Effects of suppression history on growth response and stem quality of extant northern hardwoods following partial harvests

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1. Introduction

The hardwood forests in northwest New Brunswick fall within the Great Lakes-Saint Lawrence forest region (Rowe, 1972). These forests are located at the northern limit of the temperate deciduous forest and possess elements of both temperate deciduous as well as boreal forests (Loo and Ives, 2003; Rowe, 1972). Although disturbances that create small gaps are characteristic of late successional forest ecosystems (Lorimer, 1977; Wein and Moore, 1977), most shade tolerant hardwood stands have undergone a combination of high-grade logging (Drinkwater, 1957; Koroleff, 1954) and large-scale clear cutting in the past (Loo and Ives, 2003). These intensive anthropogenic disturbances have reduced the quality of the residual stands (Seymour et al., 2002). Thus, partial harvesting, which emulates natural treefall by creating small gaps and reducing competition within residual stands (Harvey et al., 2002), is increasingly being practiced for sustainable management of these hardwood stands (Swift et al., 2013). Single-tree selection, group selection or single-tree with group selection are the common variants of an uneven-aged silvicultural system used in tolerant hardwood stands of eastern North America (MacLean et al., 2010).

Several studies have reported species-specific growth responses to partial harvesting (Forget et al., 2007; Fortin et al., 2008; Rose et al., 2014). Although tolerant hardwoods show positive growth response to canopy opening (Eyre and Zillgitt, 1953; Nicholson et al., 2010; Swift et al., 2012); the magnitude of tree growth response following partial harvesting varies with tree age or size (Bedard and Majcen, 2003; Jones and Thomas, 2004; Thorpe et al., 2007), intensity of cutting (Eyre and Zillgitt, 1953; Swift et al., 2012) and site productivity (Duchesne et al., 2002; Fortin et al., 2008). In addition, Jones and Thomas (2004) reported a slow but increasing growth trend of sugar maple (Acer saccharum Marsh.) for several years after gap creation. The same study also concluded that the response to gap creation varied with position of the tree in the gap and prior history of tree damage.

Sugar maple and yellow birch (Betula alleghaniensis Britton) trees often endure long periods of suppression (Canham, 1985; Erdmann, 1990). Longer suppressed trees are more prone to repeated damage by wildlife (Rea, 2011) and harvesting operations...
The size and intensity of such damage may reduce the growth potential (vigor) of trees (Duchesne et al., 2002) and stem quality (Eyre and Zillgitt, 1953; Ostrofsky, 1988). The degree of growth decline may vary with tree size and species because a tree's ability to cope with these damages varies with species and tree characteristics (Shigo, 1984).

Although several studies have assessed the diameter growth response of sugar maple and yellow birch in other jurisdictions (Bedard and Majcen, 2003; Fortin et al., 2008; Jones and Thomas, 2004; Kiernan et al., 2009; Nicholson et al., 2010), few have been done in New Brunswick (Swift et al., 2012) and none have considered the influence of suppression history on tree growth response to partial harvest. However, in a recent study, Gauthier et al. (2015) presumed that suppression history may influence the growth potential of northern hardwood tree species. In this context, this study aims to explore the effects of suppression history on (1) the probability of a tree being damaged and (2) growth response of trees after partial harvesting. We hypothesize that trees that have experienced a longer period of suppression are more likely to be damaged as they would be more susceptible to several biotic and abiotic injury events in their suppression phase. As a consequence, we further expect that growth response of trees to partial harvest would be negatively influenced by their suppression history due to loss of vigor. The results of this study would allow ecologists and forest managers to predict basal area growth of different sized sugar maple and yellow birch trees in second growth tolerant hardwood stands subjected to different types and levels of partial harvesting in the past. Additionally, understanding the effects of suppression history on tree growth, as well as stem damage at a specific site, would enhance better silvicultural decision-making and forest-level planning (Schmidt et al., 2006).

2. Methodology

2.1. Study site

The study was conducted in the northern hardwood forests of the Great Lakes-Saint Lawrence forest region in northwest New Brunswick (Fig. 1) on sites that had previously received some degree of partial cutting. A total of 44 different stands located northeast of Edmundston, New Brunswick were selected. The stands were located within a longitudinal range between 67°11.6°W and 68°31.7°W, and a latitudinal range between 47°28.14°N and 47°42.25°N. The average altitude, slope, and depth to the water table of the research sites were 356 m (range: 245–520 m), 13% (range: 0–45%), and 22.6 cm (range: 0–250 cm), respectively (Murphy et al., 2009, 2007). Different types and intensities of partial harvest were carried out in the study sites between 1974 and 2007. Individual tree or group selection and small patch cutting were the treatment types. The resultant stands had post cut tree basal area ranging from 5 to 40 m²/ha at the time of harvest (Table 1).

