An examination of the relationship between stand history and composition, and American beech (*Fagus grandifolia*) regeneration in tolerant hardwood forests in Ontario, Canada

by

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Abstract

Within beech bark disease (BBD)-impacted stands in North America, BBD-mediated crown decline favours abundant American beech (*Fagus grandifolia* Ehrh.) root suckering, which can inhibit regeneration of desirable species such as sugar maple (*Acer saccharum* Marsh). Methods for treating beech regeneration are effective, but monetary and effort costs limit the ability to apply such treatments, resulting in the need to be able to predict beech thicket occurrence across the managed landscape. A retrospective analysis was conducted using a multivariate regression approach to identify key relationships between beech understory densities and: (1) Past management; and (2) Stand composition, in study plots (n = 1,334) within tolerant hardwood stands in the Great Lakes – St. Lawrence Forest region of Ontario, Canada. Beech sapling (p < 0.0001) and regeneration (p < 0.0001) densities were significantly higher in plots where recent logging had occurred, with the highest densities within 1-10 years following harvest. For saplings, density was also high 21-30 years post-harvest. Beech regeneration density was significantly higher among mixed composition plots where sugar maple was not the dominant canopy species (p < 0.0001). Beech sapling density, however, was higher among mixed composition plots compared to monospecific plots of sugar maple (p < 0.0001), and was not affected by sugar maple canopy dominance among mixed stands. Both sapling (r_s = 0.449, p < 0.0001) and regeneration (r_s = 0.600, p < 0.0001) densities were strongly correlated with beech basal area. Managers may expect to encounter abundant beech regeneration in recently disturbed, non-sugar maple-dominated stands with mixed overstory composition, while abundant beech saplings may be found in recently harvested stands with a mixed overstory composition. To limit propagation of beech in the understory, it is recommended that harvesting occur in stands where sugar maple is the leading overstory species, and beech basal area is low. Though results suggest logging disturbance increases the abundance of beech saplings and regeneration, past research has indicated that pre-logging stand composition also contributes to beech regeneration dominance post-harvest. Due to the strong monotonic relationship between beech sapling and regeneration densities and beech basal area, avoidance of harvest in stands with high beech basal area in the overstory may therefore limit beech proliferation in the understory.
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Introduction

American beech (*Fagus grandifolia* Ehrh.) is common within the hardwood forests of eastern Canada and the United States, and a dominant canopy species in late-successional communities (Eyre, 1980; Cale, et al., 2013). In Ontario, Canada, roughly 600,000 hectares of tolerant hardwood forest in the area of undertaking are comprised by 10% or more American beech (Trevor Jones, unpublished data). However, within the last 20 years, beech scale insect (*Cryptococcus fagisuga* Lind.) has been found across the geographic range of beech in Ontario, which could lead to heavy aboveground mortality from beech bark disease (BBD) (Cale, et al., 2017). The BBD complex consists of an insect component, *C. fagisuga*, and a phytopathogenic fungal component, of the genus *Neonectria*. Though the exact method of interaction is unclear, *C. fagisuga* feeding on the bark tissues of mature beech enables inoculation by *Neonectria* species (Houston, 2005). Growth of these fungi produces perennial lesions in the bark (cankers) that coalesce and can eventually girdle the vascular cambium, killing the stem and crown, while leaving the root system alive (Ehrlich, 1934; Houston, 1994; Houston, 2001).

In a stand, BBD progresses through three defined phases: (1) the advance front; (2) the killing front; and (3) the aftermath forest (Shigo, 1972). The advance front begins with the arrival and spread of beech scale. During this time, the fungal components of BBD are absent, and beech mortality remains at a baseline level (Shigo, 1972; Cale, et al., 2017). When the stand progresses to the killing front, beech scale has become highly abundant, *Neonectria* cankers are present, and elevated levels of beech mortality occur (Shigo, 1972). BBD infection results in 20-40% reductions in growth relative to uninfected trees, and increases in tree vulnerability to windthrow, or ‘beech snap’ (Papaik, et al., 2005; Busby & Canham, 2011; Gavin & Peart, 1993; Mize & Lea, 1979). Once a stand reaches the aftermath stage, beech scale and *Neonectria* species levels are reduced, and remaining beech may undergo attack by other pathogens, such as heartrot-decay fungi (Shigo, 1972; Cale, et al., 2015). As BBD preferentially infects stems 25 centimeters (cm) in diameter at breast height (*D*) or larger, beech populations shift over time towards smaller stems as larger trees fail (Houston, 1994; Forrester, et al., 2003).

