



Modelling stand development after partial harvesting in boreal mixedwoods of eastern Canada



Arun K. Bose^{a,*}, Brian D. Harvey^a, K. David Coates^b, Suzanne Brais^a, Yves Bergeron^a

^a Institut de recherche sur les forêts & Centre d'étude de la forêt, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, QC, Canada J9X 5E4

^b Ministry of Forests, Lands and Natural Resource Operations, Skeena Region, Bag 6000, Smithers, BC, Canada V0J 2N0

ARTICLE INFO

Article history:

Received 18 August 2014

Received in revised form 3 December 2014

Accepted 2 January 2015

Available online 5 February 2015

Keywords:

Boreal mixedwood

Partial harvesting

Variable retention

Stand modelling

SORTIE-ND

Stand dynamics

ABSTRACT

Multi-cohort-based forest management has been proposed as a strategy to conciliate wood supply and biodiversity conservation objectives. At the stand-level, the approach involves using partial harvesting to generate structurally complex stands, notably in terms of tree age, size and species mixtures, conditions that are not easily integrated into yield tables. Using SORTIE-ND, a spatially explicit stand dynamics model, we simulated 100-year development patterns following different partial harvesting treatments in two trembling aspen (*Populus tremuloides* Michx.)-dominated stands in eastern Canada, one 76-year old (pure aspen) and the other 90 years old (mixed aspen). The two stand types differed primarily in the nature of their understory: pure aspen stands had little advance conifer growth and a dense understory of a woody shrub species whereas mixed aspen stands were characterized by a dense regeneration layer of shade-tolerant conifers. To do this, we first evaluated model performance using short (12 years) and long (168 years) term empirical data. We then modelled stand dynamics following a range of simulated partial harvesting treatments of different intensities (33, 61 and 80% basal area removal), and gap sizes (400, 900 and 1600 m²). Following mortality of the first cohort of aspen, simulations projected dominance of conifer species, white spruce in particular, in unharvested controls of pure aspen stands and balsam fir in mixed aspen stands. Aspen recruitment increased with intensity of partial harvesting. All gap treatments and the 80% dispersed harvesting favored recruitment of aspen over conifer species. After 100-year simulation runs, the 1600 m² gap treatment resulted in highest stand basal areas, 38.0 and 34.1 m² ha⁻¹, of which 18% and 28% consisted of intermediate- to shade-tolerant conifer species in pure aspen stands and in mixed aspen stands, respectively. Concerns surrounding partial harvesting have tended to focus on absolute retention levels and standing residence times of trees; however, our results demonstrate that both stand structure and timber production rates are influenced not only by retention levels after partial harvesting but also by spatial configuration of the residual trees. We identified several model functions that are likely responsible for divergences between empirical conditions and those simulated by SORTIE-ND for the boreal mixedwood and suggest specific empirical studies to improve parameter functions of this modelling tool.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Mixedwood forests are the most productive and structurally heterogeneous forests in boreal Canada (Rowe, 1972; Chen and Popadiouk, 2002) and an important source of timber supply (Penner, 2008). Mixedwood stands composed of intolerant hardwoods, in particular trembling aspen (*Populus tremuloides* Michx.), and shade-tolerant conifers are abundant across the southern

Canadian boreal forest (Nlungu-Kweta et al., 2014). During mixedwood stand development, partial disturbances such as insect outbreaks and windthrow and tree- and stand-level processes such as competition and senescence, facilitate establishment and growth of shade-tolerant conifers by creating small gaps (Bergeron, 2000). However, some studies have shown that trembling aspen can also maintain continuous recruitment even in small gaps (Cumming et al., 2000) resulting in a succession of multi-cohort aspen stands (LeBlanc, 2014). As a result, successional development of boreal mixedwood stands can be extremely complex (Bergeron et al., 2014) and the degree of complexity may be influenced by several factors: pre-disturbance stand attributes

* Corresponding author. Tel.: +1 819 279 4883.
E-mail address: arun.bose@uqat.ca (A.K. Bose).

and their relative importance, intensity and spatial configuration of disturbances and time since disturbance, and relative importance of post-disturbance attributes (Kneeshaw and Gauthier, 2003).

In boreal mixedwood forests where fire cycles exceed the life expectancy of early successional species, stand-level processes including tree mortality of this first tree cohort and recruitment of mid- and late-successional species tend to transform structurally simple stands into more complex multi-cohort forest structures (Kneeshaw and Bergeron, 1998; Bergeron and Harper, 2009). Based partly on an understanding of these natural dynamics, a multi-cohort-based forest management approach has been proposed for the eastern Canadian boreal mixedwood forest as a means of conciliating industrial demand for wood fiber and biodiversity concerns (Bergeron et al., 2002; Harvey et al., 2002). At the forest-level, the approach uses the regional fire cycle to set objectives for maintaining acceptable levels of forest types associated with different stand development stages on the landscape, and structurally complex old growth forests are of critical importance. At the stand level, the approach proposes greater use of partial cutting treatments to better incorporate natural dynamics associated with canopy succession and partial disturbances to promote the structural attributes associated with over-mature or old growth stands. This concept has led to greater experimentation of novel silvicultural practices including partial harvesting and variable retention (Gauthier et al., 2009). Partial harvesting may retain a range of densities of residual trees, either in aggregated groups, strips or dispersed patterns or a combination of these patterns, depending on stand conditions and management objectives (Franklin et al., 1997; Bose et al., 2014c). Residual trees may serve several functions including maintaining – or eventually producing – key habitat attributes, providing seed sources for future regeneration or reducing the visual impacts of harvesting (Lieffers et al., 1996; Bergeron and Harvey, 1997). It is expected that partial harvesting will be increasingly applied in boreal mixedwood stands, particularly where intolerant hardwoods reach commercial maturity before more shade-tolerant conifers (Lieffers et al., 1996; Bose et al., 2014c).

Most partial harvesting experiments have only recently been set up in the Canadian boreal mixedwood forest (e.g., Brais et al., 2004; Man et al., 2008; Prévost et al., 2010; Solarik et al., 2010). Therefore, little field-based information exists concerning how partially harvested stands develop over long time scales. According to Weiskittel et al. (2011), foresters are generally familiar with empirical yield tables and recognize their utility for predicting volume yields for fairly homogenous and simple stand conditions (even-aged, mono-specific or low species mixtures). However, growth estimations of structurally complex stands are not easily or accurately predicted using existing yield tables. Individual tree-based models are generally more flexible than yield tables, allow the exploration of different silvicultural options and can potentially provide more detailed forecasts of tree sizes (Coates et al., 2003; Groot et al., 2004; Papaik et al., 2010). Besides the flexibility generally offered by modelling and the obvious economies in time and resources compared to long-term field monitoring, stand dynamics modelling provides a complementary analysis tool to field trials for investigating and comparing different silvicultural options and outcomes (Thorpe et al., 2010; Ligot et al., 2014).

SORTIE-ND, a spatially-explicit, individual-based stand dynamics model, has been used to explore natural forest dynamics in a number of forest systems, such as mixed aspen boreal forests in eastern (Papaik et al., 2010; Beaudet et al., 2011) and western Canada (Astrup, 2006; Stadt et al., 2007), black spruce forests in eastern Canada (Thorpe et al., 2010; Vanderwel et al., 2011), mixed temperate forests (Haeussler et al., 2013) and elsewhere in

the World (Canham et al., 2010; Ameztegui et al., 2012; Yasuda et al., 2013). It is particularly suitable for applications involving mixed species stands and partial disturbances (Coates et al., 2003) and has been used to explore and forecast outcomes under alternative silvicultural systems over longer time scales than those covered by existing empirical studies (Vanderwel et al., 2011).

In this study, we adapted SORTIE-ND for boreal mixedwood stands in north-western Quebec, and evaluated model performance using short- and long-term empirical data. We then simulated stand dynamics over 100 years following a range of partial harvesting intensities and spatial configurations applied to mature pure aspen and mixed aspen stands. The study aimed to (i) evaluate whether SORTIE-ND captures short- and long-term stand dynamics of eastern boreal mixedwood stands, (ii) identify the range and configuration of partial harvesting treatments that accelerate the development of multi-cohort complex stands and (iii) assess how similar partial harvesting treatments applied to pure aspen and mixed aspen stands with contrasting understories (dense advance conifer regeneration with sparse understory shrubs versus sparse advance regeneration with dense understory shrubs) affect stand development over a period of 100 years.

2. Methods

2.1. Study area

Field sites were located in the Lake Duparquet Research and Teaching Forest (LDRTF) in the Abitibi region of north-western Quebec, 45 km northwest of the city Rouyn-Noranda (48° 86'N–48° 32'N, 79° 19'W–79° 30'W). This region is characterized by the presence of extensive clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977) and rich clayey soils on upland sites (Canada Soil Survey Committee, 1987). The climate is continental and cold with a mean annual temperature of 0.7 °C and mean annual precipitation of 889.8 mm (Environment Canada, 2011).

The LDRTF is located within the balsam fir (*Abies balsamea* (L.) Mill.) – white birch (*Betula papyrifera* Marsh) bioclimatic domain (Saucier et al., 1998). Forests of the region are characterized by a mixed composition of boreal conifers, and shade-intolerant broadleaved species. Trembling aspen, white birch, and jack pine (*Pinus banksiana* Lamb.) are the dominant early successional species. Balsam fir is the dominant species in late-successional forests on mesic sites, and is associated with white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P.), and eastern white cedar (*Thuja occidentalis* L.) in this region (Bergeron, 2000).

The natural disturbance regime is characterized primarily by a mix of influences of wildfires and defoliating insect outbreaks. For a ca. 16,000 km² area surrounding the study sites, Bergeron et al. (2001) estimated mean forest age (time since fire) to be 139 years and calculated lengthening fire cycles from 83 to 146 to 325 years for the following three periods: prior to 1850, 1850–1920 and 1920–1999, respectively. Three outbreaks of eastern spruce budworm (*Choristoneura fumiferana* (Clem.)), a defoliator of balsam fir and spruce, have been documented in the twentieth century by Morin et al. (1993) (see Section 2.5). The forest tent caterpillar (*Malacosoma disstria*), a defoliator of broadleaf species, particularly trembling aspen, has shorter outbreak cycles than the budworm (Cooke et al., 2009), but with a more minor effect on host species mortality (Cooke and Lorenzetti, 2006). Gap dynamics associated with these secondary disturbances and successional processes also influence stand-level composition and structure (Kneeshaw and Bergeron, 1998).

2.2. Sites used for starting condition and for short-term model evaluation

Empirical data from two separate partial harvesting experiments (SAFE-1 and SAFE-3) established in the late 1990s–early 2000s were used for short-term evaluation of model simulations. Both experiments are part of the SAFE project (*Sylviculture et aménagement forestier écosystémiques*) (Brais et al., 2004, 2013), situated in the Lake Duparquet Forest.

Pure aspen stands of the SAFE-1 project originated from a stand-replacing fire in 1923. Average pre-treatment stand basal area was $44.0 \text{ m}^2 \text{ ha}^{-1}$ of which 92.6% was trembling aspen and 3.3% conifer species. Four harvesting treatments, including a no harvest control, two intensities of partial harvesting and a clearcut, were applied during the winter of 1998–1999. The two partial harvesting treatments were designed to remove 33% (1/3 partial cut) and 61% (2/3 partial cut) of merchantable basal area (primarily aspen) in an evenly dispersed spatial pattern. Stands in the 1/3 partial cut were low thinned while stands in the 2/3 partial cut were primarily crown thinned (Brais et al., 2004). Harvesting treatments were applied according to complete randomized block design with three replications (blocks) of each treatment. Forest inventories were conducted in 1998 and 2010 in five 400 m^2 sampling plots per treatment unit.

Mixed aspen stands in the SAFE-3 project originated from a wildfire fire in 1910. Average pre-treatment stand basal area was $41.0 \text{ m}^2 \text{ ha}^{-1}$ of which 80.8% was trembling aspen and 17.8% conifer species. In the winter of 2000–2001, four harvesting treatments including a no harvest control, two intensities of partial harvesting (intermediate-intensity free thin; 45% BA removal and 400 m^2 gap cut; 54% BA removal) and a clearcut were applied. Similar to the pure aspen stands, treatments were applied according to complete randomized block design with three replications (blocks) of each treatment (see details in Brais et al., 2013). Forest inventories were conducted in 2000 and 2012 in five 400 m^2 permanent sampling plots per treatment unit.