2.2. Sampling design and data collection

Three clusters of stands (Fig. 1) were identified in the Central Uplands Eco-region of New Brunswick (Zelazny et al., 2003). Stands were selected on the basis of stand types, time since treatment, and treatment type in order to have a large variety of stand combinations in a relatively small geographic area. A variable radius plot (metric BAF 3 m²/ha angle gauge) was the basic sampling unit. Sampling points were distributed across different residual stand basal areas. The number of sampling units in each stand varied based on the size of the stand the variation in openings created by harvesting (see Kershaw et al., 2012).

All live trees ≥ 10.0 cm diameter at breast height (DBH) that were larger than the projected angle were considered as “selected” by the angle gauge. Selected trees were tallied by species and DBH was measured to the nearest 0.1 cm. Trees near the borderline of inclusion were checked using tree diameter and horizontal limiting distance. Live tree basal area in 2012, net basal area growth rate per year for a stand of given residual basal area, and years since harvest were used to estimate residual stand basal area at the time of harvest. Net basal area growth rate per ha per year for a stand of given residual basal area (m²/ha) for northern tolerant hardwoods, was obtained from Forget et al. (2007) and used for estimating stand basal area at the time of harvest (detailed in Appendix A).

Four DBH classes were used for sample tree selection: (1) 10.0–15.9 cm; (2) 16.0–21.9 cm; (3) 22.0–27.9 cm; and (4) 28.0 cm and above. Two trees for each species and DBH class combination were sampled provided that the possible combination was available in the sample plot. Trees were randomly selected in cases where there were more than two trees for a species and DBH class combination. Presence or absence of damage on the tree stem was assessed using the Northern Hardwood Research Institute’s (NHRI) tree classification system (Pelletier et al., 2014). Using this tree classification guide, survey crews assessed the presence of fruited bodies, holes, splits and/or mechanical damage on the main stem. All sample trees were cored at breast height for age and growth response determination in 2012. Cores were extracted from the side of the tree facing the plot center, placed in straws, labeled and stored in ice. In the laboratory, cores were dried, mounted on grooved wooden blocks and sanded. Then, rings were dated gradually from the outermost ring (starting from 2012) toward the pith. Ring widths were measured with a VelMex Unislide (Velmax Computer Systems, UK). Crossdating was done to validate tree ring-dates matching ring width patterns between samples coming from the same site using the dplR package in R (Bunn, 2010) and corrected for missing and false rings. Quality of ring dating was also assessed statistically (checking between ring correlation and expressed population signal).

Cross-dated individual tree ring series were used for (1) reconstructing tree DBH at the time of harvest, (2) counting years of suppression period (detailed in Fig. 2) defined as intervals in which there were 4 or more years of radial growth below 0.5 mm/year, during which there were no periods of 3 or more years of consecutive growth greater than 0.5 mm/year (Canham, 1985), and (3) computing tree basal area growth after the last harvest. Tree diameter (inside bark) at the time of harvest was computed by summing up the width of annual rings from pith to the year of harvest and multiplied by 2. Tree diameter (over bark) at the time of harvest was estimated from inside bark diameter using the relationship developed by Weiskittel and Li (2012). Individual tree basal area increment for each year after partial harvesting was calculated from the tree ring series using Eq. (1).

\[
BAI = \frac{\pi}{4} \cdot \left(\frac{[DI_{t0} + DI]^2 - DI_{t0}^2}{2 \times \pi \times \text{ring width}}\right)
\]

where

- \( BAI \) = annual increment of individual tree basal area in \( \text{cm}^2/\text{year} \)
- \( DI_{t0} \) = inside bark diameter of the tree (at 1.3 m) at time \( t_0 \) in cm
- \( DI \) = annual increment of tree diameter (2 × ring width) in cm

2.3. Data analysis

2.3.1. Assessing tree stem quality

As tree vigor and stem quality are related to stem damage (Boulet, 2007; Duchesne et al., 2002; Monger, 1991), the probability of a tree being damaged was examined for sugar maple and yellow birch trees. Since occurrence of damage on a tree stem is
a discrete event, a dummy variable with 0 (no damage) or 1 (damage) was created. A generalized linear model with a binomial distribution was calibrated separately for sugar maple and yellow birch to predict the occurrence of stem damage, because the probability of a tree being damaged (dependent variable) is designed as a binary response. This study examined the effects of tree diameter, age, period of suppression, number of harvest entries, stand basal area, slope of the land, altitude, and site quality on stem damage of trees. The site quality index used here, biomass survivor growth index (BSGI), was developed by Hennigar et al. (2015). It uses climate, soil, drainage and topographic information along with stand information to predict biomass survivor growth (ton/ha/year) for the Acadian forest region. The list of predictor variables used in modeling and their description are presented in Table 2. Akaike Information Criterion (AIC) scores for the possible candidate models were compared (Table 3) using the MuMin (Multi-Model Inference) package (Barton, 2014) in R (R Development Core Team, 2011) to choose predictor explanatory variables. A model with the lowest value of AIC for each species (sugar maple: Table 3, model 2 and yellow birch: Table 3, model 3) was chosen as the best model. The parameter estimates and fit statistics of the final model (Eq. (2) for yellow birch and SBA2012 was dropped from (2) for sugar maple) are presented in Table 4.

\[ D_p = \frac{1}{1 + e^{-\left(a_0 + a_1/TSP + a_2/SQI + a_3/SBA2012\right)}} \]  

where

- \( D_p \) = probability of a tree being damaged
- \( TSP \) = total length of suppression period (years)
- \( SBA_{2012} \) = plot level basal area measured in 2012 (m²/ha)
- \( SQI \) = site quality index (ton/ha/year)
- \( a_i \) = the parameters to be estimated.

