A comparative study of long-term stand growth in eastern Canadian boreal forest: Fire versus clear-cut

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Abstract

Clear-cutting and fire are the two main disturbances affecting the boreal forest of eastern Canada. These two disturbance types exert different effects on forest dynamics, which can have major implications in terms of economic and ecological sustainability. This study compared the long-term effects of these two disturbance types on stand composition, stand density, and merchantable volume on eastern Canadian mesic boreal forests dominated by black spruce and balsam fir. We used 157 permanent sample plots (PSP), 41 of which originated from fire and 116 were from clear-cuts. Model selection with finite-sample corrected Akaike Information Criterion (AICc) was used to understand which factors had the greatest influence on relative stand density and merchantable volume. Our results indicate that merchantable volume was positively influenced by stand density, which in turn was primarily influenced by disturbance origin, with post-cutting stands being denser than post-fire stands. These results indicated that an increase in stand density is an important mechanism through which disturbance acts upon merchantable volume. We also found differences in forest composition between stand-origin categories, with balsam fir being more abundant post-clearcutting; this was likely because advance regeneration was mainly composed of balsam fir, whereas post-fire stands are dominated by black spruce. Differences in merchantable volume between post-fire and post-clearcut stands become non-significant with time, mainly because of higher tree growth and lower mortality in the dominant canopy of clearcut-origin stands. Overall, the results indicate that stand origin is an important determinant of stand composition and stand yield, but that the latter effect tends to disappear after a few decades. The higher balsam fir content generally observed in naturally regenerated, clear-cut origin stands could have potentially negative economic and ecological impacts at the landscape scale, which may call for mitigation strategies.

Keywords: Boreal forest; Clear-cutting; Fire; Stand density; Merchantable volume; Forest composition.

1. Introduction

Boreal forest is the most extensive forest ecosystem worldwide, in that it covers 11% of the Earth's terrestrial surface (Kuusela, 1992). Moreover, the boreal forest biome represents the largest terrestrial reserve of carbon (Shugart et al., 1992). In the last few decades, many studies have documented natural disturbances processes in boreal forest ecosystems, in order to maintain these processes as much as possible through forest management (Johnson et al., 1998; Bergeron et al., 2002; Harvey and Brais, 2002). Wildfire is the principal agent of natural disturbance in the boreal forest (Bonan and Shugart, 1989; Viereck, 1983), but over the last century, at least in Canada, the area clear-cut has increased substantially (Brumelis and Carleton, 1989; Hart and Chen, 2006). The higher rate of clear-cut compared to fire is particularly obvious in parts of the boreal forest where the fire cycle (i.e., the time needed to entirely burn an area equivalent to the study area) is longer than the clear-cut rotation age (i.e., the age at which forest is to be harvested). Understanding differences in stand growth and compositional trajectories between clear-cutting and fire is important for a better understanding of the effects of management activities on natural ecosystems, and to improve management tools such as timber supply models.

Although fire and clear-cutting are both stand-replacing disturbances, they have different effects in terms of stand dynamics (Haeussler and Kneeshaw, 2003; Johnson et al., 2003). Fires leave an abundance of dead trees and some patches of residual unburned live trees, which create structural heterogeneity at the stand and landscape levels (Johnson et al., 1998). Patches of live trees may act as source habitats for plant species with poor dispersal capabilities (Dettki et al., 2000), whereas dead trees, snags and decaying logs provide an important habitat for a range of specialized plant species (Bradbury, 2006). In comparison, traditional clear-cutting generally results in removal of all merchantable trees, the felling...
of most non-merchantable tree species, and the retention of few dead and live standing trees (Haeussler and Kneeshaw, 2003). Severe fires also generally eliminate advance regeneration and consume much of the surface organic matter layer, thereby producing suitable mineral seedbeds for regeneration (Johnson, 1992), whereas clear-cuts often maintain advance regeneration and the understory plants (Rees and Juday, 2002), especially when the ground is snow-covered during harvesting operations (Nguyen-Xuan et al., 2000; Reich et al., 2001).

While equal wood volume yields from stands originating from fire and clear-cutting can be observed when their compositions are similar (Reich et al., 2001; Ruel et al., 2004), differences in species composition can markedly affect wood production, regardless of the disturbance being considered (Reich et al., 2001). If different disturbances induce different patterns of species succession, we can expect differences in stand production between these two types of disturbance. In eastern Canada, late-successional species may represent much of the regeneration in clear-cut stands, particularly when careful logging practices that protect advance regeneration and soil are used (Morin and Gagnon, 1991; Pothier et al., 1995; Parent and Ruel, 2002). In contrast, stands originating from fire are expected to be mostly composed of pioneer species that have established after the disturbance (Bergeron, 2000; Bouchard et al., 2008). Stand density and initial size of the recruited trees following disturbance could also have important implications in terms of wood production (Seeide and Chen, 2010).

It is important to compare forest productivity that is associated with both types of stand-replacing disturbance to accurately predict volume increases and to insure sustainable forest management over the long-term. Hence, the main purposes of this study are: (1) to compare stand-level wood production in clearcut-origin and fire-origin stands over the long term on a large territory; (2) to examine if potential differences can be explained by stand characteristics such as relative stand density or forest composition; and (3) to examine the implications of these findings for sustainable forest management in boreal forests.

