T), edge (E), and residual strip (RS).

Data analysis

We conducted a permutational multivariate analysis of variance (PERMANOVA) based on a Euclidian distance matrix (Anderson 2001). PERMANOVA evaluated the effects of stand type, harvesting method, species, height, spatial location (distance or position), and their interactions on seedling defoliation. We compared mature stand defoliation between stand types and harvesting method. When factors were significantly dissimilar ($P < 0.05$), we ran post hoc permutational *t*-tests to highlight pairwise differences between levels. The analyses were performed using type II sum of squares with 199 permutations of residuals under a reduced model using Primer 6.1.16 (PRIMER-E 2013). These criteria are recommended when the design is unbalanced (Langsrud 2003).

We conducted separate tests for each seedling species to reduce the overestimation of black spruce defoliation induced by elevated balsam fir defoliation. We also ran separate analyses for the spatial distribution of seedlings to evaluate the distance effect (clear-cutting) and the position

Table 1. Seedling characteristics by species, height, and spatial location.

Stand type by harvesting method	Seedling species	No. seedlings	Height (cm) 0–14.9	15–29.9	30–44.9	45–100.0	≥100.1	Spatial location (distance or position) C	N or T	I or E	D or RS
Clear-cutting											
Pure black spruce stand	Black spruce	684	4	60	103	194	323	158	184	178	164
	Balsam fir	36	0	0	4	4	28	4	3	19	10
	Total	720	4	60	107	198	351	162	187	197	174
Mixed stand	Black spruce	490	12	64	76	110	228	113	138	150	89
	Balsam fir	407	37	84	55	49	182	124	112	80	91
	Total	897	49	148	131	159	410	237	250	230	180
Total		1617	53	208	238	357	761	399	437	427	354
Partial cutting											
Pure black spruce stand	Black spruce	2134	667	759	350	246	112	221	1118	530	265
	Balsam fir	377	70	133	47	53	74	140	76	67	94
	Total	2511	737	892	397	299	186	361	1194	597	359
Mixed stand	Black spruce	482	46	131	89	92	124	88	146	123	125
	Balsam fir	429	49	84	79	75	142	91	125	70	143
	Total	911	95	215	168	167	266	179	271	193	268
Total		3422	832	1107	565	466	452	540	1465	790	627

Note: Spatial locations within clear-cutting plots correspond to distance (abbreviations are C, control; N, near; I, intermediate; and D, distant), and position category (abbreviations are C, control; T, trail; E, edge; and RS, residual strip) refers to partial cutting plots.

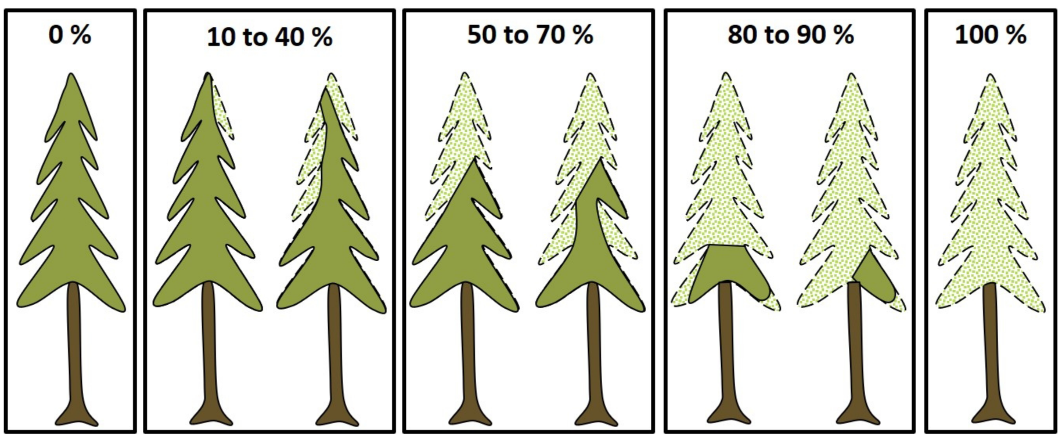

Fig. 3. Methodology used to estimate the cumulative defoliation (adapted from Lavoie et al. [2019]). Defoliation varied between 0% and 100%; light green branches represent defoliation, and dark green branches represent unaffected foliage.

effect (partial cutting) because of the differences in the post-harvesting stand structures.