This shift in forest composition has been compounded by the regeneration characteristics of beech, which reproduces both through seedlings and vegetatively, by root suckering or stump sprouting (Ward, 1961; Wagner, et al., 2010). Root suckers are the more abundant form of vegetative reproduction, developing following canopy disturbances such as logging, and often
from wounds to shallow root systems (Wagner, et al., 2010; Nyland, et al., 2006). Root suckers and seedlings can persist in the understory for decades due to their high shade-tolerance, but also possess a more rapid growth response to canopy gap formation than other shade-tolerant species, such as sugar maple (*Acer saccharum* Marsh.) (Canham, 1990). In addition to reduced ungulate preference for beech as browse in temperate forests, this provides a competitive advantage for beech regeneration following formation of small canopy gaps, such as from partial harvests (Wagner, et al., 2010; Bohn & Nyland, 2003). Such conditions occur even in unmanaged stands due to the presence of BBD, where BBD-mediated crown decline and death provide the surface disturbance and ground light levels to favour root suckering (Nyland, et al., 2006; Krasny & DiGregorio, 2001).

Under these conditions, beech regeneration of seed and sucker origin can occur at high densities, forming what are referred to as beech thickets (Giencke, et al., 2014). Thickets produce dense shade, inhibiting regeneration of desirable timber species such as sugar maple, yellow birch (*Betula alleghaniensis* Britt.), and red maple (*Acer rubrum* L.), and reducing overall plant biodiversity (Collin, et al., 2017; Cale, et al., 2013). Greenhouse experiments have also demonstrated that the leaf litter leachate of beech is phytotoxic to sugar maple seedlings, suggesting a second potential mechanism for inhibition of other species’ growth (Hane, et al., 2003). An additional concern is that root suckers are clonal, and new stems that have resulted from death of or disturbance to BBD-infected trees are equally susceptible to the disease (Houston, 1975). Remaining overstory beech provide an inoculum source for regenerating stems, resulting in low vigour understory beech that eventually succumb to BBD prior to attaining a position in the overstory (Houston, 1975; Gauthier, et al., 2015; Houston, 2005). Incidences of such secondary killing fronts have been observed in areas where BBD has long been endemic, such as the aftermath forests of Maine (Houston, 1975; Kasson & Livingston, 2012). Consequently, beech dominance in the understory will be expected to increase over time in BBD-impacted areas, alongside lack of replacement of mature canopy beech (Cale, et al., 2017).

Management for the control of beech regeneration, such as mechanical tending and use of glyphosate and triclopyr herbicides, is effective but costly and impractical for application across large areas (Cale, et al., 2017; Bohn & Nyland, 2003). Only 57,600 hectares of hardwood stands in Ontario underwent stand improvement initiatives over a 15-year period between 1994 to 2008, suggesting that only 0.6% of tolerant hardwood stands composed of 10% or more American
beech could be treated for beech regeneration each year (Stinson, 2010). Due to the cost, effort, and limited ability to apply treatments, it is essential that managers have methods to predict where beech thickets occur on the landscape, and thus the ability to identify stands to avoid for harvest, or where understory treatment may be necessary if harvesting is to occur (Bohn & Nyland, 2003). Thus far, the factors associated with beech proliferation in the understory are incompletely understood, but biotic variables such as stand basal area and beech basal area have been found to be important determinants of beech dominance in the understory (Bose, et al., 2017; Cale, et al., 2017; Ramage & Mangana, 2017). The influence of past management is also of interest, given that selection silviculture is commonly practiced in tolerant hardwood stands, and smaller gap sizes have been observed to promote beech regeneration due to the competitive advantages of beech at low light levels (Houston, 2001; Jones, et al., 1989). An additional concern is that most research has been conducted in the northeastern United States and eastern Canadian provinces, where BBD has been present up to 90 years longer than in Ontario, and differences in time since introduction of the disease may prohibit direct comparison (Cale, et al., 2017; Salmon, et al., 2016). For example, spatiotemporal analysis has indicated that beech saplings cluster around cankered canopy beech at broadening spatial scales as BBD progresses, and such relationships may therefore not be observable in more recently infected stands (Giencke, et al., 2014).

To address this gap, a retrospective analysis of tolerant hardwood stands across the Great Lakes – St. Lawrence (GLSL) forest region was conducted, to explore the relationships between understory beech densities and: (1) past management; and (2) stand composition. More specifically, the potential factors of harvesting intensity, years since harvest, total stand basal area, and basal areas of different species were examined for their relationship with high densities of beech in the understory. Due to the opportunistic nature of this study, multivariate regression techniques, specifically principal components regression, were used as robust statistical methods to identify significant relationships.