2. Materials and methods

2.1. Study area

The study area covered most of the North Shore region, a provincial administrative district in eastern Québec, Canada. The study area covered 62,962 km² and extended northward from the north shore of the Saint Lawrence River to 51°N (Fig. 1). It is located on the Canadian Shield, which is composed mostly of Precambrian rocks that are covered by glacial till of various thicknesses and by fluvialglacial deposits. According to 30-year meteorological records at two different locations along the river (1971–2001, Environment-Canada, 2012), the climate is boreal humid, with mean annual precipitation varying from 1014 to 1156 mm and mean annual temperature ranging from 0.8 to 1.5 °C. Further inland, the climate is expected to be colder and drier (Proulx, 1987). Forests in this region are dominated by black spruce (Picea mariana (Mill.) BSP and balsam fir (Abies balsamea (L.) Mill.), with minor components of jack pine (Pinus banksiana Lamb.), white or paper birch (Betula papyrifera Marsh.), and trembling aspen (Populus tremuloides Michx.). Other species that were present in lower proportions include white spruce (Picea glauca (Moench) Voss) and eastern larch or tamarack (Larix laricina (Du Roi) K.Koch), together with yellow birch (Betula alleghaniensis Britt.) and red maple (Acer rubrum (L.) in the southern portion of the North Shore region. In this region, fire is the major natural stand-replacing disturbance, with a relatively long mean return interval that ranges from 250 to 500 years along a west–east longitudinal gradient (Bouchard et al., 2008). Mesic sites tend to be dominated by black spruce and hardwood pioneers after fire, with a gradual increase in balsam fir content that can occur when the initial post-fire cohort begins to die some 100 years or more after the stand-initiating fire (Bouchard et al., 2008). In pre-industrial conditions, fire was the only disturbance capable of creating patches of mortality larger than several tens of km² across the whole region. Other types of natural disturbances are widespread, but are of relatively secondary importance in terms of landscape-scale forest composition; stand-replacing windthrows (defined as severe mortality that is incurred over areas >5 ha) have affected a mean 0.0255% of the area per year, which is equal to a cycle of about 3900 years (Bouchard et al., 2009), while severe spruce budworm (Choristoneura fumiferana (Clem.) outbreaks have historically affected only the southern part of the study area, with a corresponding cycle of about 9200 years over the entire study area (Bouchard and Pothier, 2010). Prior to 1900, anthropogenic disturbances were mainly restricted to selective logging of large trees along major rivers. Clear-cut logging (defined as removal of at least 75% of the original dominant canopy cover) began in the early 1920s, i.e., during the pulp and paper industry boom (Frenette, 1996). Clear-cut occurrence mostly in the southern part of the region and were gradually expanded northward away from the main rivers with the progressive development of the road network, particularly after the 1950s (Bouchard and Pothier, 2011). Even today, however the northern and eastern sectors of the North Shore region have not experienced extensive forest management (Bouchard et al., 2008) such as 57% of the forest stands are overmature (MRNFP, 2004).

2.2. Disturbance maps

A fire history map, which had been constructed by Bouchard et al. (2008), was used to determine stand origin in the eastern part of the territory for the period 1900–2000. For the western part of the territory, a fire map was constructed for the same period by using archival information (aerial photographs and forest maps), which were complemented with ground surveys (dendrochronology); details of the methodology are presented in Bouchard et al. (2008). Maps of clear-cutting history were created using maps found in forest company archives, as well as aerial photographs (between 1930 and 2000) (Bouchard and Pothier, 2011). For the older cuts, for which company archives were scarce, field surveys were conducted using dendrochronological methods to confirm the year in which clear-cutting had occurred at different points.
within the territory, and to confirm the occurrence of past clearcuts by looking at remaining legacies, such as old sown tree stumps.

2.3. Permanent sample plot selection

For this study, we used a network of permanent sample plots (PSP) that had been established in the study area by the Ministère des Ressources Naturelles du Québec (MRNQ) from 1970 onward. Within each permanent plot, the diameters of all merchantable trees (>9.0 cm) were measured at breast height (DBH at 1.3 m) within a 400 m² circular plot, and the ages and heights (±0.1 m) of 2–13 dominant and co-dominant trees were determined. Further, the number of saplings (1.0 < DBH ≤ 9.0 cm, in 2-cm diameter class increments) was determined for each species in a 40 m² subplot that was located near the 400 m² plot centres. Following their establishment, the plots were re-measured 1–3 times, typically with an interval of 10 years (range, 5–21 years).