Results

Effect of stand type and harvesting method on stand defoliation

We evaluated stand defoliation through the overall defoliation of mature trees. Black spruce–balsam fir stands presented 1.7× more defoliation than pure black spruce stands, with mean defoliation levels of 66% and 39%, respectively (Table 2). Both harvesting methods affected mature trees equally, producing a mean defoliation of 47%. We identified no significant interaction between the stand type and harvesting method for the defoliation of mature trees.

Factor influencing the defoliation severity of regeneration

The effect on seedling defoliation differed between stand types (Appendix S1: Table S1). Black spruce seedlings were more than twice as defoliated in black spruce–balsam fir stands (23%) than in pure black spruce stands (10%; $F_{1.3666}$ = 79.72, P = 0.005; Fig. 4A), whereas balsam fir seedlings presented 1.6× more defoliation in black spruce–balsam fir stands (47%) than in pure black spruce stands (29%; $F_{1.1223}$ = 69.26, P = 0.005; Fig. 4B).

Harvesting methods influenced the degree of seedling defoliation (Fig. 4C, D). For both species of seedling, clear-cutting resulted in greater defoliation than partial cutting. Clear-cutting also affected black spruce seedlings three times as much (24%) as those in partial cutting plots (8%; $F_{1.3666}$ = 7.24, P = 0.01). Balsam fir seedlings were twice as defoliated in clear-cutting plots (42%) than partial cutting plots (20%; $F_{1.1223}$ = 14.93, P = 0.005). Interactions between stand type and harvesting method were not significant for black spruce seedlings ($F_{1.3666}$ = 2.21, P = 0.19), whereas these interactions were significant for balsam fir seedlings ($F_{1.1223}$ = 11.13, P = 0.005). Balsam fir seedlings associated with clear-cutting presented similar levels of defoliation for both stand types (t = 1.34, P = 0.175; 54% in pure black spruce stands and 46% in black spruce–balsam fir stands). Balsam fir seedlings in clear-cutting plots, however, were more affected than balsam fir seedlings in partial cutting plots (t = 2.69, P = 0.015). Finally, in the partial cutting plots, balsam fir seedlings in black spruce–balsam fir stands experienced greater defoliation than in pure black spruce stands (t = 10.225, P = 0.005; 38% for black spruce–balsam fir and 17% for pure black spruce).

Seedling characteristics also influenced the level of defoliation (Appendix S1: Table S1). Balsam fir seedlings presented 2.7× more defoliation than black spruce seedlings ($F_{1.4925}$ = 755.26, P = 0.01)—mean defoliation of 35% and 13% for balsam fir and black spruce, respectively.

Seedling defoliation differed between distance categories in the clear-cutting plots (black spruce $F_{3.1166}$ = 27.83, P = 0.005; balsam fir $F_{3.435}$ = 7.75, P = 0.005; Fig. 5A–D). When we combined stand types, black spruce seedlings within the near, intermediate, and distant categories presented similar levels of defoliation, with a mean defoliation of 27% (t = 1.59, P = 0.12). All values were, however, higher than those of the control plots (13%; t = 6.18, P = 0.005). For balsam fir, defoliation with all stand types combined most affected the distant category, at an average defoliation of 59% (t = 2.35, P = 0.02). Defoliation of balsam fir seedlings in the near category was greater than in the control plots, with mean defoliations of 49% and 38%, respectively (t = 2.34, P = 0.005). Seedlings within the intermediate category (44%; t = 1.49, P = 0.165) did not differ in defoliation from either the control plots or the near category. For both seedling species, we did not observe an interaction between stand type and distance category (black spruce, $F_{3.1166}$ = 0.97, P = 0.455; balsam fir, $F_{3.435}$ = 1.03, P = 0.380).

For both species, when stand types were combined, the intensity of seedling defoliation differed between position categories in the partial cutting plots (Fig. 5E–H; black spruce, $F_{3.2472}$ = 16.558, P = 0.005; balsam fir, $F_{3.790}$ = 7.79, P = 0.005). Black spruce seedlings in the residual strips experienced the most defoliation (average 14%; t = 2.78, P = 0.01). Seedlings in the control and edge zones showed similar

Table 2. Results of permutational multivariate analysis of variance (PERMANOVA) for the overall defoliation of mature trees for stand type, harvesting method, and interaction of stand type × harvesting method.

Factor	df	SS	MS	Pseudo-F	P(perm)
Stand type	1	58,018	58,018	116.83	0.005**
Harvesting method	1	74.431	74.431	0.14988	0.73
Stand type × harvesting method	1	1478.4	1478.4	40.844	0.005**
Residuals	381	189,210	496.6		
Total	384	250,060			

Notes: Fixed factors: stand type (2 levels); harvesting methods (2 levels). Number of permutations: 199. df, degrees of freedom; SS, sum of squares; MS, mean squares; P(perm), significance.
** P < 0.01.