Besides differences in overstory composition, the main difference between the two stand types was in the seedling and sapling layers: balsam fir was very dense in mixed aspen stands, whereas total conifer regeneration was very low and a woody shrub, mountain maple (*Acer spicatum* Lamb.), dominated the regeneration layer in pure aspen stands.

2.3. Site used for long-term model evaluation

For long-term (168 years since stand initiation) evaluation of simulations of development of unharvested control stands in SAFE-1 and -3, data were obtained from an area of the LDRTF that originated from a wildfire in 1823. This will be referred to as the “1823 reference stand”. The area was inventoried in 1991, which corresponds to 168 years after stand initiation. Sixty temporary sample plots of 256 m^2 ($16 \text{ m} \times 16 \text{ m}$) were established at 50 m intervals along transects located within the fire-affected area. In each plot, all live and dead (standing) trees greater than 5 cm DBH were identified, measured and categorized by size classes of 5 cm DBH (Bergeron, 2000). To decrease the variability caused by the small size of plots, we merged every four consecutive plots into 15 larger inventory units ($256 \times 4 = 1024 \text{ m}^2$).

2.4. Simulator

SORTIE-ND is a spatially explicit, individual-based forest stand dynamics model (Murphy, 2011). It originated from the SORTIE model developed and tested in the early 1990s for transitional oak-northern hardwood forests in the northeastern US (Pacala et al., 1996). Since then, it has been improved upon with a greater

emphasis on forest management considerations being incorporated into the modeling research (e.g., LePage et al., 2000; Astrup et al., 2008; Coates et al., 2009). SORTIE-ND simulates changes in tree populations over time. The model uses a combination of empirical and mechanistic behaviors to predict forest dynamics.

In SORTIE-ND, the forest is represented by a large collection of interacting trees (individuals) that are followed both in time (in steps of 1 year) and space. Individual trees are categorized as seedlings, saplings, adult trees or snags. Population-level dynamics are simulated by summing the collective activities of numerous individuals. Each tree is a discrete object that is described with various attributes (size, growth rate, age, crown morphology, and so on). Each tree's (individual) behavior is modelled with rules that describe the interactions with other individuals (e.g., effect of species and distance of neighbors on growth of individual trees) or its environment (e.g., growth of seedlings in relation to available light levels). In SORTIE-ND, many of the interactions have non-linear relationships and/or have random events associated with them. The non-linearity of many interactions, the stochastic behavior of some objects and processes, and the large number of objects, rules and stochastic events makes SORTIE-ND a good example of a modelling approach aimed at being able to represent complex behavior in forests (Haeussler et al., 2013). See more details on model structure in Appendix or at <http://www.sortie-nd.org/help/manuals/help/index.html>.

SORTIE-ND is driven by a parameter file based on local conditions and field data. The Lake Duparquet Forest parameter file has been developed, tested and modified over the course of the last number of years. This has been done either through individual field experiments or studies that have allowed parameterization of specific functions in the different sub-models constituting SORTIE-ND (tree allometry, light, tree growth, tree mortality, and recruitment) or through concerted efforts to calibrate the model to adhere to our current understanding – based on empirical studies – of natural stand dynamics (Poulin and Messier, 2008; Beaudet et al., 2011; Leduc and Coates, 2013). The parameterized model for LDRTF includes six tree species trembling aspen, balsam fir, white spruce, white birch, eastern white cedar and jack pine and one woody shrub, mountain maple.

2.4.1. Growth

SORTIE-ND is designed to provide growth predictions for individual seedlings, saplings and adult trees in multi-species, complex-structured stands (Fig. 1). Seedlings and saplings grow as a function of understory light availability (e.g., Wright et al., 1998) to a size of 3–10 cm diameter (DBH), depending on species, and then shift to adult tree growth functions based on tree size and neighborhood competition (e.g., Coates et al., 2009). In cases where there is insufficient data on neighborhood competition a simple species-specific diameter increment function is used (e.g., Pacala et al., 1996). This was the case for jack pine and mountain maple in our northern Quebec simulations. For the other species, a neighborhood competition index (NCI) reduces the predicted maximum potential growth rate of a tree based on the species, size and proximity of neighbors. The NCI sums up the competitive effect of all neighbors out to the estimated maximum distance of effect, in m. The competitiveness of a neighbor increases with the neighbor's size and decreases with distance to the neighbor. It also incorporates species-specific competitive effects, with the effect depending on the relationship between the target species and the neighbor species. Once diameter growth is determined, and incremented on to an individual tree, tree height is calculated using species-specific allometric equations based on DBH. The list of parameters of different model behaviors (e.g., growth, mortality, substrate) used in the present study is described in Appendix.

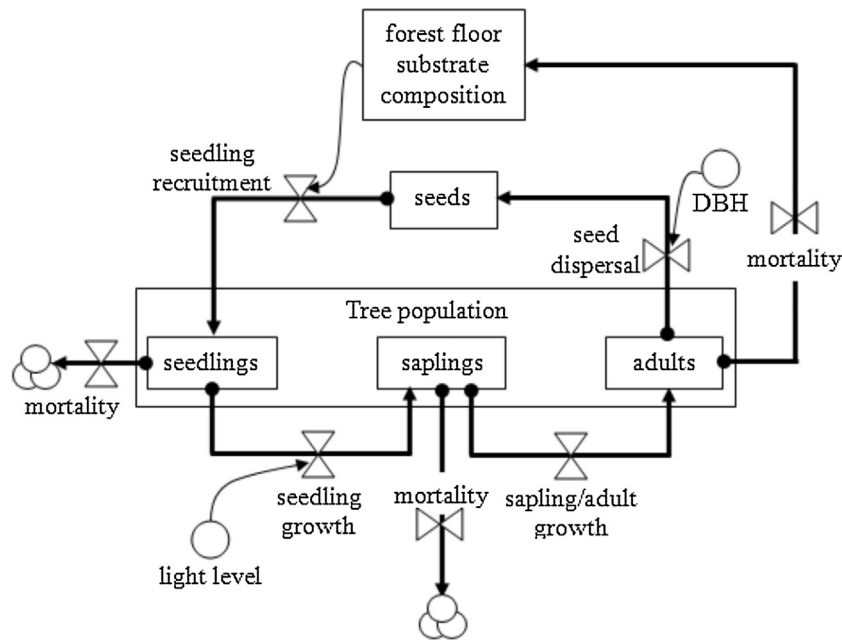


Fig. 1. Conceptual modelling diagram of SORTIE-ND.

Source: Lora Murphy, <http://www.sortie-nd.org/help/manuals/help/index.html>.

2.5. Model development

In addition to the model development described above, using repeated measurements data from the SAFE project (Brais et al., 2004; Robert et al., 2012; Bose et al., 2014b), we tested and calibrated the following parameters: senescence mortality of mountain maple, juvenile mortality of trembling aspen, white spruce and balsam fir, competition mortality of trembling aspen and sucker recruitment of trembling aspen.

We also accounted for conifer mortality caused by spruce budworm (episodic mortality in SORTIE-ND). The frequency of budworm incidents over a 100-year period was based on the chronology of three outbreaks that occurred in the region during the 20th century from 1919 to 1929, 1930 to 1950 and 1970 to 1987 (Morin et al., 1993). As mentioned previously, the pure aspen stands originated from a fire in 1923; therefore, we simulated budworm mortality at years 2024, 2040 and 2078, that is, at stand ages 101, 117 and 155 years, respectively. The mixed aspen stands originated from a fire in 1910 so we induced budworm mortality at years 2011, 2027, 2065 and 2095, or stand ages of 101, 117, 155 and 185 years, respectively. We simulated an additional budworm mortality episode for mixed aspen stands because we expected another budworm occurrence in the remaining 35 years of simulation.

In each time step, the budworm induced mortality was based on Bergeron et al. (1995) for balsam fir in the region and on Blais (1981) for white spruce in the eastern Canadian boreal region. For balsam fir, we set different mortality rates for the following three diameter classes, 5–10, 10–15 and ≥ 15 cm DBH, and we also accounted for stand composition (relative proportions of budworm-susceptible conifers and non-host hardwoods) that influence the magnitude of mortality according to Bergeron et al. (1995). We assumed deciduous-dominated stand conditions during the first budworm occurrence (101 years), mixed-deciduous during the second budworm occurrence (117 years) and conifer-dominated stand conditions during third budworm occurrence (155 years). These stand compositions at different time steps were adjusted by noting relative (to total) basal area of each species in simulation outputs. For white spruce, we set the mortality for only one size class (>10 cm DBH) but for two stand compositions,

mixedwood and conifer (see Table 1 of Blais (1981)). We adjusted stand composition (mixedwood or conifer) for white spruce following a procedure similar to that described above for balsam fir.

2.6. Simulation runs

Simulations were conducted using a 4 ha ($200\text{ m} \times 200\text{ m}$) plot (stem map) (Beaudet et al., 2011; Vanderwel et al., 2011) with a time step = 1 year. Harvest episodes (Table 2) were created at time step 1. The SORTIE-ND simulation plot is a torus, where each edge connects to the edge of the opposite side (see <http://www.sortie-nd.org/help/manuals/help/data/plot.html>).

2.6.1. Model evaluation

2.6.1.1. Short-term evaluation. We used inventory data from 15 permanent sample plots (PSP – 400 m^2) of pre-treatment conditions of unharvested controls and the 1/3 partial cuts in the pure aspen stands and unharvested controls and 400 m^2 gap cuts in mixed aspen stands (60 PSPs in all). Therefore, we created 15 starting conditions for each of the four treatments based on inventory data collected in 1998–1999 in the pure aspen stands and in 2000–2001 in the mixed aspen stands. For the 1/3 partial cut in pure aspen stands and the 400 m^2 gap cuts in the mixed aspen stands, we implemented basal area removal by partial harvesting treatments (harvest episode in SORTIE-ND) (Table 1). We then compared empirical values of stand stem density and basal area from 12-year post-treatment field measurements in permanent sample plots with simulated values for the same year.

2.6.1.2. Long-term evaluation. We also used the 15 permanent sample plots of pre-treatment conditions of unharvested controls of both the pure aspen and mixed aspen stands for long-term evaluation of model simulations. We simulated each plot for a 100-year period and evaluated the simulation outputs at 168 years since stand initiation of the pure aspen stands (76 years initially + 92 years simulated = 168 years) and mixed aspen (90 years initially + 78 years simulated = 168 years) using empirical data of the 1823 reference stand (168 years old when inventoried in 1991). We ran two separate simulations for each study site: one including

Table 1
Stand conditions, simulation periods and sources of empirical data used to evaluate short- and long-term simulations.

Stand type	Treatment	Starting condition (stand age)	Simulation period (years)	Source of empirical data used for model validation
Short-term evaluations				
Pure aspen	Control	76	12	Same treatment
Pure aspen	1/3 partial cut	76	12	Same treatment
Mixed aspen	Control	90	12	Same treatment
Mixed aspen	Gap cut	90	12	Same treatment
Long-term evaluations^a				
Pure aspen	Control	76	92	168-Year-old stands ^b
Mixed aspen	Control	90	78	168-Year-old stands

^a For long-term evaluations, two separate simulations were run for both stand types: one included spruce budworm outbreak incidents that induced balsam fir and white spruce mortality (see details in Section 2.5) and the other did not.

^b Inventory plots in stands that originated from a fire in 1823 (see Dansereau and Bergeron, 1993; Bergeron, 2000).

and the other excluding spruce budworm outbreak “incidents” (Table 1).

2.6.2. Simulated silvicultural treatments over a 100-year period

Using pre-treatment data from the 15 permanent sample plots of unharvested controls in pure aspen stands and unharvested controls in mixed aspen stands, we implemented six different partial harvesting scenarios: three dispersed partial cut patterns with 33%, 61%, and 80% BA removal and three aggregated cut scenarios that removed trees in 400 m², 900 m² and 1600 m² gaps corresponding to 37%, 43% and 54% BA removal, respectively (Table 2). An unharvested 15 m wide band was maintained between adjacent gaps in all gap-harvested stands. We averaged and calculated 95% CI of replicate model outputs ($n = 15$) for each harvest scenario and post-harvest time interval to account for the random variability in stand composition, structure and dynamics.