Disturbance origin of each plot was determined by overlapping plot location with the disturbance maps for the period 1920–1990. All plots that were not located inside the mapped disturbances were excluded from the dataset. We cross-checked ages of the dominant trees to ensure that the plots located inside mapped disturbances were not located in small stands that escaped disturbance. We removed from the datasets those PSPs that had not regenerated naturally, for example, those that had been planted following the disturbance. We further excluded any plot that had been affected by other stand-initiating disturbances, such as severe spruce budworm epidemics (defined as the death of at least 75% of the original dominant canopy cover) or windthrow. To control for a potential latitudinal effect on stand growth and composition, we retained only PSPs that were located south of 51°N. We also limited variation in stand growth that was due to site conditions by retaining only PSPs that were established on mesic sites, which were defined by soils deeper than 50 cm and by drainage conditions that were neither excessive (xeric) nor poor (hydric). In the study area, mesic sites that respect these conditions represent about 70% of the total productive land base (Bouchard et al., 2008). Finally, we only retained PSPs that had been re-measured at least once. According to these criteria, we selected a total of 157 PSPs, of which 41 originated from fires that occurred from 1921 to 1976, and 116 that had originated from clear-cutting that had been applied between 1932 and 1990. A total of 361 plot measurements were made, with an average of 2.34 measurements per PSP.

2.4. Computed variables

The volume of merchantable living trees was estimated for each species with a volume equation developed by Fortin et al. (2007). Stand-level volume was obtained by summing tree-level volumes for each measurement period. We also calculated the site index (SI) for each plot, i.e., the stand dominant height at 50 years of age, by using the age–height relationship that had been developed by Pothier and Savard (1998) for the main merchantable tree species across the Québec province. However, as suggested by Garet et al. (2009), we used the time that had elapsed since the last disturbance as the temporal variable in the SI equation instead of mean age of sampled dominant and co-dominant trees, as this variable is a better predictor of stand yield on the long-term for this region (Garet et al., 2009). To compute SI, we first estimated the dominant height (Hd), which was defined as the height of the 100 largest trees per hectare (Pardé and Bouchon, 1988), and which corresponded to the 4 largest trees within a 400 m² PSP. Because tree height was not systematically measured on dominant trees, we estimated Hd with an equation that was developed by Bégin and Raulier (1995) and parameterised by Pothier and Savard (1998) using a large number of PSPs and temporary sample plot distributed throughout the province of Québec:

\[
H_d = 1.3 + \left( \frac{D_4}{(H - 1.3)} \right) + \beta_2(D_4 - D_4) \]

(1)

where \(D_4\) is the mean DBH (cm) of the 4 largest trees per PSP, \(D\) is the mean DBH (cm) of dominant and co-dominant trees, \(H\) is the mean height of the dominant and co-dominant trees, which were measured in the field, and \(\beta_2\) is the value of the parameter calculated for each merchantable species. This parameter changed with the plot dominant species (determined in basal area) and allowed us to take into account the potential species effect on site index.

Site index was then calculated for each plot using the following equation:

\[
SL = \beta_2[H_d^{1/4}(1 - \exp(-\beta_2\overline{A}))^{1/4}H_d^{1/2}]
\]

(2)

where \(H_d\) is dominant height (m), \(\overline{A}\) is the time elapsed since the last disturbance (years) and \(\beta_1, \beta_2\) are regression parameters calculated with the same sample plots used in Eq. (1) and that are specific to each dominant tree species.

The influence of stand density on volume production over time was evaluated through the calculation of a relative density index (\(\rho\)), as proposed by Drew and Flewelling (1979) and based on the self-thinning rule. To compute \(\rho\), we used the following equation that was parameterised by Pothier and Savard (1998):

\[
\rho = N(D_4/10)^{1/b_2}
\]

(3)

where \(N\) is the total number of trees per hectare, including saplings (DBH ≥ 1.1 cm), \(D_4\) is the mean quadratic diameter (cm) of saplings and merchantable trees, and \(b_1\) and \(b_2\) are coefficients that were based on calculations made over a great number of temporary plots across the province (Pothier and Savard, 1998). Values of \(b_1\) and \(b_2\) were determined from the species that dominated basal area in each measurement period.

Finally, because a spruce budworm outbreak occurred in the study area from 1975 to 1990, i.e., during the period in which most PSPs were surveyed, and that this outbreak differentially affected the growth of trees among PSPs, we computed an index that took into account the specific effects of the outbreak on each PSP. This variable, the ring-width reduction index (RWRI, Pothier et al., 2005), has proved successful in estimating the overall impact of the insect defoliator on stand production by integrating the effects of annual defoliation that occurred between two successive PSP measurements (Pothier and Mailly, 2006; Pothier et al., 2012). In using this index, we explained variation in stand production that could have otherwise been attributed to the type of disturbance. Defoliation intensity was evaluated according to aerial surveys that had been performed annually by the MRNQ, and which assigned a defoliation category (0, no observable defoliation; 1, light defoliation (<35%); 2, moderate to severe defoliation (>35%)) to each cell, and which averaged 58 km² in size. Since each PSP was associated with a cell, we could determine the recent defoliation history of each permanent plot. These defoliation histories were included in an equation that had been parameterised by Pothier et al. (2012) to calculate the RWRI that was associated with each period between two successive measurements of each PSP. Although growth reduction due to defoliation is generally lower for spruce species than balsam fir, Pothier et al. (2012) demonstrated that these species have proportional radial growth loss patterns for a given defoliation level, making possible to predict radial growth loss of spruce from that of balsam fir as already suggested by Hennigar et al. (2008).
2.5. Statistical analyses