Probability of a tree being damaged ranges between 0 and 1.

2.3.2. Modeling basal area growth

In general, individual tree diameter or basal area growth is found to be related to tree size, competition and site quality (Wykoff, 1990). We chose to model basal area growth rather than diameter growth because basal area growth is more linearly related to tree volume growth (Hokka and Groot, 1999). Hence, an individual tree basal area growth model was calibrated using tree diameter, suppression history, residual stand characteristics and site quality information. As model fitting using a potential times modifier approach uses multiple steps, we adopted the approach suggested by Pokharel and Dech (2012), which is structured in Eq. (3).
Sample tree and stand characteristics.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Sugar maple</th>
<th>Yellow birch</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>DBH&lt;sub&gt;2012&lt;/sub&gt; (cm)</td>
<td>29.9</td>
<td>8.9</td>
</tr>
<tr>
<td>DBH&lt;sub&gt;0&lt;/sub&gt; (cm)</td>
<td>18.2</td>
<td>6.3</td>
</tr>
<tr>
<td>SBA&lt;sub&gt;2012&lt;/sub&gt; (m&lt;sup&gt;2&lt;/sup&gt;/ha)</td>
<td>24.3</td>
<td>7.8</td>
</tr>
<tr>
<td>SBA&lt;sub&gt;0&lt;/sub&gt; (m&lt;sup&gt;2&lt;/sup&gt;/ha)</td>
<td>15.6</td>
<td>6.0</td>
</tr>
<tr>
<td>QMD&lt;sub&gt;2012&lt;/sub&gt; (cm)</td>
<td>34.3</td>
<td>7.3</td>
</tr>
<tr>
<td>Tree age&lt;sub&gt;2012&lt;/sub&gt; (years)</td>
<td>81.7</td>
<td>35.9</td>
</tr>
<tr>
<td>Tree age&lt;sub&gt;0&lt;/sub&gt; (years)</td>
<td>61.5</td>
<td>33 19.0</td>
</tr>
<tr>
<td>Trees with periods of suppression (%)</td>
<td>38.3</td>
<td></td>
</tr>
<tr>
<td>TSP&lt;sup&gt;a&lt;/sup&gt; (years)</td>
<td>18.5</td>
<td>4.0</td>
</tr>
<tr>
<td>SQI (ton/ha/year)</td>
<td>1.9</td>
<td>0.2</td>
</tr>
<tr>
<td>Number of sample trees&lt;sup&gt;b&lt;/sup&gt;</td>
<td>170.0</td>
<td></td>
</tr>
<tr>
<td>Number of plots</td>
<td>112.0</td>
<td></td>
</tr>
<tr>
<td>Number of stands</td>
<td>40.0</td>
<td></td>
</tr>
</tbody>
</table>

Table 1

See Table 2 for the explanation of the variables.

<sup>a</sup> Calculated only for the trees that have gone through at least one period of suppression.

<sup>b</sup> Indicates number of trees used for growth modeling.

Annual basal area increment (BAI, cm<sup>2</sup>/year) was regressed to available tree, stand and site characteristics. The list of predictor variables includes time since harvest (years), DBH at the time of harvest (cm), residual stand basal area at the time of harvest (m<sup>2</sup>/ha), residual stand basal area in trees with DBH's larger than the subject tree's DBH at the time of harvest (m<sup>2</sup>/ha), type of partial harvest, harvest intensity, previous disturbance, competitive position of the tree (ratio of tree DBH to quadratic mean diameter of the stand), total suppression period, proportion of softwood and hardwood, and site quality index (ton/ha/year) quantified as biomass survivor growth index. As tolerant hardwoods trees in uneven-aged stands often remain suppressed for a few decades to more than a century (Canham, 1990, 1985), tree vigor might be diminished by such long periods of suppression. Thus, period of suppression was used as an explanatory variable in the model. A limitation of the model was that it lacked tree vigor attributes (e.g., crown ratio or visually assessed vigor class) at time of harvest as it is difficult to backcast this parameter to the time of harvest from the observation made in 2012.