2.7. Analysis of model simulated outputs

For both short- and long-term evaluations, we examined tree size distribution, live stem density (≥ 5 cm at DBH) and total live stem basal area (≥ 5 cm at DBH) for trembling aspen, white birch, balsam fir and white spruce. Additionally, we examined the effect of spruce budworm outbreaks (included in or excluded from simulations) on stand dynamics for long-term simulations. For the 100-year simulation following partial harvesting, we analyzed separately live merchantable trees (≥ 10 cm at DBH) and the live sapling layer (5–10 at DBH). We averaged and calculated 95% CI of replicate model simulated outputs ($n = 15$) for each treatment to account for the variability among the 15 plots (starting conditions). We compared the average with 95% CI between simulated treatments at years 25, 50 and 100.

Table 2
Simulated harvesting scenarios applied to pure aspen and mixed aspen stands.

Silvicultural treatments	Scenario no.	Scenario description		
		Spruce budworm	Basal area removed	Harvesting pattern
Control	1	×	×	×
	2	✓	×	×
	3	✓	33%	Dispersed
Dispersed partial cut	4	✓	61%	Dispersed
	5	✓	80%	Dispersed
	6	✓	37%	400 m ² gaps
Gap partial cut	7	✓	43%	900 m ² gaps
	8	✓	54%	1600 m ² gaps

All stems ≥ 5 cm DBH were considered in harvesting prescriptions. The same simulated treatments were applied to both pure aspen and mixed aspen stands with 15 replications (one for each PSP) for each site.

3. Results

3.1. Model evaluation

3.1.1. Short-term evaluation

At the end of 12-year simulation runs, simulated unharvested controls in both the pure aspen and mixed aspen stands showed good agreement with empirical data in terms of tree size distribution (Fig. 2A–D for the pure aspen stands and Fig. 2I–L for the mixed aspen stands), live stem density and live stem basal area of whole stand, aspen, birch, fir and spruce (Table 3). Higher mortality (expressed in terms of BA) of trembling aspen was the most notable difference between simulated outputs and the empirical results (7% and 13% higher mortality for the pure aspen stands and mixed aspen model results, respectively). This resulted in slightly lower aspen and total stem density and BA values in simulated outputs compared to empirical data (Table 3).

In the 1/3 partial cut (low-light thinning) in pure aspen stands, 12-year simulated outputs captured all dynamics of tree size distribution with the exception of mortality associated with smaller stems (5–10 cm DBH) of white birch (Fig. 2E–G). Simulated density and BA for total stand, aspen, fir and spruce showed good agreement with the empirical data (Table 3). The simulation did, however, project somewhat lower sapling recruitment of aspen saplings (5–10 cm DBH) than the empirical data, although sapling densities of other species were in good agreement with empirical data (Fig. 2H).

Simulated outputs of 400 m² gap cuts in mixed aspen stands did not capture initial logging-induced mortality of residual trembling aspen and spruce, and showed higher survival of these two species than empirical data (Fig. 2M–O). Such survivability of residual trees translated into 9.3 m² ha⁻¹ more BA in simulated outputs (Table 3). Balsam fir regeneration (<5 cm at DBH) recruitment into sapling

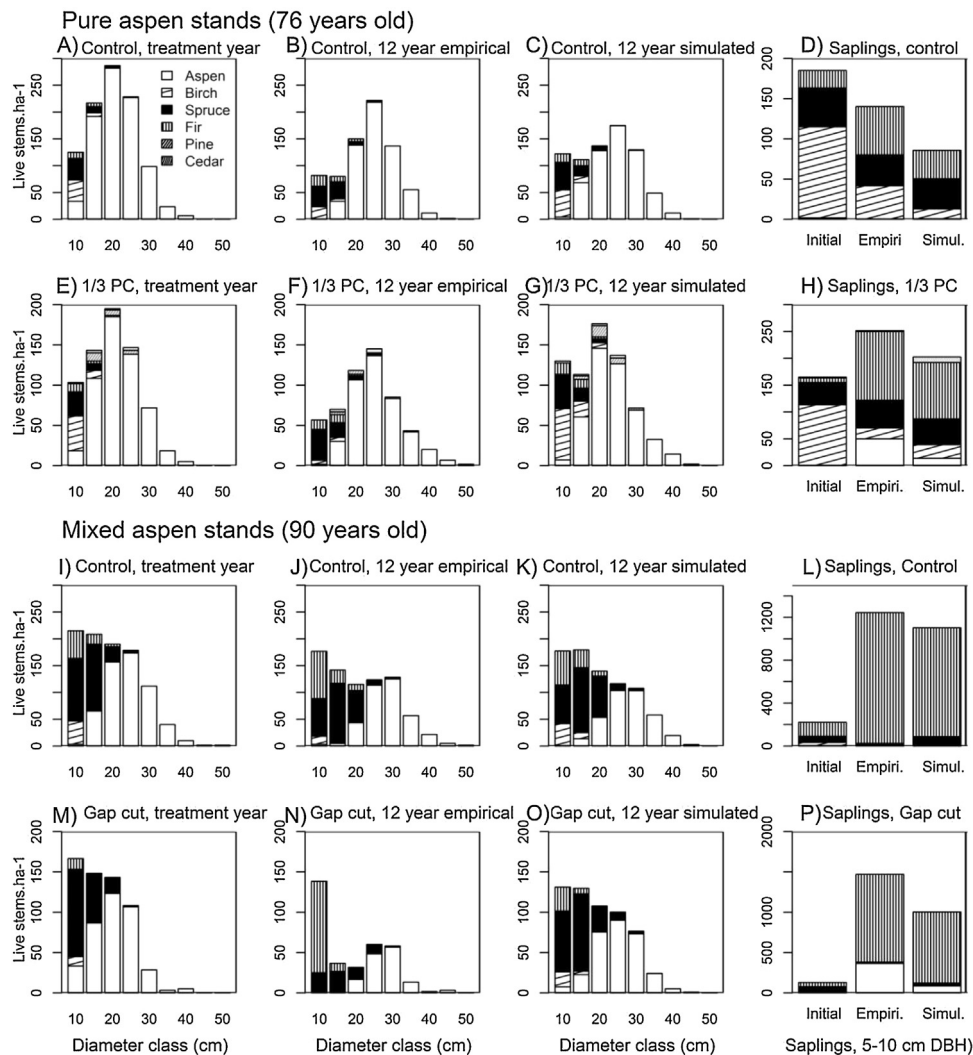


Fig. 2. Comparison between empirical values and model simulated results of DBH size distribution 12 years after partial harvesting treatment application of two sites, pure aspen and mixed aspen stands. (A–C) Merchantable trees (≥ 10 cm DBH) and (D) sapling layer (5–10 cm DBH), of uncut controls in pure aspen stands, (E–G) merchantable trees (≥ 10 cm DBH) and (H) sapling layer (5–10 cm DBH), of 1/3 PC (partial cut: 33% harvesting) in pure aspen stands, (I–K) merchantable trees (≥ 10 cm DBH) and (L) sapling layer (5–10 cm DBH), of uncut controls in mixed aspen stands and (M–O) merchantable trees (≥ 10 cm DBH) and (P) sapling layer (5–10 cm DBH), of gap cut (400 m²) in mixed aspen stands. Initial: Treatment year, Empiri: Empirical, Simul: Simulated. *Note.* Each graph represents the average condition of 15 permanent sample plots.

layer (5–10 cm DBH) was slightly lower in simulated outputs than in empirical data (Fig. 2P).

3.1.2. Long-term evaluation

Simulations that incorporated periodic spruce budworm “incidents” (punctual outbreaks) showed closer agreement with empirical data of the 1823 reference stand than simulations that did not (Fig. 3A vs B and C for pure aspen stands, Fig. 3A vs D and E for mixed aspen). Hence, we retained simulations that included spruce budworm dynamics for long-term model evaluation and for running 100-year simulations of partial harvesting scenarios (Table 2).

At the end of 92-year simulation runs of pure aspen stands (76 years at starting condition + 92-year simulation = 168 years), the overall stand basal area, aspen density, balsam fir density, birch basal area, balsam fir basal area and the dynamics of balsam fir showed a good agreement with the 1823 reference stand (Table 3). The major differences between the 1823 reference stand and the simulated pure aspen stands appeared in the dynamics of spruce and aspen (Fig. 3A vs B). Higher densities of small sized (5–15 cm at DBH) spruce in the simulated aspen stands resulted in higher

stand density at 168 years than in the 1823 reference stand (Table 3). Additionally, aspen appeared in all size classes of the 1823 reference stand, whereas simulated outputs showed aspen only in small size classes (5–15 cm at DBH) (Fig. 3A vs B).

At the end of the 78-year simulation of mixed aspen stands (90 years at starting condition + 78-year simulation = 168 years), stand BA and birch BA and the dynamics of balsam fir showed good agreement with the 1823 reference stand (Table 3). The main difference between the 1823 reference stand and simulated output of the mixed aspen stands appeared in the dynamics of spruce and aspen (Fig. 3A vs D). The simulations projected higher densities of small-sized (5–15 cm at DBH) spruce than empirical data of the 1823 reference stand (Table 3). Additionally, while aspen appeared in all size classes of the 1823 stand, simulated outputs of the mixed aspen stands presented virtually no aspen (Fig. 3A vs D).

3.2. Simulated stand dynamics of unharvested controls

After the mortality of first cohort aspen, simulations projected dominance of conifer species, white spruce in particular, in unharvested controls of pure aspen stands and balsam fir in mixed aspen

Table 3 Results of short-term (12 years) and long-term (92 years and 78 years for pure aspen and mixed aspen stands, respectively) model evaluations: comparison between empirical and simulated outputs.