Modeling was performed using a mixed-model procedure that accommodated repeated measures and unbalanced data (Pinheiro and Bates, 2000). We first tested different covariance structures, including or excluding random effects, to determine the model form that best accounted for autocorrelation between successive measurements of each PSP. For this purpose, we used a fixed set of explanatory variables (viz., initial volume or initial relative density index; time elapsed since the last disturbance (TSD); time interval between first measurement and consecutive ones and disturbance type) to select the most appropriate covariance structure according to restricted maximum likelihood method (REML) in order to compare models with the same fixed effects (Pinheiro and Bates, 2000). The model form with the smallest values of both the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) was assumed to be the most reliable. The most parsimonious model form was found to be the general least-squares procedure with an autoregressive correlation structure of order 1, and a continuous temporal variable represented by the time interval between two PSP measurements without any random effect.

The influence of explanatory variables upon stand production and density were examined using an information-theoretic approach (Burnham and Anderson, 2002) to select the most parsimonious fit to the data among a set of candidate models. For model selection, we used maximum likelihood (ML) method that is appropriate to compare model with different fixed effects (Pinheiro and Bates, 2000). We performed two distinct model selection analyses to examine which explanatory variables best explained the observed changes in stand density and to examine the effect of explanatory variables on merchantable volume. For each model selection procedure, a set of candidate models was formulated according to a priori hypotheses (Burnham et al., 2011).

Several explanatory variables were considered in the models, including disturbance type, site index, TSD, time interval, RWRI, which represented the occurrence of spruce budworm outbreaks, and predicted relative stand density index (values from the best model) for modeling change in merchantable volume. In addition, the volume or the relative stand density corresponding to the first measurement of each PSP was used as a fixed covariate (e.g., Kiernan et al., 2008; Garet et al., 2009). Model selection among the a priori candidate models was performed with the finite-sample corrected Akaike Information Criterion (AICc, Burnham and Anderson, 2002) using ML method.

\[
\text{AICc} = -2 \log(L) + 2K + [2K(K+1)]/(n-K-1)
\]

where \(\log(L)\) is the log-likelihood of the model, \(K\) is the number of parameters of the model including the intercept, and \(n\) is the sample size. The parameter values of the final prediction model were chosen according to the AICc weight of the best model. When the top ranking model had an AICc weight greater than or equal to 0.90, we computed predictions and associated standard errors based on the parameters of this model only. Otherwise, we computed the model-averaged predictions and unconditional standard errors based on the entire set of candidate model estimates (Mazerolle, 2012). Standard errors were then used to compute confidence intervals (CI) around the predicted temporal changes of relative density or volume to determine the time period during which significant differences occurred between disturbance types. We corrected for potential biases that were associated with the conversion from logarithmic to arithmetic units by multiplying each transformed prediction by the correction factor (CF) of Sprugel, 1983:

\[
CF = e^{(SEE^2/2)}
\]

where \(SEE\) is the standard error of the estimate of the model. Data analyses were performed using the NLME package (Pinheiro and Bates, 2000) for mixed-model procedures in R (R Development Core Team, 2012). When necessary, variables were in-transformed to respect model assumptions, especially homogeneity of variance and normality of residuals. Model curves were displayed for each disturbance type when at least disturbance effect or its interaction with TSD was statistically significant at \(\alpha < 0.05\). Standard errors associated with predicted values of the model curves were approximated with the delta method (Oehlert, 1992) with the AICcmodavg R package (Mazerolle, 2012). Because we used 10-year time steps to determine the temporal trajectories of stand density and production, we used the estimates calculated at the preceding step as the initial volume or the initial relative density index of each succeeding step. Thus, we added the error of these estimates to compute the confidence interval of each curve.

3. Results

The most parsimonious model that explained variation in stand density was the model with the largest number of explanatory variables (model #10, Table 1). This model performed much better than the second-best model (model #9), as indicated by a difference of 17.9 between their respective AICc values. The strong AICc weight of model #10 (close to 1) meant that coefficients of this model (Table 2) could be used directly for prediction without resorting to model-averaging. The parameter values for model #10 indicated that the relative density index at time \(i + 1\) was positively affected by relative density index at time \(i\) and by site index, while it was negatively affected by the ring-width reduction index (RWRI), which represented the effects of defoliation during the last spruce budworm outbreak. The two last interaction terms in Table 2 indicate that the relative density index exhibit different temporal patterns between disturbance types as seen in Fig. 2, and that RWRI differently affects stand density between disturbance types. Based on model #10, a visual representation of disturbance effects on relative density has been illustrated in Fig. 2 with the 95% confidence intervals. These confidence intervals indicated that after 38 years, the relative density index values of both disturbances were no longer statistically different at \(\alpha = 0.05\).