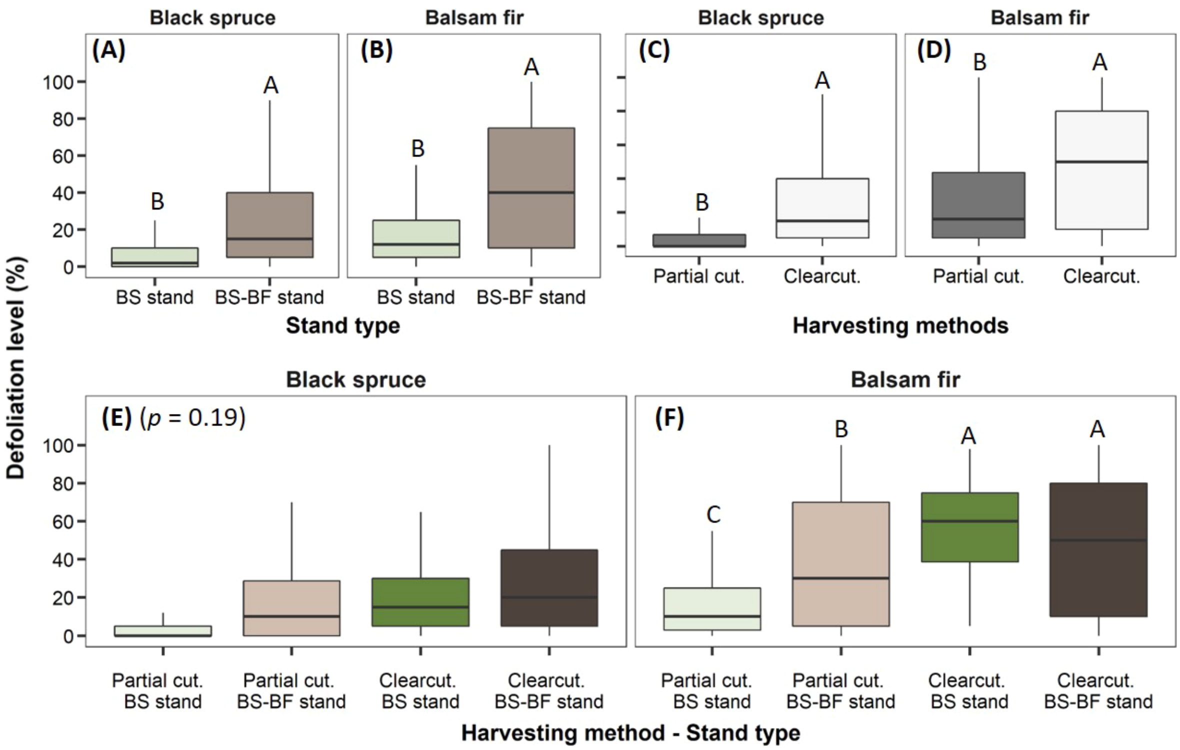

Fig. 4. Defoliation levels (%) for black spruce and balsam fir seedlings in relation to stand type, harvesting method, and the combined stand characteristics (harvesting method + stand type). Different letters represent significant differences between levels ($P < 0.05$), following A > B > C > D.

levels of defoliation (10% and 9%, respectively; $t = 0.38$, $P = 0.73$), although at defoliation levels higher than for seedlings in the trail zone (5.5%; $t = 2.80$, $P = 0.005$). Balsam fir seedlings in the residual strips experienced higher levels of defoliation than in the other position zones (35%; $t = 2.25$, $P = 0.035$), except for trail (32%; $t = 0.95$, $P = 0.355$). Balsam fir seedlings in the trail and edge zones were similarly affected (32% vs. 27%, respectively; $t = 1.47$, $P = 0.155$). All seedling positions in the partial cutting plots experienced greater defoliation than the control zone seedlings (19%; $t = 3.02$, $P = 0.015$). The interaction between stand type and position categories affected black spruce seedling defoliation (black spruce, $F_{3.2472} = 3.92$, $P = 0.005$; balsam fir, $F_{3.790} = 3.92$, $P = 0.02$). For all position categories, black spruce seedlings in pure black spruce stands presented lower levels of defoliation than those in the black spruce–balsam fir stands (6% vs. 19%; $t = 15.01$, $P = 0.005$; Fig. 5G). We observed a similar result for balsam fir seedlings—with the exception of seedlings in the residual strips of pure stands that experienced similar defoliation levels as seedlings in the control plots and in the edge category of black spruce–balsam fir stands (27% vs. 29% vs. 35%; $t = 1.75$, $P = 0.07$; Fig. 5H).