Stand types and treatment	Period	Live stem density ≥ 5 cm DBH (stems ha ⁻¹)					Live basal area ≥ 5 cm DBH (m ² ha ⁻¹)				
		Stand	Aspen	Birch	Fir	Spruce	Stand	Aspen	Birch	Fir	Spruce
Short-term evaluations											
Pure aspen Control	Treatment-year	1190 ± 97	857 ± 88	161 ± 41	40 ± 22	102 ± 36	44.0 ± 2.4	40.6 ± 2.4	1.2 ± 0.3	0.4 ± 0.3	1.0 ± 0.4
	12-Year empirical	895 ± 106	592 ± 76	73 ± 23	95 ± 36	117 ± 39	41.5 ± 3.4	37.7 ± 3.1	0.7 ± 0.3	0.9 ± 0.5	1.7 ± 0.6
	12-Year simulated	822 ± 73	566 ± 69	76 ± 25	64 ± 29	114 ± 42	38.3 ± 1.6	35.0 ± 1.8	1.0 ± 0.3	0.6 ± 0.3	1.5 ± 0.6
Pure aspen 1/3 partial cut	Treatment-year	856 ± 82	545 ± 79	168 ± 67	23 ± 26	80 ± 51	30.9 ± 3.1	27.3 ± 3.7	1.3 ± 0.8	0.3 ± 0.3	0.7 ± 0.5
	12-Year empirical	813 ± 119	478 ± 89	30 ± 25	153 ± 76	115 ± 54	32.8 ± 4.2	29.0 ± 4.2	0.3 ± 0.3	1.0 ± 0.5	1.5 ± 0.7
	12-Year simulated	818 ± 147	459 ± 76	115 ± 60	83 ± 67	112 ± 63	31.9 ± 2.2	26.5 ± 3.0	1.6 ± 1.1	0.9 ± 0.7	1.3 ± 0.8
Mixed aspen Control	Treatment-year	1178 ± 128	568 ± 81	75 ± 55	205 ± 88	330 ± 94	42.2 ± 4.9	33.7 ± 4.8	0.8 ± 0.4	1.7 ± 0.8	6.1 ± 1.3
	12-Year empirical	2013 ± 262	377 ± 74	17 ± 16	1343 ± 310	277 ± 89	42.3 ± 4.3	29.3 ± 4.4	0.2 ± 0.2	6.1 ± 1.1	6.7 ± 1.8
	12-Year simulated	1902 ± 292	357 ± 55	59 ± 33	1120 ± 231	366 ± 131	41.9 ± 3.5	26.8 ± 3.3	0.9 ± 0.4	5.3 ± 1.2	8.2 ± 1.8
Mixed aspen Gap cut	Treatment-year	653 ± 194	387 ± 99	22 ± 16	67 ± 33	257 ± 152	21.7 ± 4.3	17.2 ± 4.2	0.2 ± 0.2	0.4 ± 0.2	3.9 ± 2.0
	12-Year empirical	1750 ± 347	503 ± 249	7 ± 8	1200 ± 322	103 ± 52	19.1 ± 3.1	11.2 ± 2.3	0.0 ± 0.0	5.4 ± 1.7	2.5 ± 1.4
	12-Year simulated	1579 ± 127	384 ± 47	27.4 ± 23	921 ± 149	246 ± 125	28.4 ± 2.0	19.1 ± 2.2	0.4 ± 0.3	3.6 ± 0.8	5.4 ± 2.4
Long-term evaluations											
168 reference stand	Empirical	1210 ± 186	472 ± 122	206 ± 58	430 ± 131	86 ± 23	20.7 ± 2.4	10.3 ± 2.2	3.6 ± 0.8	3.7 ± 1.3	2.7 ± 0.8
76-Year-old pure aspen stands	92 years simulated with budworm	1583 ± 83	635 ± 169	101 ± 43	269 ± 120	571 ± 174	22.5 ± 2.0	6.3 ± 1.4	5.6 ± 1.9	2.4 ± 1.2	8.1 ± 2.4
76-Year-old pure aspen stands	92 years simulated without budworm	2185 ± 153	456 ± 182	75 ± 30	715 ± 269	932 ± 260	37.4 ± 5.4	4.6 ± 1.6	5.4 ± 1.9	10.2 ± 4.4	17.1 ± 4.6
90-Year-old mixed aspen	78 years simulated with budworm	1659 ± 198	37 ± 17	49 ± 29	1037 ± 179	536 ± 109	24.1 ± 1.0	0.9 ± 0.3	4.2 ± 2.0	10.3 ± 1.0	8.6 ± 1.5
90-Year-old mixed aspen	78 years simulated without budworm	1802 ± 89	7 ± 4	48 ± 28	1424 ± 140	323 ± 70	51.9 ± 3.1	0.8 ± 0.3	3.7 ± 1.7	26.2 ± 2.9	21.2 ± 5.3

Note. All values presented represent mean ± 95% confidence interval (n = 15), elements in bold indicate significant difference (mean ± 95% confidence interval) between empirical field data simulated outcomes.

stands. At the end of 100-year simulation runs, these intermediate and shade-tolerant conifers had accumulated 13.9 m² ha⁻¹ and 18.6 m² ha⁻¹ of BA, or 51% and 78% of total stand BA in pure aspen stands and in mixed aspen stands, respectively. The sapling layer (5–10 cm DBH) was equally dominated by balsam fir and white spruce in the pure aspen stands, but balsam fir occupied a larger proportion of saplings in the mixed aspen stands at the end of 100 simulations (Tables 4 and 5). In addition, balsam fir maintained a higher proportion of merchantable BA in mixed aspen stands than in the pure aspen stands whereas the second cohort of aspen was more important in the pure aspen stands than in the mixed aspen stands (Tables 4 and 5, Figs. 4 and 5).

3.3. Stand dynamics following simulated partial harvesting treatments

Simulated gap harvesting, in particular 1600 m² gaps (54% BA removed), produced the highest merchantable BA of all simulated treatments at years 50 and 100 (Figs. 4 and 5). At year 100 of simulations, total stand BA values for pure aspen stands and mixed aspen stands were 38.0 and 34.1 m² ha⁻¹, of which conifer species accounted for 18% and 28%, respectively (Tables 4 and 5). Total stand regeneration, and in particular aspen suckers, responded proportionally to simulated gap size at both stand types. Sucker recruitment into the sapling layer (5–10 cm DBH) started between 12 and 15 years of simulation runs and aspen sucker density increased with gap size (Figs. 4 and 5). Simulated gap cuts created higher aspen sucker densities than dispersed partial cuts in both stand types. Aspen sapling recruitment into merchantable tree size (≥ 10 cm DBH) began 40 years after partial harvesting (Figs. 4B and 5B). Similar to sucker density, merchantable aspen stems responded proportionally, in terms of both density and BA, to gap size (Figs. 4B,C and 5B,C) in both stand types. No differences appeared between unharvested controls and the 33% dispersed cut in the case of pure aspen stands or among unharvested controls, 33 and 61% dispersed cuts in the mixed aspen stands in terms of aspen and conifer density and basal area (Figs. 4A–C and 5A–C).

At years 25, 50 and 100 of simulation runs, mixed aspen stands had higher balsam fir sapling density and higher merchantable stem density and BA than pure aspen stands. Contrary to the response of aspen to gap size, balsam fir decreased in simulated gap cuts in both stand types. Compared to gap cuts, unharvested controls and dispersed partial cuts favored balsam fir (Tables 4 and 5, Figs. 4D–F and 5D–F). Between spruce and fir, the latter dominated the sapling layer of the mixed aspen stands whereas white spruce dominated in the pure aspen stands (Figs. 4D,G and 5D,G). At simulation years 25, 50 and 100 in the pure aspen stands, white spruce produced higher stem density and BA (≥ 5 cm DBH) than balsam fir, irrespective of simulated treatments (Table 4). In the mixed aspen stands, stem density and BA values were higher for balsam fir at years 25 and 50, but white spruce dominated at year 100, regardless of simulated treatments (Table 5).

4. Discussion

The two central questions of this study were: (1) Does the SORTIE-ND reasonably simulate short- and long-term stand dynamics of aspen-dominated mixedwoods and (2) Can partial harvesting accelerate the development of complex, multi-cohort stands and, if so, which treatments perform best? To do this, we used the SORTIE-ND model which has been parameterized for the study area. Short-term (12 years) simulation outcomes were very similar to empirical values of species composition and size distribution, and although long-term simulations showed some

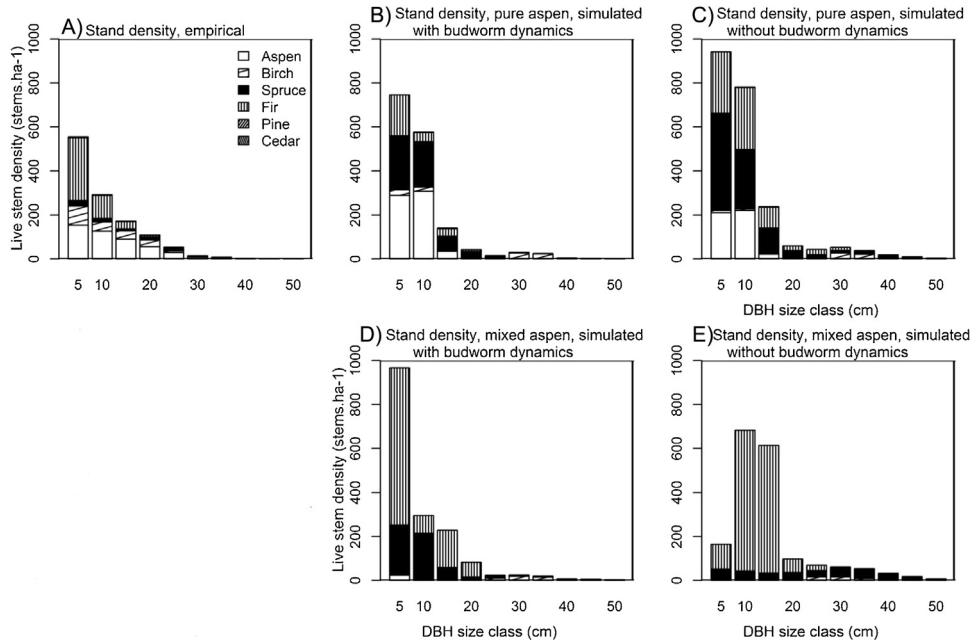


Fig. 3. Comparison between empirical values and model simulation results of DBH size distribution for long-term model evaluation. (A) 168-Year-old growth stand using empirical data from Bergeron (2000). (B and C) 76-Year-old pure aspen stands simulated 92–168 years (76 + 92 = 168) using empirical data from pure aspen stands. (D and E) 90-Year-old mixed aspen stands simulated 78–168 years (90 + 78 = 168) using empirical data from mixed aspen stands. Each graph represents the average condition of 15 permanent sample plots of each study site.

unexpected trends, these were not solely due to problems with model parameter functions or values (discussed below). Stand dynamics similar to those of unharvested controls occurred in both stand types following the simulated 33% partial harvesting. All gap harvesting and the 80% dispersed harvesting promoted aspen recruitment and maintained mixed compositions with higher stand productivity than that in 33% and 61% dispersed harvesting treatments.

4.1. Short-term evaluation

Over the short term (12 years), simulated treatments generally agreed with field data for most parameters including species-level stem density and basal area, but showed higher survival of residual aspen trees in the forest matrix of the 400 m² gap cuts in mixed aspen stands. The observed short-term mortality not captured by the model was likely both endogenous (death of small, low-vigor

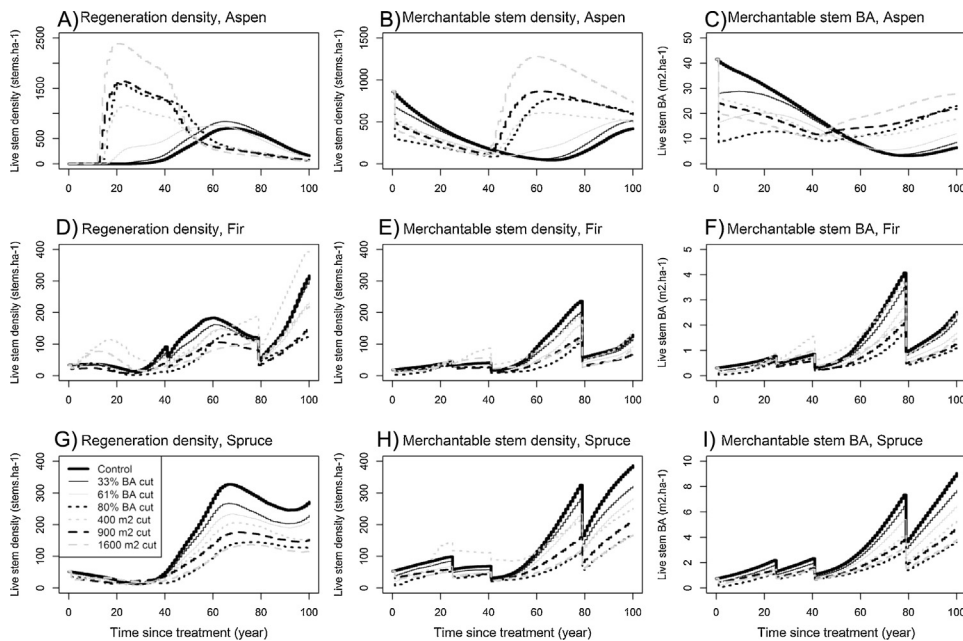


Fig. 4. Stand dynamics of live stems after six levels of partial harvesting and unharvested controls in pure aspen stands. Note. Each graph represents the average condition of 15 permanent sample plots. Regeneration size: 5–10 cm DBH, Merchantable stem: ≥ 10 cm DBH. Sharp declines at years 25, 41 and 79 are due to simulated spruce budworm mortality of balsam fir and white spruce invoked by outbreak incidents (see details in Section 2.5).