Changes in merchantable volume were best explained by models #9 and #10, which both included the relative density index, site index, and the time that had elapsed since the last disturbance (Table 3). The second-best model (model #9), which excluded RWRI, does not separate effectively with #10 (AICc < 2) and is empirically supported with an AICc weight of 0.4634. The variable “disturbance” was not present in these two models. When combined with results from the previous model selection procedure, the effect of disturbance was mostly capture by its effects on stand density. When models including relative density are excluded from the model selection process, variation in merchantable volume was best explained by model #7, which included the effect of disturbance (Table 3). The effect of disturbance on merchantable volume is illustrated in Fig. 3, and the parameters that were associated with this model have been summarized in Table 4. According to these results, the merchantable volume of PSPs originating from clear-cuts increased faster than those from fire (Fig. 3), which corresponded to the higher relative stand density observed in clear-cut stands (Fig. 2). Differences in merchantable volume decreased with increasing time-since-disturbance while confidence intervals increased with increasing projection period so that an overlapping of the confidence intervals was apparent after about 33 years. At the end of the observation period, the merchantable volume of clear-cutting stands averaged 228 m\(^3\), whereas that of fire-origin stands averaged 179 m\(^3\). Temporal changes in merchantable
Table 1
Candidate models for assessing changes in relative density index ln(p1 + 1).

<table>
<thead>
<tr>
<th>No.</th>
<th>Models</th>
<th>K</th>
<th>AICc</th>
<th>AICcWt</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI + RWRI × Disturb</td>
<td>12</td>
<td>253.02</td>
<td>0.00</td>
</tr>
<tr>
<td>9</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>11</td>
<td>270.92</td>
<td>17.90</td>
</tr>
<tr>
<td>8</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>10</td>
<td>280.43</td>
<td>27.41</td>
</tr>
<tr>
<td>6</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>9</td>
<td>281.01</td>
<td>27.99</td>
</tr>
<tr>
<td>7</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>8</td>
<td>287.15</td>
<td>34.13</td>
</tr>
<tr>
<td>5</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>9</td>
<td>288.26</td>
<td>35.24</td>
</tr>
<tr>
<td>4</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>8</td>
<td>298.20</td>
<td>45.18</td>
</tr>
<tr>
<td>3</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>7</td>
<td>299.24</td>
<td>46.22</td>
</tr>
<tr>
<td>2</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>6</td>
<td>331.99</td>
<td>78.97</td>
</tr>
<tr>
<td>1</td>
<td>ln(p1) + ln(Δt) + ln(p1) + ln(Δt) + ln(TSDt + 1) + Disturb + ln(TSDt + 1) + Disturb + ln(S1) + RWRI</td>
<td>5</td>
<td>426.33</td>
<td>173.30</td>
</tr>
</tbody>
</table>

Note: p1 is the initial value of p (relative density index) for each PSP; TSDt is the time since the last disturbance of the next PSP measurement; Δt is the time interval between two PSP measurements; Disturb is a binary variable which takes the value of 0 for clear-cut and 1 for fire.

Table 2
Parameter estimates of model #10, which predicts changes in relative density index ln(p1 + 1).

<table>
<thead>
<tr>
<th>Covariate</th>
<th>β</th>
<th>SE</th>
<th>t-Value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.316</td>
<td>0.781</td>
<td>-1.685</td>
<td>0.0936</td>
</tr>
<tr>
<td>ln(p1)</td>
<td>1.082</td>
<td>0.194</td>
<td>5.575</td>
<td>0.0000</td>
</tr>
<tr>
<td>ln(Δt)</td>
<td>-0.111</td>
<td>0.165</td>
<td>-0.674</td>
<td>0.5009</td>
</tr>
<tr>
<td>ln(TSDt + 1)</td>
<td>0.027</td>
<td>0.119</td>
<td>0.229</td>
<td>0.8191</td>
</tr>
<tr>
<td>Disturb</td>
<td>-4.112</td>
<td>1.195</td>
<td>-3.442</td>
<td>0.0007</td>
</tr>
<tr>
<td>ln(S1)</td>
<td>0.440</td>
<td>0.138</td>
<td>3.181</td>
<td>0.0017</td>
</tr>
<tr>
<td>RWRI</td>
<td>-0.159</td>
<td>0.030</td>
<td>-5.222</td>
<td>0.0000</td>
</tr>
<tr>
<td>ln(p1) × ln(Δt)</td>
<td>-0.271</td>
<td>0.071</td>
<td>-3.791</td>
<td>0.0002</td>
</tr>
<tr>
<td>ln(TSDt + 1) × Disturb</td>
<td>0.261</td>
<td>0.063</td>
<td>4.489</td>
<td>0.0000</td>
</tr>
</tbody>
</table>

Standard Error of Estimate: 0.445847.

Note: Disturb is a binary variable which takes the value of 0 for clear-cut and 1 for fire.

Fig. 2. Patterns of change of relative density index over time after clear-cut and after fire. White filled circles and black filled triangles correspond to measured values of relative density index (0.001 and 0.009 after clear-cut and fire, respectively). Confidence bands (α < 0.05) are represented by grey areas around the thicker model lines. Site index was set at 17 and 15 for clear-cut and fire, respectively, while RWRI was set at 0 for both disturbance types. Lower dashed horizontal line represents the relative density index at crown closure while the upper dashed horizontal line represents the relative density index, at which mortality induced by competition begins (Drew and Flewelling, 1979; Newton and Weetman, 1993).