We observed a positive correlation between defoliation level and height class for both species (Fig. 6; black spruce, $F_{4.3666} = 321.76$, $P = 0.005$; balsam fir, $F_{4.1223} = 230.91$, $P = 0.005$), and the interaction between height class and stand type affected both species (black spruce, $F_{4.3666} = 16.04$, $P = 0.005$; balsam fir, $F_{4.1223} = 11.16$, $P = 0.005$). For each height class, black spruce–balsam fir stands had generally higher levels of seedling defoliation than observed in pure black spruce stands (black spruce, $t = 0.90$, $P = 0.335$; balsam fir, $t = 1.89$, $P = 0.045$), and defoliation was correlated positively with height class. The defoliation of black spruce seedlings varied between 2% and 35% in

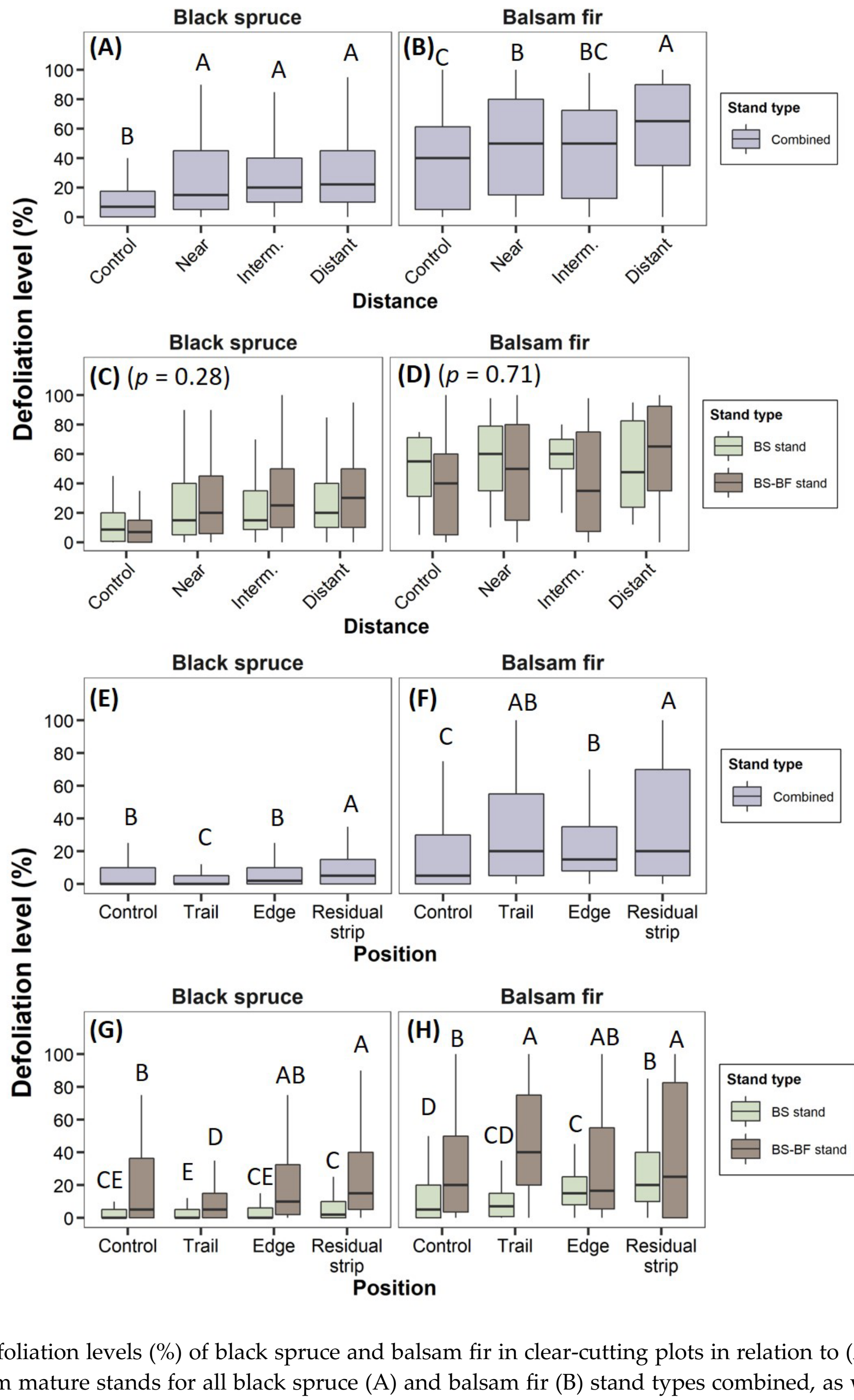

Fig. 5. Defoliation levels (%) of black spruce and balsam fir in clear-cutting plots in relation to (A–D) seedling distance from mature stands for all black spruce (A) and balsam fir (B) stand types combined, as well as for different stand types (C, D). Defoliation levels (%) of black spruce and balsam fir within partial cutting plots in relation to seedling position for all black spruce (E) and balsam fir (F) stand types combined, as well as for different stand types (G, H). Different letters represent significant difference between levels ($P < 0.05$), following A > B > C > D.

pure black spruce stands, whereas defoliation in black spruce–balsam fir stands ranged between 5% and 40%. Balsam fir seedling defoliation in pure black spruce stands varied between 6% and 43%, whereas in black spruce–balsam fir stands, the balsam fir seedlings experienced defoliation levels between 3% and 69%. We did not observe any significant differences between the harvesting methods for the height classes of both species (black spruce $F_{4.3666} = 2.13$, $P = 0.105$; and balsam fir, $F_{4.1223} = 0.56$, $P = 0.715$).

Discussion

Over the last millennia, the Canadian boreal forest has been affected by SBW outbreaks, which have contributed to shaping forest dynamics (Morin 1994, Montoro Girona et al. 2018*a*). Most research on SBW has focused solely on the effects of SBW outbreaks on mature stands while neglecting their effects on regeneration (Bauce et al. 1994, Nie et al. 2018). Most seedling from balsam fir regeneration that reaches a height of more than 30 cm die when they had more than 80% of defoliation (Nie et al. 2018). Under 80% of defoliation, the lost of foliage reduces regeneration growth and the canopy opening increases competition with other