A multiple linear regression model was developed using these predictor variables, along with their various transformations and interactions as suggested in the literature (Hann and Larsen, 1991; Pokharel and Dech, 2012; Zhang et al., 2004). Non-significant variables at the 95% confidence level were dropped during the modeling process. The resultant model is presented in Eq. (4).

\[
\ln(BAI)_{ijk} = (\beta_0 + b_i + b_j) + \beta_1 \cdot (TSH) + \beta_2 \cdot (TSH)^2 + \beta_3 \cdot (DBH_{0}) + \beta_4 \cdot (DBH_{0})^2 + \beta_5 \cdot (\ln(BAI_{0}) + 1)^2 / DBH_{0} + \beta_6 \cdot (TSP) + \beta_7 \cdot (SQI_i) + \epsilon_{ijk}
\]

where

- \( BAI_{ijk} \) = basal area increment of tree \( j \) in stand \( i \) in year \( k \) (cm<sup>2</sup>/year)
- \( TSH_i \) = time since harvest for stand \( i \) (years)
- \( DBH_{0} \) = diameter at breast height of tree \( j \) in stand \( i \) at the time of harvest (cm)
- \( BAI_{0} \) = residual stand basal area of the trees larger than the subject tree at the time of harvest (m<sup>2</sup>/ha)
- \( SQI_i \) = site quality index (ton/ha/year) for stand \( i \)
- \( TSP_i \) = suppression period (years) of tree \( j \) in stand \( i \)
- \( b_i \) = stand level random effects, where; \( b_i \sim N(0, \sigma_i^2) \)
- \( \beta \) = regression parameters to be estimated
- \( \epsilon_{ijk} \) is the residual error of tree \( i \) in year \( j \), \( \epsilon_{ijk} \sim N(0, \epsilon) \)
- \( R_\sigma^2 = \sigma_{\text{residuals}}^2 \times \left[ \begin{array}{cccc} 1 & \gamma & \gamma \delta & \gamma \delta^2 & \ldots \\ \gamma & 1 & \gamma & \gamma \delta & \ldots \\ \gamma \delta & \gamma & 1 & \gamma & \ldots \\ \gamma \delta^2 & \gamma \delta & \gamma & 1 & \ldots \\ \ldots & \ldots & \ldots & \ldots & \ldots \end{array} \right] \) (5)

\( \sigma_{\text{residuals}}^2 \) = within tree variance of residuals
- \( \gamma \) = moving average parameter
- \( \delta \) = autoregressive parameter

Heteroscedasticity was modeled using a power variance function (Eq. (6)) described by Pinheiro and Bates (2000).

\[
\Var(\epsilon_{ijk}) = \sigma_{\text{residuals}}^2 \cdot |DBH_{ij}|^{2p}
\]

Eq. (4) was fitted for sugar maple and yellow birch trees separately. A mixed modeling technique was used to estimate regression parameters of Eq. (4) using the nlme package (Pinheiro and Bates, 2000) in R (R Development Core Team, 2011) because of its effectiveness for fitting longitudinal data arising from repeated measurements (Gregoire et al., 1995). As temporal and/or spatial autocorrelation may violate the assumptions of independence and homogeneity in growth models (Fox et al., 2001), different error covariance structures were used to fit the desired model. The model fit was evaluated based on AIC, Bayesian Criterion (BIC), and Likelihood Ratio Test (LRT) (Gregoire et al., 1995). Since appropriate specification of the error covariance structure is an important part of the model identification process (Gregoire et al., 1995), five models with different covariance structures were evaluated: (1) an ordinary least squares (OLS) model, (2) a mixed-effects model, (3) a mixed-effects model with first-order autoregressive (AR(1)), (4) a mixed-effects model with first-order autoregressive moving average (ARMA(1,1)) and (5) a mixed-effects model with second-order autoregressive moving average (ARMA(2,0)). They were used to determine whether both repeated
and random effects improved model performance for the given data. The one associated with the smallest values of AIC and BIC was selected as the final model.

The mixed effect model with first-order autoregressive moving average (model 4, ARMA(1,1)) was found to be the most suitable as it produced the smallest AIC and BIC for both sugar maple and yellow birch (Table 5). Therefore, the first-order autoregressive moving average (ARMA(1,1)) error covariance structure was used to fit Eq. (4) for both species. The logarithmic transformation of BAI in Eq. (4) provided good fit by linearizing the relationship between the response variable and predictor variables. The residual plots (Fig. 3) as well as other diagnostic plots (figure not shown) revealed no violations of model assumptions for both sugar maple and yellow birch. The residuals (in logarithmic scales) were plotted against tree diameter class (Fig. 4) and other predictor variables (figure not shown) to check any trends in residuals.