Volume were statistically different between disturbance types as attested by the interaction of this variable with TSD. Changes in merchantable volume were also positively associated with site index, temporal variables (TSDt + 1 and Δt) and initial volume whereas they were negatively affected by spruce budworm defoliation (Table 4).

Species composition of merchantable volume differed between stands originating from each disturbance type, particularly in the case of balsam fir (Fig. 4). Balsam fir constituted 30–53% of merchantable volume in clear-cut stands, whereas its contribution to post-fire stands was negligible for all age classes that were observed in this study. When the 60-year age-class was examined separately, this difference was highly significant (15g = 4.1066, P < 0.001). In addition, the proportion of hardwood species was smaller after clear-cutting than after fire while reverse was observed for coniferous species other than balsam fir and black spruce. Finally, the black spruce fraction increased over time for both disturbance types and, at the end of the observation period, represented 33% and 61% of the merchantable volume for clear-cut and burned stands, respectively.

4. Discussion

4.1. Post-disturbance stand density and wood production

Stand volume trajectories during the decades following disturbance (Fig. 3) were mainly influenced by stand density (Fig. 2), which was largely determined by the disturbance type. Higher stand densities after clear-cutting than after fire were also observed in other boreal regions (Ilisson and Chen, 2009), and were attributed to the presence and the survival of advance regeneration in post-clear-cut stands (Ilisson and Chen, 2009). In the province of Québec, most clear-cut-origin stands < 25-years-old have been harvested by purposefully preserving the advance growth, which can result in regeneration densities > 30,000 trees/ha (Harvey and Brais, 2002), depending upon harvesting methods that were employed, the machinery that is used, and the season in which logging is conducted (Harvey and Bergeron, 1989; Harvey and Brais, 2002).

Our results also support those of Seedre and Chen (2010) who also found a higher vegetation biomass (living vegetation C) in post-logged stands than in post-fire ones for the first 27 years after disturbance. Seedre and Chen (2010) attributed this result to a faster stand establishment in managed stands which facilitates an effective capture of the nutrients that are made available after disturbance (Simard et al., 2001; Thiffault et al., 2008). As a consequence, the height of the advance regeneration at time of cutting allows young post-cut stands to be taller that post-fire stands, which results in higher calculated values of site index. Thus, the mean SI values were 17 and 15 for post-cut and post-fire stands, respectively (Figs. 2 and 3) even though both post-disturbance plots were established on the same soils at the same latitude.
**Table 3**

Model selection for assessing changes in merchantable volume $\ln(V_i + 1)$ over time since the last disturbance.

<table>
<thead>
<tr>
<th>No.</th>
<th>Models</th>
<th>$K$</th>
<th>AICc</th>
<th>AAIcc</th>
<th>AICcWt</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>$\text{ln}(V_i) + \text{ln}(\text{Disturb}) + \text{ln}(\text{TSD}_i + 1) + \text{ln}(V_i + 1) + \text{ln}(\text{TSD}_i + 1) + \text{ln}(\text{SI}) + \text{RWRI}$</td>
<td>10</td>
<td>326.56</td>
<td>0.00</td>
<td>0.5359</td>
</tr>
<tr>
<td>9</td>
<td>$\text{ln}(V_i) + \text{ln}(\text{Disturb}) + \text{ln}(\text{TSD}_i + 1) + \text{ln}(V_i + 1) + \text{ln}(\text{TSD}_i + 1) + \text{ln}(\text{SI})$</td>
<td>9</td>
<td>326.85</td>
<td>0.29</td>
<td>0.4634</td>
</tr>
<tr>
<td>7</td>
<td>$\text{ln}(V_i) + \text{ln}(\text{Disturb}) + \text{ln}(\text{TSD}_i + 1) + \text{ln}(V_i + 1) + \text{ln}(\text{TSD}_i + 1) + \text{ln}(\text{SI})$</td>
<td>8</td>
<td>340.17</td>
<td>13.61</td>
<td>0.0006</td>
</tr>
<tr>
<td>6</td>
<td>$\text{ln}(V_i) + \text{ln}(\text{Disturb}) + \text{ln}(\text{TSD}_i + 1) + \text{ln}(\text{SI})$</td>
<td>9</td>
<td>345.53</td>
<td>18.97</td>
<td>0.0000</td>
</tr>
<tr>
<td>8</td>
<td>$\text{ln}(\text{Disturb}) + \text{ln}(\text{TSD}_i + 1) + \text{ln}(\text{SI})$</td>
<td>8</td>
<td>348.87</td>
<td>22.31</td>
<td>0.0000</td>
</tr>
<tr>
<td>5</td>
<td>$\text{ln}(\text{Disturb}) + \text{ln}(\text{TSD}_i + 1)$</td>
<td>8</td>
<td>392.78</td>
<td>66.22</td>
<td>0.0000</td>
</tr>
<tr>
<td>4</td>
<td>$\text{ln}(\text{TSD}_i + 1)$</td>
<td>6</td>
<td>394.80</td>
<td>68.24</td>
<td>0.0000</td>
</tr>
<tr>
<td>3</td>
<td>$\text{ln}(\text{TSD}_i + 1)$</td>
<td>5</td>
<td>442.11</td>
<td>115.56</td>
<td>0.0000</td>
</tr>
<tr>
<td>2</td>
<td>$\text{ln}(\text{Disturb})$</td>
<td>4</td>
<td>459.97</td>
<td>133.41</td>
<td>0.0000</td>
</tr>
<tr>
<td>1</td>
<td>$\text{ln}(\text{TSD}_i + 1)$</td>
<td>3</td>
<td>591.38</td>
<td>264.83</td>
<td>0.0000</td>
</tr>
</tbody>
</table>