species that can compromise regeneration viability and increase hardwood contained in the stand (Ruel 1992, Nie et al. 2019). In the last decades, intensive use of clear-cutting as the main harvesting method had resulted in a vast territory to become occupied by early-stage stands (National Forestry 2017). The economic and ecological consequences of this intense use of clear-cutting have led to a reconsideration of existing paradigms in forest management and the development of novel management methods, such as partial cutting, to ensure the sustainability of silvicultural activities and long-term forest production (Gauthier et al. 2009). Thus, understanding the relationship between SBW outbreaks and harvesting methods in regard to the severity of seedling defoliation is vital for optimizing long-term forest management strategies. For this reason, our study represents a major contribution in providing a diagnosis of defoliation severity on conifer regeneration for the two main harvesting methods used within the Canadian boreal forest.

Effect of stand type and harvesting method on stand and seedling defoliation

*Stand types.—*Stand type—in this study referring to pure black spruce or black spruce–balsam fir stands—plays a major role in determining a forest's resilience to natural disturbances, such as fire, windthrow, and insect outbreaks (MacLean and MacKinnon 1997, Martin et al. 2020). Stand type has a major influence on mature tree susceptibility and vulnerability to SBW defoliation, also confirmed by our observations of defoliation in mature trees and the resulting NDVI values (Appendix S1: Fig. S3; MacLean 1980, Su et al. 1996, Colford-Gilks et al. 2012). We also observed that stand type influenced the level of defoliation of seedlings.

Mature trees and seedlings are therefore subject to greater defoliation in black spruce–balsam fir stands than in pure black spruce stands (MacLean and MacKinnon 1997, Bognounou et al. 2017).

Harvesting methods

Intensive harvesting affects regeneration, canopy dynamics, and other ecological processes, including seed dispersion, growth, and tree mortality. Many of these factors affect and are influenced by SBW defoliation because the modification of the canopy characteristics also has consequences for egg abundance and larval dispersion within the canopy (Régnière and Fletcher 1983). For sustainable ecosystem-based management, factors affecting forest productivity (e.g., natural and anthropogenic disturbance regimes) and SBW life cycles must be considered conjointly.