As Eq. (4) predicts BAI on a natural logarithmic scale, it was necessary to back transform the predicted values to the original scale when making predictions. This back transformation of predicted values from a log-transformed model produces an associated log-transformation bias (Baskerville, 1972; Sprugel, 1983). Therefore, a correction factor was used to transform the model predictions back to the original units (Eq. (7)). An empirical ratio estimator (Eq. (8)) was computed to use as a correction factor for log transformation bias as suggested by Snowdon (1991).

\[
\text{BAI}' = \text{BAI} \times CF
\]  

where

\[
\begin{align*}
\text{BAI}' & = \text{predicted back transformed value of BAI after correcting log transformation bias} \\
\text{BAI} & = \text{predicted natural logarithmic value of BAI from Eq. (4)} \\
\text{CF} & = \frac{\text{BAI}}{e^{\text{log}_{e}\text{BAI}}}
\end{align*}
\] (8)

Fig. 2. Measurement of suppression history. Suppression period was defined as the intervals of 4 or more years below horizontal dashed line (0.5 mm), during which there were no periods of 3 or more years of consecutive growth above the horizontal dashed line (Canham, 1985). The vertical dashed lines indicate the beginning of the canopy recruitment.
Table 2
Description of predictor variables used to develop models.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAI</td>
<td>Basal area increment of a tree at breast height (cm²/year)</td>
</tr>
<tr>
<td>TST</td>
<td>Time since treatment (years)</td>
</tr>
<tr>
<td>DBH₀₂₀₁₂</td>
<td>Tree diameter at breast height measured in 2012 (cm)</td>
</tr>
<tr>
<td>DBH₂₀₁₂</td>
<td>Tree diameter at breast height at the time of harvest (cm)</td>
</tr>
<tr>
<td>Age₀₂₀₁₂</td>
<td>Total number of annual rings at breast height in 2012</td>
</tr>
<tr>
<td>Age₀₂₀₁₂</td>
<td>Number of annual rings counted from pith to the year of harvest</td>
</tr>
<tr>
<td>SBA₀₂₀₁₂</td>
<td>Plot level basal area measured in 2012 (m²/ha)</td>
</tr>
<tr>
<td>SBA₀</td>
<td>Estimated plot residual basal area at the time of harvest</td>
</tr>
<tr>
<td>QMD₂₀₁₂</td>
<td>Quadratic mean diameter of the plot in 2012 (cm)</td>
</tr>
<tr>
<td>BAL₂₀₁₂</td>
<td>Plot level basal area of trees with DBH (DBH₀₂₀₁₂) larger than the subject tree's DBH in 2012 (m²/ha)</td>
</tr>
<tr>
<td>BAL₀</td>
<td>Estimated basal area in trees larger than the subject tree at the time of harvest (m²/ha) at the plot level</td>
</tr>
<tr>
<td>SQI</td>
<td>Plot site quality index defined as biomass survivor growth (ton/ha/year)</td>
</tr>
<tr>
<td>TSP</td>
<td>Total length of suppression period (years)</td>
</tr>
<tr>
<td>NHE</td>
<td>Number of previous harvest entries</td>
</tr>
<tr>
<td>Slope</td>
<td>Average slope of the plot (%)</td>
</tr>
<tr>
<td>Altitude</td>
<td>Altitude of the plot (m)</td>
</tr>
<tr>
<td>Trt_type</td>
<td>Treatment type</td>
</tr>
</tbody>
</table>

DBH₀ was reconstructed using tree ring chronology. SBA₀ and BAL₀ were estimated by discounting the mean annual basal area net growth rate given by Forger et al. (2007) for tolerant hardwoods in northern North America for the time interval between 2012 and the year of harvest from SBA₀₂₀₁₂ and BAL₀₂₀₁₂, respectively. TSP (suppression period); see Fig. 2 for detailed explanation. Treatment types include: (1) selection cutting (single tree selection or group tree selection) in which size of suppression period: see Fig. 2 for detailed explanation. Treatment types include: (1) selection cutting (single tree selection or group tree selection) in which size of the canopy opening ranges between 0.05 ha and 0.14 ha; and (2) small patch cutting in which size of the canopy opening ranges between 0.04 ha and 0.25 ha.

Table 3
Model selection for predicting probability of tree damage.

<table>
<thead>
<tr>
<th>Model</th>
<th>Predictor variables</th>
<th>AIC (SM)</th>
<th>AIC (YB)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>TSP</td>
<td>221.7</td>
<td>226.7</td>
</tr>
<tr>
<td>2</td>
<td>TSP + SQI</td>
<td>212.0</td>
<td>219.2</td>
</tr>
<tr>
<td>3</td>
<td>TSP + SQI + SBA₀₂₀₁₂</td>
<td>213.7</td>
<td>214.8</td>
</tr>
<tr>
<td>4</td>
<td>TSP + SQI + SBA₀₂₀₁₂+ DBH₂₀₁₂</td>
<td>213.4</td>
<td>216.6</td>
</tr>
<tr>
<td>5</td>
<td>TSP + SQI + SBA₀₂₀₁₂+ DBH₂₀₁₂+ Age₀₂₀₁₂</td>
<td>215.5</td>
<td>218.7</td>
</tr>
<tr>
<td>6</td>
<td>TSP + SQI + SBA₀₂₀₁₂+ DBH₂₀₁₂+ Age₀₂₀₁₂+ NHE</td>
<td>217.2</td>
<td>220.6</td>
</tr>
<tr>
<td>7</td>
<td>TSP + SQI + SBA₀₂₀₁₂+ DBH₂₀₁₂+ Age₀₂₀₁₂+ NHE + Slope</td>
<td>215.7</td>
<td>227.1</td>
</tr>
<tr>
<td>8</td>
<td>TSP + SQI + SBA₀₂₀₁₂+ DBH₂₀₁₂+ Age₀₂₀₁₂+ NHE + Slope + Altitude</td>
<td>216.5</td>
<td>230.0</td>
</tr>
<tr>
<td>9</td>
<td>TSP + SQI + SBA₀₂₀₁₂+ DBH₂₀₁₂+ Age₀₂₀₁₂+ NHE + Slope + Altitude + Trt_type</td>
<td>224.9</td>
<td>236.4</td>
</tr>
</tbody>
</table>