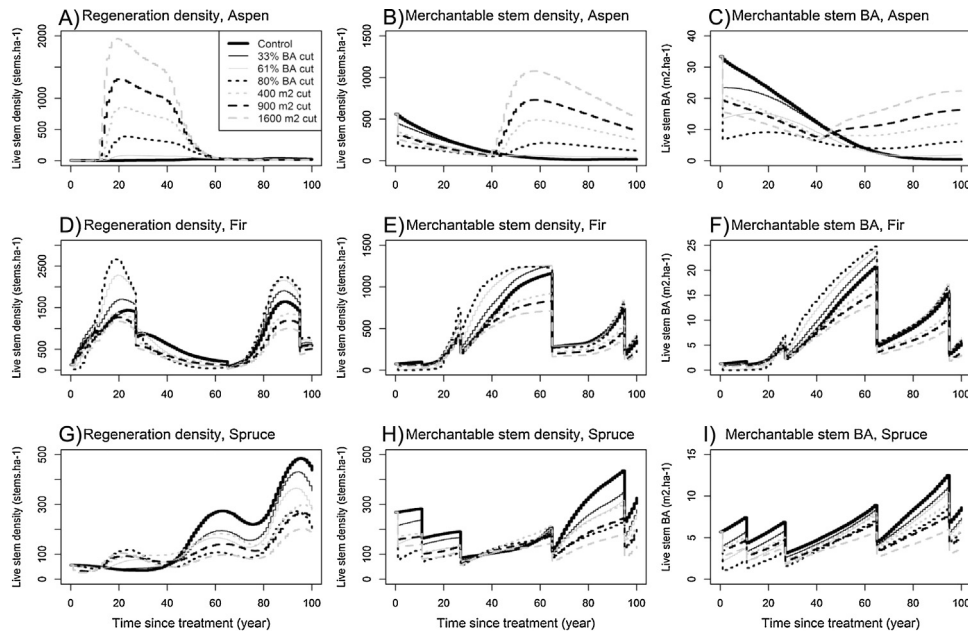


Fig. 5. Stand dynamics of live stems after six levels of partial harvesting and unharvested controls in mixed aspen stands. *Note.* Each graph represents the average condition of 15 permanent sample plots. Regeneration size: 5–10 cm at DBH, Merchantable stem: ≥ 10 cm at DBH. Sharp declines at years 11, 27, 65 and 95 are due to spruce budworm mortality of balsam fir and white spruce manually invoked by outbreak incidents (see details in Section 2.5).

residual aspen stems) and exogenous. These latter sources of mortality include combined effects of harvesting machinery on some residual stems, 2 years of partial defoliation of aspen by the forest tent caterpillar and dry summers in 2001 and 2002, and moderate windthrow, particularly in the mixed aspen stands (Harvey and Brais, 2007; Bose et al., 2014a). None of these sources of mortality are incorporated into the model, and occurring individually, their effects may not be very important to overall stand dynamics; however, their combined and cumulative effects probably contributed to discrepancies between field observations and simulations.

4.2. Long-term evaluation

Simulated development of un-harvested controls of 76-year-old pure aspen stands and 90-year-old mixed aspen stands forecasted conifer dominance in the old stands with lower basal areas than those at starting conditions of simulations. Old stands (150–200 years) in this region are generally composed of at least two cohorts of shade-tolerant conifers (balsam fir, white and black spruce, eastern white cedar), possibly with some residuals of the initial intolerant hardwood cohort and minor subsequent cohorts of

Table 4

Comparison of seven simulated partial harvesting treatments in pure aspen stands at time steps 25, 50 and 100 years of simulations.

	Live stem density ≥ 5 cm DBH (stems ha ⁻¹)				Live basal area ≥ 5 cm DBH (m ² ha ⁻¹)			
	Stand	Aspen	Fir	Spruce	Stand	Aspen	Fir	Spruce
Simulation values at year 25								
Uncut (control)	548 ± 54	347 ± 49	44 ± 22	74 ± 31	31.6 ± 1.9	28.1 ± 2.1	0.5 ± 0.3	1.4 ± 0.5
33% dispersed cut	535 ± 47	351 ± 34	40 ± 20	62 ± 29	28.4 ± 1.6	25.4 ± 1.9	0.5 ± 0.2	1.1 ± 0.5
61% dispersed cut	754 ± 104	572 ± 91	33 ± 18	55 ± 26	23.3 ± 0.9	20.7 ± 1.2	0.4 ± 0.2	0.9 ± 0.4
80% dispersed cut	1855 ± 165	1676 ± 210	28 ± 18	53 ± 38	20.9 ± 0.3	18.5 ± 0.7	0.4 ± 0.2	0.8 ± 0.3
400 m ² gap cut	1606 ± 66	1371 ± 54	114 ± 70	48 ± 20	26.5 ± 1.0	23.3 ± 1.2	0.9 ± 0.4	0.9 ± 0.4
900 m ² gap cut	1963 ± 43	1811 ± 45	28 ± 13	55 ± 27	26.4 ± 0.9	23.8 ± 1.1	0.4 ± 0.2	1.0 ± 0.4
1600 m ² gap cut	2637 ± 143	2457 ± 129	75 ± 41	55 ± 16	26.3 ± 1.1	23.8 ± 1.1	0.6 ± 0.3	0.8 ± 0.2
Simulation values at year 50								
Uncut (control)	915 ± 150	461 ± 94	172 ± 116	204 ± 81	20.6 ± 1.5	14.0 ± 1.9	1.1 ± 0.7	2.2 ± 0.8
33% dispersed cut	1005 ± 127	620 ± 124	133 ± 93	177 ± 69	19.9 ± 1.4	14.1 ± 1.7	0.9 ± 0.5	1.9 ± 0.7
61% dispersed cut	1125 ± 114	807 ± 131	93 ± 67	151 ± 55	18.7 ± 1.1	13.4 ± 1.4	0.8 ± 0.4	1.6 ± 0.6
80% dispersed cut	1446 ± 92	1262 ± 102	50 ± 36	73 ± 30	19.0 ± 0.9	14.9 ± 0.7	0.5 ± 0.3	1.1 ± 0.5
400 m ² gap cut	1320 ± 83	993 ± 70	131 ± 68	126 ± 55	19.9 ± 1.8	14.7 ± 1.1	1.2 ± 0.5	1.3 ± 0.6
900 m ² gap cut	1546 ± 60	1281 ± 61	82 ± 52	118 ± 44	21.6 ± 0.8	17.0 ± 1.1	0.6 ± 0.3	1.4 ± 0.5
1600 m ² gap cut	1931 ± 128	1719 ± 129	81 ± 37	85 ± 26	23.8 ± 1.1	19.9 ± 1.1	0.8 ± 0.3	1.2 ± 0.3
Simulation values at year 100								
Uncut (control)	1790 ± 156	579 ± 154	446 ± 210	658 ± 190	27.1 ± 2.5	7.5 ± 1.7	3.7 ± 1.8	10.2 ± 3.0
33% dispersed cut	1727 ± 163	669 ± 162	415 ± 206	551 ± 187	26.9 ± 2.4	9.6 ± 2.0	3.4 ± 1.7	8.6 ± 2.9
61% dispersed cut	1558 ± 165	649 ± 123	326 ± 174	494 ± 172	27.9 ± 2.5	12.8 ± 2.0	2.8 ± 1.4	7.2 ± 2.5
80% dispersed cut	1210 ± 126	660 ± 56	194 ± 102	299 ± 115	32.7 ± 2.1	23.4 ± 2.4	1.6 ± 0.8	4.2 ± 1.5
400 m ² gap cut	1592 ± 174	566 ± 76	553 ± 212	400 ± 139	32.6 ± 1.9	18.7 ± 1.3	4.1 ± 1.4	5.6 ± 2.1
900 m ² gap cut	1330 ± 98	672 ± 70	220 ± 96	365 ± 110	33.8 ± 1.6	22.4 ± 1.3	1.9 ± 0.8	5.4 ± 1.6
1600 m ² gap cut	1427 ± 125	785 ± 73	360 ± 149	283 ± 73	38.0 ± 0.8	28.1 ± 1.3	2.4 ± 1.0	4.3 ± 1.1

Note. All values presented represents mean ± 95% confidence interval (n = 15). All simulations incorporated spruce budworm outbreak incidents that induced balsam fir and white spruce mortality (see details in Section 2.5).

Table 5
Comparison among seven simulated partial harvesting treatments in mixed aspen stands at time steps 25, 50 and 100 years of simulations.

	Live stem density ≥ 5 cm DBH (stems ha^{-1})				Live basal area ≥ 5 cm DBH ($\text{m}^2 \text{ha}^{-1}$)			
	Stand	Aspen	Fir	Spruce	Stand	Aspen	Fir	Spruce
Simulation values at year 25								
Uncut	2298 \pm 278	216 \pm 33	1794 \pm 248	225 \pm 73	38.8 \pm 2.7	20.3 \pm 2.9	10.3 \pm 1.6	6.8 \pm 1.6
33% dispersed cut	2601 \pm 315	213 \pm 29	2126 \pm 287	209 \pm 68	38.0 \pm 2.6	18.8 \pm 2.6	12.4 \pm 1.5	5.8 \pm 1.4
61% dispersed cut	2997 \pm 365	233 \pm 112	2514 \pm 391	207 \pm 78	34.1 \pm 2.4	14.3 \pm 1.6	14.4 \pm 1.6	4.5 \pm 1.1
80% dispersed cut	3363 \pm 331	437 \pm 271	2695 \pm 459	200 \pm 131	30.7 \pm 2.0	10.4 \pm 1.1	16.0 \pm 2.2	3.6 \pm 1.0
400 m^2 gap cut	2878 \pm 242	957 \pm 130	1647 \pm 322	228 \pm 100	32.9 \pm 2.3	16.6 \pm 1.7	10.1 \pm 1.3	5.2 \pm 1.2
900 m^2 gap cut	3121 \pm 211	1352 \pm 180	1511 \pm 326	218 \pm 112	32.7 \pm 2.1	17.6 \pm 1.7	9.4 \pm 1.4	4.9 \pm 1.1
1600 m^2 gap cut	3497 \pm 171	1898 \pm 287	1359 \pm 374	206 \pm 128	31.2 \pm 1.9	17.9 \pm 1.4	8.4 \pm 1.8	4.2 \pm 1.0
Simulation values at year 50								
Uncut	1769 \pm 169	78 \pm 19	1339 \pm 165	294 \pm 74	32.8 \pm 1.8	7.5 \pm 1.6	15.7 \pm 1.7	6.8 \pm 1.6
33% dispersed cut	1808 \pm 146	82 \pm 30	1425 \pm 153	251 \pm 74	33.2 \pm 2.1	7.2 \pm 1.5	17.5 \pm 1.6	6.2 \pm 1.5
61% dispersed cut	1797 \pm 138	120 \pm 88	1373 \pm 201	262 \pm 84	32.5 \pm 2.2	5.8 \pm 1.0	18.9 \pm 2.1	5.8 \pm 1.3
80% dispersed cut	1861 \pm 151	272 \pm 194	1348 \pm 237	211 \pm 112	32.2 \pm 2.2	5.7 \pm 1.5	19.8 \pm 2.6	5.2 \pm 1.7
400 m^2 gap cut	2021 \pm 100	625 \pm 98	1057 \pm 167	296 \pm 82	31.0 \pm 2.0	9.5 \pm 0.9	13.5 \pm 1.8	6.1 \pm 1.3
900 m^2 gap cut	2115 \pm 74	900 \pm 129	941 \pm 165	236 \pm 86	31.1 \pm 1.8	11.8 \pm 1.2	12.2 \pm 1.9	5.3 \pm 1.3
1600 m^2 gap cut	2307 \pm 68	1286 \pm 204	800 \pm 182	189 \pm 89	31.2 \pm 1.7	14.4 \pm 1.5	10.7 \pm 2.3	4.5 \pm 1.3
Simulation values at year 100								
Uncut	1800 \pm 105	43 \pm 14	945 \pm 79	764 \pm 156	23.7 \pm 1.2	0.6 \pm 0.4	7.8 \pm 0.8	10.8 \pm 1.9
33% dispersed cut	1784 \pm 95	45 \pm 16	1066 \pm 68	633 \pm 137	22.9 \pm 1.1	0.8 \pm 0.7	9.0 \pm 0.8	9.2 \pm 1.5
61% dispersed cut	1791 \pm 81	61 \pm 37	1158 \pm 71	539 \pm 119	23.1 \pm 1.9	2.0 \pm 2.3	9.6 \pm 0.9	8.5 \pm 1.4
80% dispersed cut	1743 \pm 104	117 \pm 79	1205 \pm 128	397 \pm 116	24.9 \pm 2.8	6.3 \pm 4.4	9.5 \pm 1.4	7.0 \pm 1.4
400 m^2 gap cut	1627 \pm 82	257 \pm 40	847 \pm 68	490 \pm 101	28.7 \pm 1.2	12.1 \pm 2.1	6.3 \pm 0.7	7.2 \pm 1.2
900 m^2 gap cut	1561 \pm 85	365 \pm 51	743 \pm 71	425 \pm 95	30.8 \pm 1.4	16.3 \pm 2.4	5.6 \pm 0.7	6.3 \pm 1.1
1600 m^2 gap cut	1479 \pm 81	520 \pm 81	619 \pm 85	315 \pm 86	34.1 \pm 1.9	22.4 \pm 3.4	4.7 \pm 0.7	4.7 \pm 1.0