**Note:** $V_i$ is the initial merchantable volume of PSPs; TSD$_i$ is the time since the last disturbance; $\text{SI}$ is the time interval between $V_i + 1$ and $V_i$; Disturb is the categorical variable for disturbance type; SI is Site Index; RWRI is the ring-width reduction index. $K$ is the number of parameters, including two additional parameters for correlation structure and standard error of regression estimates; AICc is Akaike's Information Criterion (corrected); AAIcc is the difference in AICc between the current model and the model with the minimum value of AICc; AICcWt is the Akaike weight or level of support for a model.

Fig. 3. Patterns of change of merchantable volume over time after clear-cutting and after fire according model #7 in Table 4. White filled circles and black filled triangles correspond to measured merchantable volume at TSD$_i + 1$ after clear-cutting and fire, respectively. Model was incremented by 10-year intervals and initialised at the first minimum measured values of merchantable volume ($0.25$ m$^3$ ha$^{-1}$ and $0.74$ m$^3$ ha$^{-1}$ after clear-cut and fire, respectively). Confidence bands ($\alpha < 0.05$) are represented by grey areas around the thicker model lines. Site index was set at 17 and 15 for clear-cut and fire, respectively, while RWRI was set at 0 for both disturbance types.

**Table 4**

Parameter estimates of model #7, which predicts changes in merchantable volume ($V_i + 1$) over time since the last disturbance.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$\beta$</th>
<th>SE</th>
<th>$t$-Value</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-4.995</td>
<td>0.705</td>
<td>-7.082</td>
<td>0.0000</td>
</tr>
<tr>
<td>$\text{ln}(V_i)$</td>
<td>0.385</td>
<td>0.042</td>
<td>9.202</td>
<td>0.0000</td>
</tr>
<tr>
<td>$\text{ln}(\text{Disturb})$</td>
<td>0.621</td>
<td>0.120</td>
<td>5.164</td>
<td>0.0000</td>
</tr>
<tr>
<td>$\text{ln}(\text{TSD}_i + 1)$</td>
<td>0.775</td>
<td>0.157</td>
<td>4.919</td>
<td>0.0000</td>
</tr>
<tr>
<td>Disturb</td>
<td>-2.922</td>
<td>1.295</td>
<td>-2.256</td>
<td>0.0252</td>
</tr>
<tr>
<td>$\text{ln}(\text{SI})$</td>
<td>1.240</td>
<td>0.165</td>
<td>7.512</td>
<td>0.0000</td>
</tr>
<tr>
<td>RWRI</td>
<td>-0.095</td>
<td>0.035</td>
<td>-2.726</td>
<td>0.0070</td>
</tr>
<tr>
<td>$\text{ln}(\text{TSD}_i + 1) \times \text{Disturb}$</td>
<td>0.693</td>
<td>0.331</td>
<td>2.096</td>
<td>0.0373</td>
</tr>
</tbody>
</table>

Standard Error of Estimate: 0.5919289.

**Note:** Disturb is a binary variable which takes the value of 0 for clear-cut and 1 for fire.

(Fig. 1). Despite this apparent difference in SI between disturbance types, Figs. 2 and 3 are representative of the average stand development following clear-cut and fire in the study area.

Crown closure and the onset of density-dependent mortality appeared to occur later in post-fire stands (Fig. 2), which is likely related to the convergence of relative density index trajectories between stands originating from clear-cut and fire after 38 years (Fig. 2). Clear-cut stands may have also been affected by higher tree mortality levels following the spruce budworm epidemic that occurred in the area during the 1980s (Bouchard and Pothier, 2010).

In this study, stand age was determined according to disturbance year, which can be different from the age of dominant trees that is often used in growth and yield studies when only cored trees from usual forest inventories are available. However, time since disturbance was found to improve the accuracy of growth predictions over the long term in the studied region (Garet et al., 2009). Age at breast height can overestimate time since disturbance when naturally regenerated stands contain many dominant trees that were relatively old suppressed saplings at time of cutting (Garet et al., 2012). However, if age at breast height had been used in the models, the difference between clear-cut-origin and fire-origin stands would have likely appeared to be less important during the earlier phase of stand development.