We observed that silvicultural treatments significantly affected the severity of seedling defoliation (Fig. 4). Harvesting intensity influences stand density, a critical driver in SBW ecology, by affecting the exposure of seedlings to egg deposition and larval dispersion within the canopy and among individual trees (Greenbank 1957). During oviposition, a female SBW selects the most easily accessible branches and locations where exposure to light radiation is high—generally in the upper crown of the tallest trees (Régnière and Fletcher 1983, Fry et al. 2009, Eveleigh and Johns 2014). Thus, in denser overstory, such as within untreated and partial cutting stands, seedlings are less susceptible to egg depositing by SBW. The result is less defoliation relative to seedlings

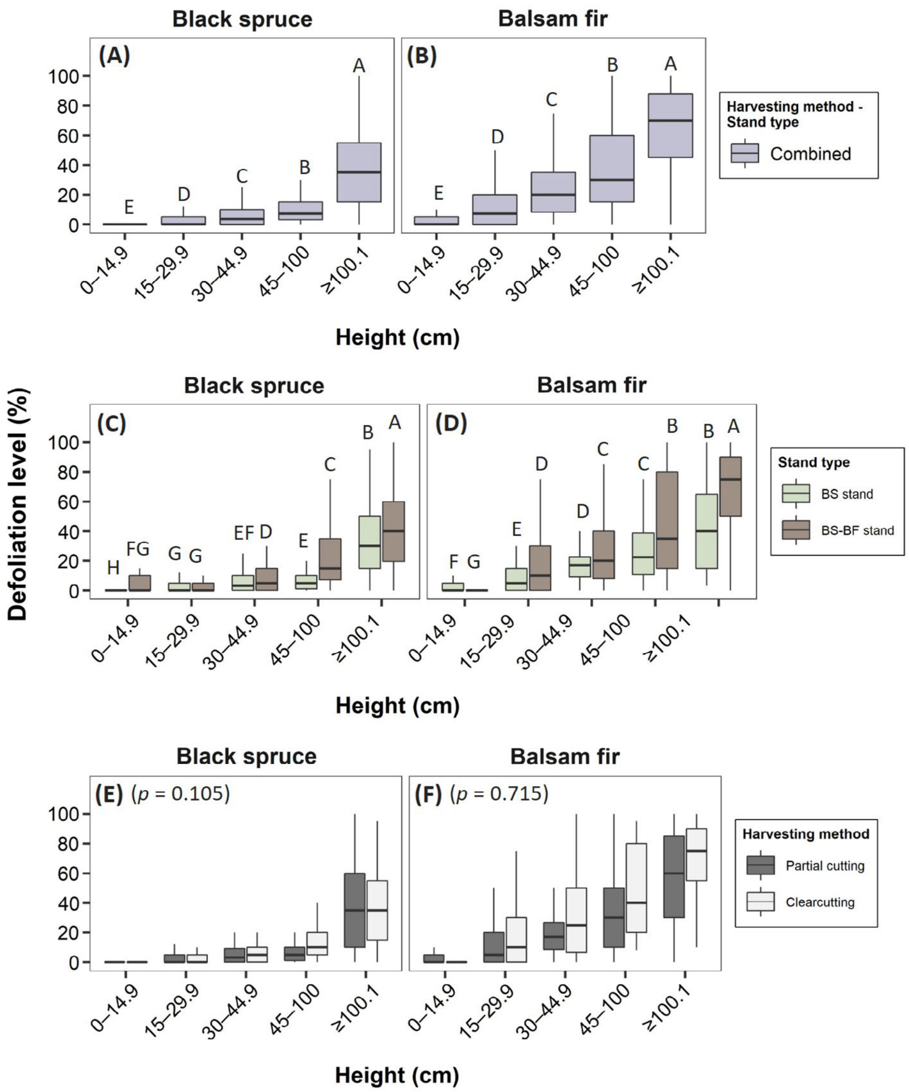

Fig. 6. Seedling defoliation level (%) for black spruce and balsam fir between seedling height classes in relation to seedling species, stand type, and harvesting method. (A, B) Seedling height class vs. seedling species with all harvesting methods and stand types combined; (C, D) seedling height class vs. seedling species and stand type; (E, F) seedling height class vs. seedling species and harvesting method. Different letters represent significant differences between levels ($P < 0.05$), following A > B > C > D.

in clear-cutting stands, where much of this canopy has been removed.