Note. All values presented represents mean \pm 95% confidence interval ($n = 15$). All simulations incorporated spruce budworm outbreak incidents that induced balsam fir and white spruce mortality (see details in Section 2.5).

intolerant hardwoods (Bergeron, 2000; Harvey et al., 2002; Pothier et al., 2004). The degree to which intolerant hardwoods recruit into older stands generally depends on several factors: density of advance conifer regeneration; canopy composition at the time of budworm or tent caterpillar outbreaks; defoliation severity and the extent of subsequent canopy mortality (Bergeron, 2000; D'Aoust et al., 2004; Bouchard et al., 2005; Moulinier et al., 2011, 2013). The 1823 stands used as a reference for the study contained small amounts of white spruce in all size classes, abundant small-sized balsam fir and decreasing densities of trembling aspen from the 5 cm diameter class (ca. 150 stems) to the 25 cm size class (ca. 50 stems), thus suggesting a multiple cohort age structure for aspen (Fig. 3A). This stand structure would appear to be driven by spruce budworm-induced mortality and recurrent aspen and fir recruitment into budworm gaps (Morin et al., 1993). We recognize, however, that the 1823 reference stands represent one portrait of a ca. 190-year-old boreal mixedwood stand on a spectrum of possible structural and compositional conditions. Indeed, numerous factors, including initial stand conditions, severity of the stand-establishing fire and subsequent budworm and tent caterpillar disturbances, seed sources and succession processes, could all influence stand development in these boreal mixedwood landscapes.

Given the occurrence of three spruce budworm outbreaks of variable duration and intensity in this region during the twentieth century (Morin et al., 1993), it is understandable that the punctual budworm "outbreak incidents" induced in the simulations deviate in their effect on stand structure and composition from the 1823 reference conditions. Certainly, the approach to incorporating budworm-induced mortality was hindered by data shortage on spruce mortality from outbreaks in the study area, and our simulated output showed higher survival of spruce than observed in the reference stand. The data that we used to estimate white spruce mortality (Blais, 1981) were from a site situated 600 km southeast of the study area so it is possible, even likely, that real budworm mortality in the 1823 reference stand was different. In addition to this, while we accounted for the percentage of budworm-induced fir and spruce mortality, we did not consider size of gaps created by

this mortality. As demonstrated by the partial harvesting simulations, if conifer mortality had been imposed in the form of medium to large gaps (900–1600 m^2 and larger) rather than in a random (dispersed) distribution, this would have resulted in higher aspen recruitment and survival and, like the 1823 reference stand, more aspen in intermediate diameter classes.

4.3. Multi-cohort management and stand productivity in pure aspen and mixed aspen stands

A multi-cohort based forest management approach proposed for the eastern boreal forest (Bergeron and Harvey, 1997) involves, at the stand level, integrating natural stand dynamics into silviculture with the objective of developing structural and compositional attributes characteristic of old growth stands. In this context, variants of partial harvesting have been suggested to promote the old-growth attributes. Our results suggest that, in the two stand types, virtually all simulated partial harvesting treatments maintained multi-cohort mixedwood compositions with a second generation of aspen and first and second generation shade tolerant conifers. The sole exception was the 33% dispersed removal (and to a certain extent, the 61% dispersed removal) in mixed aspen stands which almost eliminated aspen by year 100 of the simulations.

By creating more area with high light incidence in the sub-canopy and forest floor, gap harvesting favored trembling aspen and increased stand productivity in terms of basal area, regardless of stand type. In contrast, dispersed harvesting promoted shade tolerant conifers (Figs. 4 and 5). A simulation study by Beaudet et al. (2011) using the light resource module of SORTIE-ND in similar forest cover types showed that dispersed removal of 30% BA created no sub-canopy microsites with $>50\%$ light availability, and only 2–3% of microsites had $>50\%$ light availability after 60% BA dispersed removal. SORTIE-ND predicts regeneration recruitment and growth as a function of light and neighborhood competition (Coates et al., 2003) and our results indicate that dispersed partial harvesting as high as 60% of BA still benefits shade tolerant conifers over trembling aspen but results in lower total stand basal area than gap

harvesting of similar intensity (Tables 4 and 5). Similar low understory light conditions have been observed after dispersed partial harvesting in aspen mixedwood stands in other studies of the eastern Canadian boreal forest (e.g., Prévost and Pothier, 2003; Man et al., 2008). Understory light could further decrease following dispersed tree removal due to crown expansion of residual neighbors in the years following partial harvesting (Man et al., 2008).

Simulations indicate that low-level (33–66%) dispersed partial harvesting impedes trembling aspen recruitment and survival. Overall results suggest that, over the long-term and after successive budworm outbreaks, these treatments would create stands with the lowest stand BA (≈ 23 – 28 m^2) but with the highest proportion of shade-tolerant conifers (36–45% in pure aspen stands and 78–80% in mixed aspen stands). The level of ingress of intolerant species depends on initial canopy opening by treatments and on the extent of subsequent canopy tree mortality induced by spruce budworm and other partial disturbances. In contrast, high intensity partial harvesting ($\geq 80\%$ BA) and particularly gap cuts $\geq 400 \text{ m}^2$ favor trembling aspen recruitment immediately after harvesting. Large gaps, in particular, have the sustained effect of maintaining high stem densities of aspen in both stand types. At year 100 of simulations, unharvested controls, 33% and 61% dispersed harvestings created more simple stand structures in both stand types, with only merchantable trees and regeneration of tolerant conifers. In contrast, by favoring a continuous recruitment of trembling aspen as well as tolerant conifers, all gap treatments and 80% dispersed harvesting created more complex stand structures in both stand types (Figs. 4 and 5 and Tables 4 and 5). Although, we did not measure the size variability/heterogeneity, graphics of stand dynamics (regenerations and merchantable stems) illustrate a more complex stand structure with regeneration and merchantable stems of both trembling aspen and tolerant conifers in all gap harvesting treatments at year 100 of simulations (Figs. 4 and 5). Pretzsch and Schütze (2009) also demonstrated the importance of mixed compositions of Norway spruce and European beech for long-term stand-level productivity. According to Pothier et al. (2004), a second-generation aspen recruitment in even-aged natural aspen stands is generally delayed until stand senescence. At this point, mortality is less density-dependant and, especially in clonal aspen stands, is probably more contagious (aggregated). If this is the case, gap cuts would certainly better mimic senescence mortality in pure aspen and mixed aspen stands than dispersed partial harvesting.

4.4. Dynamics of pure aspen versus mixed aspen stands

After 25 and 50 years of simulation runs, unharvested controls of the two stand types showed different development patterns, largely as a result of differences in pre-treatment understory conditions (Tables 4 and 5). Besides the low initial densities of conifer regeneration in the pure aspen stands, the presence of mountain maple impaired the recruitment of shade tolerant conifers into larger tree layers and is likely at least partly responsible for lower stand basal area than the mixed aspen stands after 25 and 50 years of simulation. The adverse impact of high woody shrubs such as mountain maple on shade tolerant conifer recruitment and growth has been well documented for eastern Canadian boreal mixedwood (MacDonald et al., 2004; Kneeshaw and Prévost, 2007; Bose et al., 2014b). Moreover, the pure aspen stands in the study site had fewer conifer seed trees than the mixed aspen stands, which also would affect conifer recruitment over the long term. Our results suggest that the differences in pre-treatment stand characteristics, that is, abundance of advance conifer regeneration, conifer seed trees and mountain maple in the understory were the primary factors driving tree and stand responses to the simulated treatments. Results showed that such differences in pre-treatment stand conditions could continue to influence stand dynamics for up to 100 years.

However, at year 100, simulated 1600 m^2 gap cuts decreased over all stand and species specific differences between the two stand types (Tables 4 and 5).

4.5. Management implications

Forecasting stand growth and development is not an exact science and, after partial harvesting, is additionally complicated because this type of intervention generally introduces more stand-level structural complexity (Zenner, 2000). This study provides insight into how partial harvesting treatments of different intensities and spatial configurations can influence dynamics in pure aspen and mixed aspen stands. Our results demonstrate – or at least strongly suggest – that the spatial configuration of residual overstory trees, the amount of residual conifer seed trees and advance conifer regeneration, conifer mortality by spruce budworm and the presence of woody shrubs like mountain maple are all factors that, ideally, should be taken into consideration when making harvest prescriptions, and particularly partial harvesting prescriptions. To promote aspen regeneration, our long-term simulations corroborate the overwhelming body of knowledge on the subject: large gaps favor aspen recruitment and growth, small gaps and low intensity canopy removal tend to be much less favorable. This is generally true for both pure aspen and mixed aspen stands. To promote conifer recruitment into the canopy layer, the contrary is generally true: small gaps and a range of intensities of dispersed harvesting will favor spruce and fir at the expense of aspen. This said, these treatments are best applied in mixedwood stands, like the ones simulated in this study, where dense conifer understories are present.

Three of the simulated gap harvesting treatments (400 m^2 , 900 m^2 and 1600 m^2) removed less than 60% of basal area but generated higher basal area values at 100 years of simulation than dispersed partial harvesting of 60% and 80% basal area removal. Such high basal area retention by gap harvesting could potentially also retain more favorable wildlife habitat than dispersed harvesting with low basal area retention. A review by Vanderwel et al. (2009) indicated that high intensity partial harvesting (70% BA removal) created unsuitable habitat for about one fourth of all late-successional species, including most forest raptors, pileated and black-backed woodpeckers, brown creeper, northern flying squirrel and woodland caribou.

4.6. Further model development and calibration

This study allowed us to identify a number of gaps in our understanding of the dynamics and interrelationships occurring within these ecosystems. The model simulations also identified areas in which the parameters estimated in SORTIE-ND could be improved upon or where more empirical studies should be undertaken to improve our understanding of specific dynamics of the eastern Canadian boreal mixedwood.

The fact that white spruce appears to have superior seedling recruitment and survival to that of balsam fir does not reflect the reality of our region in the eastern Canadian boreal forest. Therefore, there is clearly a need to better understand spruce recruitment and dynamics at the juvenile (seedling and sapling) stage. Installation of long-term monitoring plots would allow the quantification of relationships between spruce seed production, seed dispersal, and germination and seedling survival rates for specific seedbed types as well as mortality at different stages (seedlings, saplings and pole size). A better understanding of the competitive effects of woody shrubs on survival is also very much of interest. In this study, we considered the competition effect of mountain maple, a high, woody shrub, but not other species in the herb and shrub layers.

It should be noted that SORTIE-ND does not incorporate below-ground effects of competition for water and nutrients on growth or regeneration recruitment.

Currently, the integration of punctual, non-catastrophic disturbances such as insect outbreaks can only be done manually with SORTIE-ND, by converting selected live trees species and tree sizes to snags at pre-determined specific time-steps. Due to the already complex nature of the model, this manual approach to integrating budworm dynamics may be a more reasonable way to go than endeavoring to model them. Budworm-forest dynamics are complex and other non-spatial models have been developed solely for the purpose of characterizing and forecasting forest dynamics under budworm-driven disturbance regimes and developing management options for optimizing wood supply (MacLean et al., 2001). Nonetheless, similar to work by D'Aoust et al. (2004), aerial photographs could be used to improve understanding of the spatial dimensions of canopy gap formations following insect outbreaks such as spruce budworm and forest tent caterpillar in mixed forest types of different ages and with varying proportions of vulnerable species. SORTIE-ND could also benefit from monitoring of budworm-induced canopy gap formation and closure and associated regeneration dynamics.