4.2. Post-disturbance stand composition and production

The observed differences in stand composition between disturbance types (Fig. 4) likely were best explained by their respective effects on advance regeneration. On the one hand, clear-cutting tended to preserve much of the advance regeneration, which is mainly composed of shade-tolerant species (Iisson and Chen, 2009; Bouchard and Pothier, 2011). In the northeastern Canadian boreal forest, these species are mainly represented by balsam fir and black spruce, with the former being proportionally more abundant in situations where the mineral soil is not exposed, as it is usually the case in mature boreal stands (Harvey and Bergeron, 1989). In general, the increased abundance of balsam fir after harvesting observed in this study is coherent with previous results from this region (Greene et al., 1999).

On the other hand, black spruce is often more abundant than balsam fir after fire as its semi-serotinous cones facilitate on-site regeneration immediately after disturbance (see review of Greene et al., 1999). In addition, the post-fire regeneration capabilities of balsam fir is constrained by distance from unburned patches containing mature seed trees (Johnson et al., 2003), and the occurrence of mast-years. Black spruce has thus remained a dominant post-fire species in the study area (Fig. 4), whereas the proportion of balsam fir becomes significant only after a period of >100 years following fire (Bouchard et al., 2008). Difference in balsam fir content between older and younger clear-cut stands (Fig. 4) may be attributed to extraction method where horse logging may allow more survival of advance regeneration than more recent mechanical forest operations.

These differences in species composition between disturbance types could partly explain the higher volume production in clear-
cut-origin stands compared with fire-origin stands (Fig. 3). Indeed, early growth responses of balsam fir after the creation of canopy openings are greater than that of spruce species, presumably because of its higher capacity to optimize and modulate growth allocation under changing light conditions (Green et al., 1999; Parent and Ruel, 2002; Messier et al., 1999; Doucet and Blais, 2000). Later during stand development, however, the greater abundance of balsam fir in clear-cut stands may have had a negative effect on volume production because of its greater vulnerability to spruce budworm-induced mortality (Pothier et al., 2012). Even if spruce budworm can also feed on black spruce foliage, it causes greater damage to balsam fir trees, mostly because early larval development of this insect is well-synchronized with balsam fir bud-break (Nealis and Régnière, 2004), and because balsam fir resistance is lower than that of spruce for an equivalent defoliation level (Erdle and MacLean, 1999). Despite its significance, the effects of the last spruce budworm outbreak on merchantable volume (Table 4) was comparatively less important than its impact on relative stand density (Table 2), likely because tree mortality that was caused by spruce budworm may have been compensated for by growth releases in the remaining living trees after the outbreak.

4.3. Implications for forest management

The results of this stand-level study imply that at the landscape level, the conversion of a natural boreal forest mosaic primarily driven by fire to a forest mosaic primarily driven by clear-cut harvesting result in a higher balsam fir content, and a lower black spruce content, which may have important consequences. First, the shift in tree dominance from black spruce to balsam fir may affect negatively some animal species that are associated with extensive black spruce stands, such as woodland caribou. Second, the higher vulnerability of balsam fir to spruce budworm could jeopardise the expected harvested wood volume in the absence of mitigation measures that would increase the proportion of black spruce (Pothier et al., 2012). Third, the wood of balsam fir has poorer mechanical properties than that of black spruce (Liu et al., 2007) and has greater susceptibility to rotting (Basham, 1991). Consequently, balsam fir has been generally considered a less desirable species by the forest products industry (Barrette et al., 2013).

Considering the preceding points, maintaining higher proportions of black spruce at both local and regional scales could contribute to sustainable management objectives in the northeastern Canadian boreal forest. At the stand level, when balsam fir dominates the advance regeneration layer, black spruce proportions could be increased by using adequate site preparation measures in post-harvest stands, thereby eliminating a substantial number of the pre-established seedlings (Pothier, 2000), followed by direct planting of spruce species. If black spruce already represents a substantial proportion of the advance regeneration, pre-commercial thinning may be used to adjust stand composition for black spruce. It would also be possible to modulate the harvest season depending on the composition of the regeneration, so that stands where the advance regeneration is dominated by balsam fir would be harvested in summer to increase soil disruption.

5. Conclusions

Clear-cutting is the most prevalent harvest treatment in the northeastern Canadian boreal forest. Our results indicate that merchantable wood output from stands of clear-cut origin would be equal to or even greater than that from fire-origin stands, at least during the initial 70 years following the disturbance. However, the composition of this volume differed markedly between the two types of disturbance. The higher proportion of balsam fir in post-cut stands not only causes the difference between natural and managed forest landscapes to increase, but also potentially reduces economic benefits by decreasing the presence of high-value black spruce stands. Replacing clear-cutting by partial logging, which may be a positive ecological alternative at the local level to preserve old-growth forest attributes (irregular vertical and horizontal structures), may not be a sound alternative to address regional-level composition issues since balsam fir also tends to dominate the regeneration of various partial-cut treatments in
the region (Cimon-Morin et al., 2010). Therefore, mitigation treatments such as scarification and/or plantation would appear to be the principal remedial measures that reduce the gap between post-clear-cut and post-fire volume composition.

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