Note: AIC = Akaike Information Criterion, SM = sugar maple, YB = yellow birch. See Table 2 for the description of the variables. Bold values indicate final model AIC.

where BAI is the mean measured basal area increment (cm²/year) and \( e^{\text{BAI}} \) is the mean estimated basal area increment (cm²/year). Snowdon (1991) confirmed that this method gives more reliable results than Finney’s approximation (Finney, 1941) or Baskerville’s method (Baskerville, 1972).

Table 4
Parameter estimates for model 2.

<table>
<thead>
<tr>
<th>Sugar maple</th>
<th>Yellow birch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameters</td>
<td>Estimates SE</td>
</tr>
<tr>
<td>( x₀ )</td>
<td>Intercept</td>
</tr>
<tr>
<td>( x₁ )</td>
<td>TSP</td>
</tr>
<tr>
<td>( x₂ )</td>
<td>SBA₀₂₀₁₂</td>
</tr>
<tr>
<td>( x₃ )</td>
<td>SQI</td>
</tr>
<tr>
<td>AIC</td>
<td>214</td>
</tr>
<tr>
<td>Residual deviance</td>
<td>206</td>
</tr>
<tr>
<td>n</td>
<td>211</td>
</tr>
</tbody>
</table>

\( ^4 \) Estimated using D-squared function of modEvA package in R (Márcia Barbosa et al., 2013).

3. Results

3.1. Stem quality development

The probability of a tree being damaged increased with increasing suppression period and decreased with site quality for both sugar maple and yellow birch. The probability also decreased with increasing stand basal area for yellow birch but not for sugar maple (Fig. 5). The probability of a tree being damaged was found to be independent of number of harvest entries, slope of the land, and size and age of the tree as these variables were found to be statistically insignificant in the model (2).

3.2. Basal area increment

The different statistics associated with the parameter estimates indicated that the coefficients for the final model for sugar maple and yellow birch were highly significant, except the \( β₀ \) for sugar maple and the \( β₁ \) for yellow birch (Table 6). Both sugar maple and yellow birch responded positively to partial harvesting by increasing individual tree basal area in a higher rate with time since harvest (Fig. 6a). However, the rate of increase was higher for yellow birch than sugar maple. The \( β₁ \) and \( β₂ \) coefficients indicated that the increasing rate of basal area increment was found to be maintained up to 18–25 years after partial harvesting for yellow birch and sugar maple respectively (Table 6, Fig. 6a). Tree size at the time of harvest (diameter at breast height) was found to have a significant effect on basal area increment for both species (Table 6). Basal area increment increased for trees smaller than 35 cm DBH, reached a plateau around 35 cm DBH, and then declined for larger trees (Fig. 6b). For both species, basal area increment was found to be higher for the trees that were growing in lower levels of competition defined here as stand basal area of trees with DBH’s larger than the subject tree’s DBH (Fig. 6a and b). Suppression history significantly influenced growth response of both sugar maple and yellow birch trees. However, the effect of suppression period on the growth response of yellow birch was more pronounced than for sugar maple. Sugar maple grew better than yellow birch when BAI was compared between trees suppressed for 50 years (Fig. 6c). The non-significant \( β₂ \) indicated that site quality defined as biomass survivor growth index (ton/ha/year) had no effect on basal area increment of yellow birch trees (Fig. 6d). Although type of partial harvest, number of previous treatments and softwood hardwood proportion were expected to influence basal area increment, these variables were not found to be statistically significant at a 95% level of significance.

4. Discussion

As suggested in our first hypothesis, trees that experienced longer periods of suppression were more likely to possess stem
damage. Similarly, supporting our second hypothesis, the longer suppressed trees’ growth response (BAI) to partial harvest was found to be significantly reduced. In addition, sugar maple and yellow birch growth response to partial harvesting was related to time since harvest, tree size, competition and site. Effects of these predictor variables on growth response and their silvicultural implications are discussed separately in the subsequent sections.