Several studies have reported on initial logging induced mortality after partial harvestings in Canadian boreal mixedwoods (e.g., MacDonald and Thompson, 2003; Bladon et al., 2008; Solarik et al., 2012). A better understanding of initial pulses of mortality after a range of partial harvesting treatments (different intensities and spatial configurations) could contribute to capture a source of mortality otherwise missed by SORTIE-ND. For example, Thorpe et al. (2010) simulated a range of partial harvesting treatments for black spruce forests of boreal Ontario and reported initial logging induced mortality for several harvesting scenarios and Arii et al. (2008) employed a complex harvesting algorithm to investigate a broader range of partial harvest scenarios.

This said, we believe that SORTIE-ND has already proved its utility for the eastern Canadian boreal mixedwood forest and will continue to be improved as new data specific to key ecosystem processes become available.

Acknowledgements

We are grateful to two anonymous reviewers, the editor of *Ecological Modelling*, Sean Thomas and Jean-Claude Ruel for helpful comments and suggestions for improving the original manuscript. The first author acknowledges the funding received through the NSERC-FQRNT-BMP scholarship program and support from Norbord Industries, British Columbia Forest Service and Bulkley Valley Research Center for logistic support during model development and parameterization in Smithers, BC, Canada. This work was supported by NSERC Collaborative Research and Development Grant CRDPJ 395368-09 (Eastern boreal mixedwoods: Multiscale analysis of stand structure, dynamics and silviculture). We are also grateful to Albanie Leduc for providing the earlier parameterized version of SORTIE-ND, Lora Murphy for model technical support, Danielle Charron for helping with the dataset of the 1823 reference stand, Marc Mazerolle for assistance with statistics and Major Mario, Alfred Coulombe, Manuella Strukelj, Jeanne Therrien, Suzie Rollin, Hannah Brais Harvey and Elizabeth Turcotte for assistance with field data collection for the SAFE project.

Appendix. Major modelling behaviors of SORTIE-ND used in present study

Growth behaviors

Three sub-models were used to predict growth:

- (i) Non limited absolute diameter growth for seedlings and saplings:

$$Y = SF \left(\frac{A \times GLI}{(A/S) + GLI} \right), \quad (1)$$

where $Y = \log_{10}(\text{radial growth} + 1)$, SF is the suppression factor, A is the asymptotic diameter growth, S is the slope of growth response and GLI is the gap light index, calculated by a light behavior. A Gap Light Index (GLI) value is calculated for each individual tree by accounting for minimum solar angle in radians, number of altitude sky divisions, number of azimuth sky divisions, beam fraction of global radiation (0–1), clear sky transmission coefficient, first day of growing season, last day of growing season, amount of canopy light transmission (0–1) and amount of light transmission through snags (0–1). GLI values range from 0 (no sun) to 100 (full sun).

Amount of diameter growth per timestep is calculated as:

$$\text{Growth} = \frac{(10^Y - 1) \times 2}{10} \times T, \quad (2)$$

where $Y = \log_{10}(\text{radial growth} + 1)$ and T is the number of years per time step.

- (ii) Constant radial growth (Y)

$$Y = \frac{g^4}{10} \times 2 \times T, \quad (3)$$

where Y is the amount of diameter growth, in cm, to add to the tree, g^4 is the species-specific adult constant radial growth parameter in $\text{mm} \cdot \text{yr}^{-1}$ and T is the number of years per timestep.

- (iii) NCI (neighborhood competition indices) growth:

$$\text{Growth} = \text{Max Growth} \times \text{Size Effect} \times \text{Shading Effect} \times \text{Crowding Effect}, \quad (4)$$

Max Growth is the maximum diameter growth the tree can attain, in $\text{cm} \cdot \text{yr}^{-1}$, entered in the NCI Maximum Potential Growth, $\text{cm} \cdot \text{yr}^{-1}$ parameter. *Size Effect*, *Shading Effect* and *Crowding Effect* are all optional factors which act to reduce the maximum growth rate and will vary depending on the conditions a tree is in. Each of these effects is a value between 0 and 1.

$$\text{Size effect, } SE = e^{-0.5 \left(\frac{\ln(\text{DBH}/X_0)}{X_b} \right)^2}, \quad (5)$$

where DBH is the DBH of the target tree in cm, X_0 is the NCI size effect mode in cm and X_b is the NCI size effect variance in cm.

$$\text{Shading effect, } ShE = e^{-m \cdot S^n}, \quad (6)$$

where m is the NCI shading effect coefficient, n is the NCI shading effect exponent and S is the amount of shade cast by neighbors, from 0 (no shade) to 1 (full shade).

$$\text{Crowding effect, } CW = e^{-C \times \text{DBH}^\gamma \times \text{NCI}^D}, \quad (7)$$

where C is the NCI crowding effect slope, DBH is the DBH of the target tree in cm, γ is the NCI size sensitivity to target tree species type, D is the NCI crowding effect steepness and NCI is the individual based tree NCI value (equation below):

$$\text{NCI}_i = \sum_{j=1}^S \sum_{k=1}^N \lambda_{ik} \frac{(\text{DBH}_{jk}/q)^\alpha}{\text{dist}_{ik}^\beta}, \quad (8)$$

where the calculation sums over $j = 1, \dots, S$ species and $k = 1, \dots, N$ neighbors of each species of at least a DBH of NCI minimum neighbor DBH, in cm, out to a distance of NCI max radius of crowding neighbors, in m, α is the NCI alpha parameter for the target tree's

species, β is the NCI beta parameter for the target tree's species, DBH_{jk} is the DBH of the k th neighbor, in cm, q is the NCI DBH divisor, λ_{jk} is the species j NCI Lambda parameter for the target species relative to the k th neighbor's species, $dist_{jk}$ is distance from target to neighbor, in m.

Mortality behaviors

Five sub models are used to predict mortality:

(i) Juvenile mortality (m)

$$m = 1 - e^{-(T \times m1)e^{-m^2 \times G}}, \quad (9)$$

where m is the probability of mortality, T is the number of years per timestep, $m1$ is the mortality at zero growth parameter, m^2 is the light-dependent mortality parameter and G is amount of radial growth, in mm yr^{-1} , added to the tree's diameter during T .

(ii) Senescence (m_s)

$$m_s = \frac{e^{(\alpha + \beta)(DBH - DBH_s)}}{1 + e^{(\alpha + \beta)(DBH + DBH_s)}}, \quad (10)$$

where m_s is the probability of mortality, α (senescence mortality alpha parameter) and β (senescence mortality beta parameter) control the magnitude of the uptick, DBH is the tree's DBH, in cm and DBH_s is the DBH at onset of senescence, in cm parameter.

(iii) Adult stochastic mortality

$$\text{Adult stochastic mortality} = \frac{Max}{1 + (Age/X_0)X_b}, \quad (11)$$

p is the probability of mortality, Max is the suppression duration mortality – max mortality rate (0–1) parameter, X_0 is the suppression duration mortality – X_0 parameter, X_b is the suppression duration mortality – X_b parameter, Age is the tree's age, in years.

(iv) Weibull snag mortality (s)

$$s = e^{-(a \times T)^b}, \quad (12)$$

where S is proportion of snags still standing, between 0 and 1, a and b are weibull parameters (weibull annual “ a ” parameter for snag size class X mortality parameter and weibull annual “ b ” parameter for snag size class X mortality parameter), T is the snag age in years.

(v) Competition mortality: competition mortality is a growth-based mortality behavior. It uses the results of the NCI growth behavior (Eq. (2)). Trees killed by this behavior have a mortality reason code of natural.

Substrate behaviors

Substrates are what seedlings germinate on. Six types of substrates of variable and species-specific suitability are incorporated into the model: forest floor litter, forest floor moss, scarified soil, tip-up mounds, decayed logs and fresh logs.

$$\text{Fresh log area, } FL = \frac{DBH \times h}{2}, \quad (13)$$

where FL is new fresh log area, in square meters, DBH is the DBH of the fallen tree, in m and h is the height of the fallen tree, in m.

$$\text{Newly exposed tip-up mounds, } OA = \pi \times (r \times F)^2, \quad (14)$$

where OA is the new tip-up mounds area in square meters, r is the tree trunk radius in meters and F is the uprooted tree radius increase factor for root rip-out parameter, which accounts for the effects of root disturbance.

Relationships among fresh logs, decayed logs, tip-up mounds and scarified soils represent the decay of the different substrates as a function of substrate age according to the following equation:

$$Y = e^{\alpha \times t^\beta}, \quad (15)$$

where t is time in years, α and β are the parameters.

Spatial disperse behaviors

We fit functions that predict the density (numbers/ m^2) of seedlings (R_i) in quadrant i using an equation of the form:

$$R_i = STR \sum_{j=1}^S C_j f_j \sum_{k=1}^T \left(\frac{dbh_k}{30} \right)^2 \frac{1}{n} e^{-Dm_{ik}^3}, \quad (16)$$

where STR (“standardized total recruits”) is the potential number of seedling recruits produced by a 30 cm DBH parent tree, c_j and f_j are the cover and favorability, respectively of the $j = 1..S$ substrate types, dbh_k is the DBH (in cm) of the $k = 1..T$ parent trees within the specified radius of quadrant i , n is a normalizer (described below), D is a species-specific dispersion parameter and m_{ik} is the distance (in meters) from the i th quadrant to the k th parent tree. The normalizer (n) serves two functions. It reduces parameter correlation between STR and the dispersion parameter (D); and scales the distance-dependent dispersion terms so that STR is in meaningful units – i.e., the total number of seedlings produced in the entire seedling shadow of a 30 cm DBH parent tree.

References

- Ameztegui, A., Coll, L., Benavides, R., Valladares, F., Paquette, A., 2012. Understory light predictions in mixed conifer mountain forests: role of aspect-induced variation in crown geometry and openness. *For. Ecol. Manag.* 276, 52–61.
- Arii, K., Caspersen, J.P., Jones, T.A., Thomas, S.C., 2008. A selection harvesting algorithm for use in spatially explicit individual-based forest simulation models. *Ecol. Model.* 211, 251–266.
- Astrup, R., (Ph.D. dissertation) 2006. Evaluation of SORTIE-ND for growth prediction in mixed boreal stands. University of British Columbia, Vancouver, BC, 156p.
- Astrup, R., Coates, K.D., Hall, E., 2008. Finding the appropriate level of complexity for a simulation model: an example with a forest growth model. *For. Ecol. Manag.* 256, 1659–1665.
- Beaudet, M., Harvey, B.D., Messier, C., Coates, K.D., Poulin, J., Kneeshaw, D.D., Brais, S., Bergeron, Y., 2011. Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: a modelling approach. *For. Ecol. Manag.* 261, 84–94.
- Bergeron, Y., 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology* 81, 1500–1516.
- Bergeron, Y., Harper, K.A., 2009. Old-Growth Forests in the Canadian Boreal: The Exception rather than the Rule? Old-Growth Forests. Springer, pp. 285–300.
- Bergeron, Y., Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. *For. Ecol. Manag.* 92, 235–242.
- Bergeron, Y., Leduc, A., Joyal, C., Morin, H., 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Can. J. For. Res.* 25, 1375–1384.
- Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Can. J. For. Res.* 31, 384–391.
- Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S., 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. *Silva Fenn.* 36, 81–95.
- Bergeron, Y., Chen, H.Y.H., Kenkel, N.C., Leduc, A.L., Macdonald, S.E., 2014. Boreal mixedwood stand dynamics: ecological processes underlying multiple pathways. *For. Chron.* 90, 202–213.
- Bladon, K.D., Lieffers, V.J., Silins, U., Landhäusser, S.M., Blenis, P.V., 2008. Elevated mortality of residual trees following structural retention harvesting in boreal mixedwoods. *For. Chron.* 84, 70–75.
- Blais, J.R., 1981. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. *Can. J. For. Res.* 11, 620–629.
- Bose, A.K., Brais, S., Harvey, B.D., 2014a. Trembling aspen (*Populus tremuloides* Michx.) volume growth in the eastern boreal mixedwood: effect of partial cutting, social status, and neighborhood competition. *For. Ecol. Manag.* 327, 209–220.
- Bose, A.K., Harvey, B.D., Brais, S., 2014b. Sapling recruitment and mortality dynamics following partial cutting in aspen-dominated mixedwoods in eastern Canada. *For. Ecol. Manag.* 329, 37–48.