Larval dispersion between the canopy and individual branches follows two main trajectories: (1) a voluntary vertical dispersal where larvae move from the upper to lower branches, via gravity, over a short distance; and (2) an involuntary horizontal dispersal where larvae are carried by the wind over a long distance before being intercepted by vegetation (Greenbank 1957, Régnière and Fletcher 1983, Johns and Eveleigh 2013). For voluntary vertical dispersal, SBW larvae are intercepted by lower branches after falling from the upper branches (Ruel and Huot 1993). In involuntary horizontal dispersal, stand density affects the distance travelled by larvae. In denser stands, SBW larvae can be intercepted relatively quickly by the nearest surrounding vegetation as opposed to sparse stands where distances are greater before larvae can reach the canopy (Régnière and Fletcher 1983). For both scenarios, the lower branches of the overstory intercept falling larvae before they reach the understory. Thus, the overstory provides a protector effect for the understory. In clear-cutting, harvesting intensity affects more than 90% of the stand basal area (Poulin 2013); this intensity is 50% in partial cutting (Montoro Girona 2017). Clear-cutting removes the protector effect, and seedlings therefore experience greater defoliation. In contrast, residual trees in partial cutting stands ensure greater stand density to protect seedlings from SBW defoliation (Régnière and Fletcher 1983).

Additionally, the regeneration process differs between the two harvesting methods. An elevated harvesting intensity, such as in clear-cutting, decreases seed trees and leads to less seed-sourced regeneration. Under partial cutting, the higher density of seed trees provides new seedlings despite the harvesting activity and regeneration is also more abundant. Consequently, the main natural regeneration in clear-cutting stands occurs through the pre-established advanced regeneration by layering (for black spruce) or seedlings (for balsam fir); partial cutting favors seed-sourced regeneration (Ruel 1989, Montoro Girona et al. 2017). Clear-cutting would be expected to increase the level of defoliation because seedlings were pre-established before harvesting; therefore, regeneration is taller and older in these plots than seedlings in partial cuttings (Ruel 1992, Ruel et al. 1998). Although our results show a clear effect of harvesting method on seedling defoliation level, we also detected complex interactions between stand type, harvesting method, and height class. Improving our understanding of harvest method effects on seedlings will require future studies to investigate these interactions and the implicated drivers.

Factors influencing the defoliation severity of regeneration

Species.—Tree species determines the stand composition and therefore influences the susceptibility and vulnerability of a stand to SBW defoliation (Fuentealba and Bauce 2016, Nealis 2016). Our results showed that seedling vulnerability to SBW defoliation differs between species. As expected, balsam fir seedlings experienced greater defoliation than black spruce seedlings. Balsam fir, white spruce, and black spruce are all equally susceptible to egg deposition, but larval survival differs between species, mainly because of phenological differences; that is, balsam fir bud burst occurs 10–14 d before that of black spruce, which leads to greater defoliation and a higher vulnerability for balsam fir (Blais 1957, Nealis and Régnière 2004, Hennigar et al. 2008). Other mechanisms affect differences in susceptibility and vulnerability between species, including foliage biomass and foliage composition. For instance, black spruce has a greater foliage biomass than balsam fir, yet the nutritional quality of black spruce foliage is less suitable for SBW, thereby reducing larval performance (Blais 1957, Lambert et al. 2005, Ung et al. 2008). Black spruce is therefore less vulnerable to defoliation because the foliage of this species can tolerate a higher level of defoliation by a given SBW population compared with other species, such as balsam fir (Blais 1957).

Seedling spatial distribution.—Changes to the canopy conditions created by harvesting alter seedling exposure to defoliation, SBW larval dispersion, seedling growth response, species distribution, and the type of regeneration (Montoro Girona et al. 2018*b*, 2019). Within our plots subjected to clear-cutting, black spruce seedlings were more affected than those located within the control plot. Mature trees offer a protective effect to the understory by intercepting falling larvae, and this protection may explain the lower levels of defoliation for seedlings in the control plots (Ruel and Huot 1993). Furthermore, the conditions within the understory are not ideal for egg deposition and thus reduce further the risk of defoliation (Greenbank 1957, Régnière and Fletcher 1983, Hébert et al. 1990, Fry et al. 2009, Eveleigh and Johns 2014). However, we did not observe a strong role for the distance from mature trees on the level of defoliation for regeneration. This lack of effect may be explained by the harvesting intervention not being conducted in the same year for all study plots (±4 yr). Our study did not measure the variability in abundance of seedlings between plots, nor did we evaluate wind direction, seedling–sourcing, and the number of cumulative years of defoliation. Future studies require this information to better constrain the influence of spatial distribution on seedling defoliation.