4.1. Suppression history and stem quality development

The probability of a tree being damaged increases with increased length of suppression period because of harvest- and wildlife-related damages to advanced regeneration (Lamson et al., 1985; Jacobs, 1974; Rea, 2011; Kittredge et al., 1995). The low probability of a tree being damaged on the better quality sites in this study might be due to a shorter time exposure to damaging agents (natural as well as anthropogenic) as trees achieve a given tree size in a relatively shorter time period than on poor quality sites. Although the likelihood of a tree being damaged decreases with increasing distance between residual trees (Tatsumi et al., 2014), our findings indicated a higher probability of a tree being damaged in lower residual basal area stands. This disparity in our findings might be due to two different reasons. Firstly, the effect of previous harvesting in which most of the quality trees were harvested (Seymour et al., 2002), and only low vigor trees were left as residual trees in the lower basal area stands. Secondly, Belanger et al. (1996) have shown that trees are more likely to be affected by wind and snow storm damages in thinner stand. The damaged trees are susceptible to be attacked by different fungus (e.g., Nectria). Hence, similar to our findings, Ward et al. (2010) suggested to keep mature trees as buffer to minimize the proportion of damaged stems.

4.2. Growth response to partial harvesting

Not surprisingly, both sugar maple and yellow birch trees growing at the northern limit of tolerant hardwoods showed a positive growth response to partial harvesting occurring 5–35 years before the sampling date. Most importantly, both species showed a persistent increase in basal area growth (BAI) for about 20 years after harvest. As has been found elsewhere (Eyre and Zillgitt, 1953; Fortin et al., 2008), trees of DBH between 30 and 40 cm had a greater growth response than smaller or larger trees. Although yellow birch responded better than sugar maple in the short term, sugar maple showed a small but continuous growth response for a longer period of time.

Sugar maple and yellow birch growth responses were quite similar to those of previous studies. Our study showed an average annual basal area increment for a 30 cm DBH tree of 14 cm²/year.

### Table 5

Model fitting statistics of the different error covariance structures for equations (Eq. (4), sugar maple) and (Eq. (4), yellow birch).

<table>
<thead>
<tr>
<th>Criterion</th>
<th>Sugar maple (Eq. (4))</th>
<th>Yellow birch (Eq. (4))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OLS</td>
<td>LME</td>
</tr>
<tr>
<td>AIC</td>
<td>5747</td>
<td>4002</td>
</tr>
<tr>
<td>BIC</td>
<td>5806</td>
<td>4072</td>
</tr>
<tr>
<td>LR</td>
<td>–</td>
<td>1749</td>
</tr>
<tr>
<td>P-value</td>
<td>–</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

AIC = Akaike Information Criterion, BIC = Bayesian Information criterion, LR = likelihood ratio.

### Fig. 3

Standardized residuals (on transformed scale) against predicted basal area increment (cm²/year on transformed scale). (a) SM = sugar maple and (b) YB = yellow birch.

### Fig. 4

Standardized residuals on transformed scale against tree diameter at breast height. (a) SM = sugar maple and (b) YB = yellow birch.
Partial harvesting generally promotes tree growth for trees between 20 and 30 cm DBH (Bedard and Majcen, 2003; Kiernan et al., 2009). The results of this study revealed the same trend. It might be due to the relative capacity of sub-canopy (co-dominant) trees to respond to increased availability of above and below ground resources in post harvesting condition. When a canopy gap is created, suppressed trees recruit themselves to intermediate canopy, but sub-canopy (co-dominant) trees close the gap by expanding their crown laterally (Fahey, 2013).

In uneven-aged stand conditions, some trees remain suppressed for a long period of time (Canham, 1990, 1985). We observed that longer periods of suppression reduced growth response to partial harvesting of such trees. This can be explained by three factors: (1) age-related tree vigor decline (Ryan et al., 1997) because longer suppressed trees are generally older for a given diameter, (2) tree health decrease (Duchesne et al., 2002) since suppressed trees are more likely to be associated with stem damages, and (3) social position of the tree, as longer suppressed trees are likely to be intermediate or sub-canopy trees (Canham, 1990, 1985). It is also explained by our result that showed the better growth performance of sugar maple trees (a shade tolerant species) that were suppressed for 50 years than the yellow birch trees (an intermediate shade tolerant species) that were suppressed for 50 years.

Increased basal area growth of sugar maple with increasing site quality index observed in this study inferred that sugar maple growth might have been limited by soil nutrients. It has been reported that sugar maple growth in the northeastern U.S. has

(diameter increment (DI) ≈ 0.28 cm/year) and 16 cm²/year (DI ≈ 0.36 cm/year) for sugar maple and yellow birch respectively, 15 years after partial harvesting at 10 m²/ha residual stand basal area. Although this is smaller than Kiernan et al. (2009) who observed a DI of 0.42 cm/year for a similar sized sugar maple, our observation is similar to Fortin et al. (2008) who observed a DI of 0.32–0.38 cm/year for yellow birch and 0.28–0.36 cm/year for sugar maple at 20 m²/ha residual stand basal area. Ondro and Love (1979) also found a similar growth rate (DI = 0.23–0.33 cm/year) for sugar maple as a response to partial cutting. However, their observation for yellow birch growth (DI = 0.18–0.23 cm/year) was smaller than the findings of this study.