- Bose, A.K., Harvey, B.D., Brais, S., Beaudet, M., Leduc, A., 2014c. Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review. *Forestry* 87, 11–28.
- Bouchard, M., Kneeshaw, D., Bergeron, Y., 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. *For. Ecol. Manag.* 204, 297–313.
- Brais, S., Harvey, B.D., Bergeron, Y., Messier, C., Greene, D., Belleau, A., Paré, D., 2004. Testing forest ecosystem management in boreal mixedwoods of northwestern Quebec: initial response of aspen stands to different levels of harvesting. *Can. J. For. Res.* 34, 431–446.
- Brais, S., Work, T.T., Robert, É., O'Connor, C.D., Strukelj, M., Bose, A., Celentano, D., Harvey, B.D., 2013. Ecosystem responses to partial harvesting in eastern boreal mixedwood stands. *Forests* 4, 364–385.
- Canada Soil Survey Committee, 1987. Canadian System of Soil Classification, 2nd ed. Publ. 1646. Agriculture Canada, Ottawa, Canada.
- Canham, C.D., Thompson, J., Zimmerman, J.K., Uriarte, M., 2010. Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42, 87–94.
- Chen, H.Y., Popadiouk, R.V., 2002. Dynamics of North American boreal mixedwoods. *Environ. Rev.* 10, 137–166.
- Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L., Messier, C., 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. *For. Ecol. Manag.* 186, 297–310.
- Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. *J. Ecol.* 97, 118–130.
- Cooke, B.J., Lorenzetti, F., 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. *For. Ecol. Manag.* 226, 110–121.
- Cooke, B., Lorenzetti, F., Roland, J., 2009. On the duration and distribution of forest tent caterpillar outbreaks in East-Central Canada. *J. Entomol. Soc. Ont.* 140, 3–18.
- Cumming, S.G., Schmiegelow, F.K.A., Burton, P.J., 2000. Gap dynamics in boreal aspen stands: is the forest older than we think? *Ecol. Appl.* 10, 744–759.
- Dansereau, P.-R., Bergeron, Y., 1993. Fire history in the southern boreal forest of northwestern Quebec. *Can. J. For. Res.* 23, 25–32.
- D'Aoust, V., Kneeshaw, D., Bergeron, Y., 2004. Characterization of canopy openness before and after a spruce budworm outbreak in the southern boreal forest. *Can. J. For. Res.* 34, 339–352.
- Environment Canada, 2011. Canadian Climate Normals 1971–2000. Canadian Climate Program. Atmospheric Environment Service, Downsview, Ontario, Canada, http://climate.weather.gc.ca/climate_normals/index_e.html
- Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. *Alternative Silvicultural Approaches to Timber Harvesting: Variable Retention Harvest Systems. Creating a Forestry for the 21st Century: The Science of Ecosystem Management.* Island Press, Washington, DC, pp. 111–139.
- Gauthier, S., Vaillancourt, M.-A., Leduc, A., Grandpré, L.D., Kneeshaw, D., Morin, H., Drapeau, P., Bergeron, Y., 2009. *Ecosystem Management in the Boreal Forest.* Presses de l'Université du Québec, Québec.
- Groot, A., Gauthier, S., Bergeron, Y., 2004. Stand dynamics modelling approaches for multicohort management of eastern Canadian boreal forests. *Silva Fenn.* 38, 437–448.
- Haeussler, S., Canham, C.D., Coates, K.D., 2013. Complexity in Temperate Forest Dynamics. In: Messier, C., Puettmann, K.J., Coates, K.D. (Eds.), *Managing Forests as Complex Adaptive Systems: Building Resilience to the Challenge of Global Change.* Routledge, New York, USA, pp. 60–78.
- Harvey, B.D., Brais, S., 2007. Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (*Populus tremuloides*) dominated boreal mixedwoods: implications for deadwood dynamics. *Can. J. For. Res.* 37, 1525–1533.
- Harvey, B.D., Leduc, A., Gauthier, S., Bergeron, Y., 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. *For. Ecol. Manag.* 155, 369–385.
- Kneeshaw, D.D., Bergeron, Y., 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* 79, 783–794.
- Kneeshaw, D., Gauthier, S., 2003. Old growth in the boreal forest: a dynamic perspective at the stand and landscape level. *Environ. Rev.* 11, S99–S114.
- Kneeshaw, D.D., Prévost, M., 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. *Can. J. For. Res.* 37, 1534–1544.
- LeBlanc, P.A., 2014. Incorporating multi-cohort old aspen and mixedwood dynamics into a long-term forest management plan. *For. Chron.* 90, 50–58.
- Leduc, A., Coates, K.D., (a report carried out as part of Master thesis) 2013. Parameterization changes to the lac Duparquet SORTIE-ND model. Département des sciences biologiques, Université du Québec à Montréal, 28p.
- LePage, P.T., Canham, C.D., Coates, K.D., Bartemucci, P., 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. *Can. J. For. Res.* 30, 415–427.
- Lieffers, V.J., Stewart, J.D., Macmillan, R.B., Macpherson, D., Branter, K., 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. *For. Chron.* 72, 286–292.
- Ligot, G., Balandier, P., Courbaud, B., Jonard, M., Kneeshaw, D., Claessens, H., 2014. Managing understory light to maintain a mixture of species with different shade tolerance. *For. Ecol. Manag.* 327, 189–200.
- MacDonald, G.B., Thompson, D.J., 2003. Responses of planted conifers and natural hardwood regeneration to harvesting, scalping, and weeding on a boreal mixedwood site. *For. Ecol. Manag.* 182, 213–230.
- MacDonald, G.B., Cherry, M.L., Thompson, D.J., 2004. Effect of harvest intensity on development of natural regeneration and shrubs in an Ontario boreal mixedwood stand. *For. Ecol. Manag.* 189, 207–222.
- MacLean, D.A., Erdle, T.A., MacKinnon, W.E., Porter, K.B., Beaton, K.P., Cormier, G., Morehouse, S., Budd, M., 2001. The spruce budworm decision support system: forest protection planning to sustain long-term wood supply. *Can. J. For. Res.* 31, 1742–1757.
- Man, R., Kayahara, G.J., Rice, J.A., MacDonald, G.B., 2008. Eleven-year responses of a boreal mixedwood stand to partial harvesting: light, vegetation, and regeneration dynamics. *For. Ecol. Manag.* 255, 697–706.
- Morin, H., Laprise, D., Bergeron, Y., 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. *Can. J. For. Res.* 23, 1497–1506.
- Moulinier, J., Lorenzetti, F., Bergeron, Y., 2011. Gap dynamics in aspen stands of the Clay Belt of northwestern Quebec following a forest tent caterpillar outbreak. *Can. J. For. Res.* 41, 1606–1617.
- Moulinier, J., Lorenzetti, F., Bergeron, Y., 2013. Effects of a forest tent caterpillar outbreak on the dynamics of mixedwood boreal forests of eastern Canada. *Ecoscience* 20, 182–193.
- Murphy, L.E., 2011. SORTIE-ND User Manual, Version 6.11. Institute of Ecosystem Studies, Millbrook, NY, <http://www.sortie-nd.org/software/index.html>
- Nlungu-Kweta, P., Leduc, A., Bergeron, Y., 2014. Conifer recruitment in Trembling Aspen (*Populus tremuloides* Michx.) stands along an east-west gradient in the boreal mixedwoods of Canada. *Forests* 5, 2905–2928.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43.
- Papaik, M.J., Fall, A., Sturtevant, B., Kneeshaw, D., Messier, C., Fortin, M.-J., Simon, N., 2010. Forest processes from stands to landscapes: exploring model forecast uncertainties using cross-scale model comparison. *Can. J. For. Res.* 40, 2345–2359.
- Penner, M., 2008. Yield prediction for mixed species stands in boreal Ontario. *For. Chron.* 84, 46–52.
- Pothier, D., Raulier, F., Riopel, M., 2004. Ageing and decline of trembling aspen stands in Quebec. *Can. J. For. Res.* 34, 1251–1258.
- Poulin, J., Messier, C., 2008. Rapport de paramétrisation du modèle de simulation de la dynamique forestière SORTIE-ND pour la forêt boréale et sub-boréale de l'ouest du Québec. Centre d'Étude de la forêt, Université du Québec à Montréal, <http://www.cef-cfr.ca/uploads/CEF/parametrisation.pdf> (in French).
- Pretzsch, H., Schütze, G., 2009. Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. *Eur. J. For. Res.* 128, 183–204.
- Prévost, M., Pothier, D., 2003. Partial cuts in a trembling aspen conifer stand: effects on microenvironmental conditions and regeneration dynamics. *Can. J. For. Res.* 33, 1–15.
- Prévost, M., Dumais, D., Pothier, D., 2010. Growth and mortality following partial cutting in a trembling aspen-conifer stand: results after 10 years. *Can. J. For. Res.* 40, 894–903.
- Robert, E., Brais, S., Harvey, B.D., Greene, D., 2012. Seedling establishment and survival on decaying logs in boreal mixedwood stands following a mast year. *Can. J. For. Res.* 42, 1446–1455.
- Rowe, J.S., 1972. *Forest Regions of Canada.* Information Canada Ottawa.
- Saucier, J.P., Bergeron, J.F., Grondin, P., Robitaille, A., 1998. Les régions écologiques du Québec méridional (3ième version): Un des éléments du système hiérarchique de classification écologique du territoire mis au point par le ministère des Ressources naturelles du Québec, L'Abelle, February–March 1998., pp. 1–12.
- Solarik, K.A., Lieffers, V.J., Volney, W.J.A., Pelletier, R., Spence, J.R., 2010. Seed tree density, variable retention, and stand composition influence recruitment of white spruce in boreal mixedwood forests. *Can. J. For. Res.* 40, 1821–1832.
- Solarik, K.A., Volney, W.J.A., Lieffers, V.J., Spence, J.R., Hamann, A., 2012. Factors affecting white spruce and aspen survival after partial harvest. *J. Appl. Ecol.* 49, 145–154.
- Stadt, K.J., Huston, C., Coates, K., David, Z., Feng, M., Dale, R.T., Lieffers, V.J., 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. *Ann. For. Sci.* 64, 477–490.
- Thorpe, H.C., Vanderwel, M.C., Fuller, M.M., Thomas, S.C., Caspersen, J.P., 2010. Modelling stand development after partial harvests: an empirically based, spatially explicit analysis for lowland black spruce. *Ecol. Model.* 221, 256–267.
- Vanderwel, M.C., Mills, S.C., Malcolm, J.R., 2009. Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. *For. Chron.* 85, 91–104.
- Vanderwel, M.C., Caspersen, J.P., Malcolm, J.R., Papaik, M.J., Messier, C., 2011. Structural changes and potential vertebrate responses following simulated partial harvesting of boreal mixedwood stands. *For. Ecol. Manag.* 261, 1362–1371.
- Vincent, J.-S., Hardy, L., 1977. L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. *Géog. Phys. Q.* 31.
- Weiskittel, A.R., Hann, D.W., Kershaw Jr., J.A., Vanclay, J.K., 2011. *Forest Growth and Yield Modeling.* John Wiley & Sons.
- Wright, E.F., Coates, K.D., Bartemucci, P., 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. *Can. J. For. Res.* 28, 1352–1364.
- Yasuda, A., Yoshida, T., Miya, H., Harvey, B., 2013. An alternative management regime of selection cutting for sustaining stand structure of mixed forests of northern Japan: a simulation study. *J. For. Res.* 18, 398–406.
- Zenner, E.K., 2000. Do residual trees increase structural complexity in Pacific Northwest coniferous forests? *Ecol. Appl.* 10, 800–810.