We did, however, observe an influence of spatial distribution on seedling defoliation in the partial cutting plots. In addition to the relationship between seedling exposition and defoliation, partial cuttings also exposed seedlings to other constraints, such as seed-sourcing and wind, which may influence the defoliation severity of seedlings. Seedlings experienced greater wind exposure along the edge of the harvest trail than within the residual strips; this difference affects the distance of larval dispersal and seedling growth response (Batzer 1968). Normally, taller seedlings located along the edge of the trail are more exposed to defoliation and should experience a priori greater defoliation; however, a greater exposition to wind also leads to lower seedling survival and/or higher larval transport by wind. Multiple studies have shown that increased windthrow in partial cutting stands can reduce the density of mature trees in residual strips, thereby increasing seedling exposure to defoliation (Ruel 1995, Thorpe et al. 2008, Cimon-Morin et al. 2010, Montoro Girona et al. 2019). Less protection from mature trees can also explain the greater defoliation of both species in the residual strips.

Height.—Seedling height had a very strong effect on SBW defoliation, with seedling defoliation correlated positively with seedling height in agreement with previous studies (Cotton-Gagnon et al. 2018). Nie et al. (2018) observed that balsam fir seedlings shorter than 30 cm experienced less defoliation than taller seedlings. Taller seedlings tend to have a wider crown and thus a higher probability of intercepting SBW larvae falling from the overstory (Régnière and Fletcher 1983). Taller seedlings are also more exposed than smaller seedlings and offer more suitable sites for egg deposition (Greenbank 1957, Hébert et al. 1990, Fry et al. 2009). Smaller seedlings are often covered by taller seedlings, thereby receiving protection from these taller forms (Ruel and Huot 1993).

Implications for sustainable forest management

Forests are dynamic and complex systems, involving multiscale interactions between natural and anthropic factors. We demonstrated that both stand type and harvesting method affect the severity of defoliation for conifer regeneration. These results are useful for guiding the selection of an appropriate harvesting method to reduce the severity of seedling defoliation. The choice of harvesting method determines regeneration growth, the source of seedlings, and defoliation severity. Maintaining a natural conifer succession and high forest productivity requires the use of harvesting practices that promote seed-sourced and pre-established regeneration. These practices must also reduce the consequences of SBW outbreak on regeneration given the ecological and the economic damage of this disturbance. In the current outbreak context and to protect regeneration from SBW defoliation, we suggest reducing the use of clear-cutting. Layering-sourced regeneration is more present in clear-cutting areas and leads to greater defoliation because this regeneration tends to be taller and older than seedlings found in partial cutting stands (Ruel 1992, Ruel et al. 1998). In contrast, partial cutting offers a very good alternative to clear-cutting because this approach reduces the defoliation severity of regeneration in severely affected landscapes and favors increased seed-sourced regeneration. Given the higher vulnerability of balsam fir–codominant stands, future forest management must consider stand type and outbreak severity when selecting the type of harvesting method.

Conclusion

This research improves our understanding of the interactions between natural and anthropogenic disturbances by evaluating the intensity of seedling defoliation within pure black spruce and spruce-fir black spruce–balsam fir stands, each subjected to two harvesting methods commonly applied within the Canadian boreal forest. Harvesting method affects the severity of seedling defoliation as clear-cutting favors greater SBW defoliation in the regeneration than partial cutting. Under partial cutting, black spruce seedlings experience 15% less defoliation than through clear-cutting, and balsam fir seedlings experienced 20% less defoliation under partial cutting relative to clear-cutting. Stand type and height class also influenced the severity of seedling defoliation. SBW most affected black spruce—balsam fir black spruce–balsam fir stands and taller seedlings. We conclude that partial cutting offers a promising alternative harvesting method that protects conifer seedlings from increased SBW-related defoliation. This approach reduces the negative effects of SBW on forest productivity and promotes a higher regeneration density. Even if the defoliation reduction under partial cutting is relatively moderate, we recommend to managers to use partial cuttings as silvicultural option, especially in severe defoliated area. Despite these important contributions of our study, many other factors influence defoliation severity in conifer regeneration. The seedling and stand defoliation history in previous years need to be known to understand factor involved in their defoliation. We suggest to conduct studies involving the long-term monitoring of stands, including from the onset of a SBW outbreak, will improve our understanding of the influence of seedling spatial distribution on seedling defoliation and survival. Further study should be conducted to evaluate whether longer transect and different wide classes include SBW biology. Additional investigations of this complex ecological phenomenon must be prioritized because SBW outbreaks are expected to increase in severity and frequency with climate warming.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3506/full