Table 6
Fixed parameters and their corresponding standard errors estimated based on REML method with intercept $\beta_0$ modeled as a tree level mixed effect parameter.

<table>
<thead>
<tr>
<th>Co-efficient</th>
<th>Estimate</th>
<th>Standard error</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta_0$</td>
<td>-0.1265</td>
<td>0.4909</td>
<td>0.80</td>
</tr>
<tr>
<td>$\beta_1$</td>
<td>0.0356</td>
<td>0.0052</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>$\beta_2$</td>
<td>-0.0007</td>
<td>0.0002</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>$\beta_3$</td>
<td>0.0609</td>
<td>0.0296</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>$\beta_4$</td>
<td>-0.0010</td>
<td>0.0005</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>$\beta_5$</td>
<td>-0.0807</td>
<td>0.0235</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>$\beta_6$</td>
<td>-0.01173</td>
<td>0.0032</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>$\beta_7$</td>
<td>0.7359</td>
<td>0.2021</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

| Variance component | $\sigma^2_{\text{stand}}$ | 0.0220 |
|                    | $\sigma^2_{\text{stand/tree}}$ | 0.2757 |
|                    | $\sigma^2_{\text{residuals}}$ | 0.2060 |
|                    | $\gamma$ | -0.2360          |
|                    | $\delta$ | 0.7206           |
|                    | $\rho$    | 0.0551           |
|                    | CF        | 1.1333           |

| Mean bias$^a$ (cm²/year) | 1.0507 |
| Bias (%)$^a$ | 9.79 |

Mean bias = \(\sum(Y_i - \bar{Y}_i)/n\)

Bias % = \( \left( \frac{\sum(Y_i - \bar{Y}_i)/n}{\sum\bar{Y}_i/n} \right) \times 100.\)

$^a$ Prediction was made using fixed effects parameters only.

(continued)
declined in the last century due to decreased soil base cations such as calcium and magnesium (Bailey et al., 2004; Horsley et al., 2002; Juice et al., 2006; Long et al., 2009, 1997). In addition, as sugar maple is less tolerant to drought (Niinemets and Valladares, 2006) than yellow birch, sugar maple growth might have been limited by soil moisture as well in poor quality sites.

5. Conclusions

Longer suppression is likely to negatively affect future stem quality of sugar maple and yellow birch. Growth response to partial harvesting was also influenced negatively by longer suppression periods. Therefore, less suppressed trees need to be released through partial harvesting as suppression history not only affects tree growth but also affects stem quality.

Sugar maple and yellow birch trees showed positive growth response to partial harvesting. As trees smaller than 35 cm DBH responded more vigorously, partial harvesting should focus on creating growing space for less suppressed healthy sub-canopy trees. In addition, diameter or basal area growth models need to consider tree suppression history, otherwise such models may overestimate growth response to partial harvesting. Since yellow birch growth response was found to be insensitive to site quality index, this species should be favored over sugar maple on poor quality sites as the future crop species in the residual stands.

Acknowledgements

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Appendix A. Stand basal area estimation

Stand basal area in 2012 (m²/ha) is a function of post-cut basal area (m²/ha), time since harvest (years) and net basal area growth rate (m²/ha/year), where net basal area growth rate is a function of residual tree growth rate (m²/ha/year), ingrowth rate (m²/ha/year) and mortality rate (m²/ha/year). Our retrospective database consists of information on stand basal area in 2012 and year of partial harvest. Forget et al. (2007) showed that net stand basal area growth rate is a function of post-cut basal area, and that stand basal area growth rate declines with increasing post-cut stand basal area due to higher levels of competition for space and resources in higher basal area stands (Fig. A1.1).

A discounting formula was used to estimate stand basal area at the time of harvest (Eq. (A1.1)).

\[
SBA_{Y0} = SBA_{Y1} \left(1 + \frac{BAGR(\%)}{100}\right)^{-T}
\]  
(A1.1)

where

- \( SBA_{Y0} \) = stand basal area at the time of harvest (m²/ha)
- \( SBA_{Y1} \) = stand basal area observed in 2012 (m²/ha)
$Y = \frac{-1.6099 \ln(x) + 0.8453}{r^2 = 0.1865}$

$T = \text{time since harvest in [years]}

\text{BAGR} = \text{mean annual basal area growth rate (m}^2/\text{ha/year)}

\text{for the given post cut SBM stand which is obtained from the equation given by Forget et al. (2007)}

\text{BAGR} = -0.1909 - \text{LNSBA}_0 + 0.8453

Eventually, the extended form of Eq. (A1.1) becomes:

\text{SBA}_{V0} = \frac{\text{SBA}_1}{(1 + ((-0.1909 - \text{LN}(\text{SBA}_0) + 0.8453)/\text{SBA}_0))^{(T)}}

In Eq. (A1.4), \text{SBA}_1 and \text{T} are known and \text{SBG}_0 was estimated using the known values of \text{SBA}_1 and \text{T}.

**References**