**Background Research**

*Past Management and Beech Understory Proliferation*

Consistent with the regeneration characteristics of American beech, partial cutting increases the proportion of beech regeneration from root sprouts (Jones & Raynal, 1987).
Analyses of the post-harvest survival of beech regeneration have also indicated that root sucker production is higher among clearcut stands than those that are partially cut, likely due to greater surface disturbance, but that survival of root suckers is greater among partially cut sites up to 10 years post-harvest (Houston, 2001; Farrar & Ostrofsky, 2006). In partially cut stands, root sprout production increases over the first five years following harvest (Houston, 2001). A recent broad-scale analysis of beech regeneration response to harvest has indicated that relative abundance and dominance of beech in the understory is positively related to higher residual live basal area post-harvest (i.e. where less of the overstory has been removed) (Salmon, et al., 2016). Creation of elevated light levels during harvest, such as among shelterwood cuts, results in a growth advantage for other shade-tolerant species, such as sugar maple and yellow birch, over newly established root suckers (Nyland, et al., 2004). Despite this, instances of beech propagation following aggressive harvesting treatments (eg. clearcuts) have also been observed, with beech persisting under shade intolerant overstory species (eg. *Populus* species) (Marquis, 1981).

**Stand Composition and Beech Understory Densities**

Recent attempts to characterize the occurrence of beech-dominated understories in BBD-impacted stands have indicated that overstories of beech-dominated understories tend to be relatively mixed and dominated by hardwoods. Though beech was not found to be necessary in the overstory for beech to dominate the understory, higher beech overstory basal area (alongside higher total basal area) increased occurrence probability of beech dominance in the understory (Bose, et al., 2017). Beech has a regeneration advantage over other shade-tolerant species in stands with high a proportion of beech in the overstory, due to reductions in light transmission to the understory and putative phytotoxic effects of beech litter leachate (Canham & Burbank, 1994; Hane, et al., 2003). However, where natural or anthropogenic disturbance has occurred, beech regeneration density is higher among stands with lower overstory basal area, likely due to the influence of forest floor disturbance in promotion of root suckering (Petrillo & Witter, 2005). For saplings, analyses of spatial relationships with beech in the overstory have indicated that saplings are only significantly associated with canopy beech that are severely cankered (Giencke, et al., 2014). This is supported by analyses in BBD-absent stands, with beech saplings being negatively associated with large conspecifics (Ramage & Mangana, 2017).
Methods

Study Area

Field observations for this study were taken from plots (n = 1,334) established within tolerant hardwood stands in the Great Lakes – St. Lawrence (GLSL) forest region of Ontario, Canada (44-48°N, 74-85°W), encompassing three ecoregions (Rowe, 1972) (Figure 1; Table 1). Tolerant hardwood forests within the GLSL forest are generally dominated by eight principal species: sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), red oak (*Quercus rubra* L.), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), basswood (*Tilia americana* L.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.), in association with other, less abundant species such as red maple (*Acer rubrum* L.) and ironwood (*Ostrya virginiana* (Mill.) K. Koch) (OMNR, 1998).

![Figure 1. Map of the study area.](image)

The study area (shaded in grey) comprised a portion of the Great Lakes – St. Lawrence forest region, within the area of undertaking (hatched with grey). Study plots (dark grey points) were chosen if they were located within tolerant hardwood stands in this area. Coordinate data is absent for the Silvicultural Effectiveness Monitoring dataset (n = 888), which are located within the French Severn Forest and Algonquin Park.
The predominant silvicultural system within managed tolerant hardwood stands in Ontario’s GLSL forest region over the past 30-40 years has been single-tree selection, wherein portions (up to 30% of basal area) of uneven-aged stands are harvested on a short cutting cycle of 15-25 years. Prior to this time, some stands in this region were selectively harvested for species such as yellow birch and white pine (*Pinus strobus* L.) (Jones & Thomas, 2004). Other silvicultural systems practiced within the region include shelterwood cuts and clearcuts, which are forms of even-aged management that remove up to approximately 50% (eg. Kreutzweiser et al., 2004) and 100% of basal area, respectively. Based on available harvest information, study plots were not harvested within the last 30 years, or were harvested either by shelterwood or selection cuts. 74 plots had undergone their second stand entry at the time of measurement.

**Table 1. Number of plots sampled across ecoregion and management status.** Ecoregions include Lake Temagami (4E), Georgian Bay (5E) and Lake Simcoe-Rideau (6E). Management includes harvested and unharvested plots, based on records of harvest within the last 30 years. Types of harvest include selection (SE) and shelterwood (SH).

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<th>Unharvested</th>
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<td>SH</td>
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<td>6E</td>
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</table>

**Data Collection**

This study used plots from five datasets established by the Ontario Ministry of Natural Resources and Forestry, in conjunction with other partners. The most geographically extensive dataset was the Growth and Yield Program network of permanent sample plots (PSPs) and permanent growth plots (PGPs) across central and part of northern Ontario (44-47°N, 76-84°W) (n = 146). For PSPs, circular 0.04 hectare (ha) sub-plots were established in groups of three, while for PGPs, one 0.04 ha sub-plot was established (Fig. B1). All trees ≥ 2.5 centimeters (cm) in diameter at breast height (*D*) were measured and recorded for *D* and species identity. Within each 0.04 ha plot, a 25-square meter (m²) vegetation plot was established, within which counts by species for saplings (*D* < 2.5 cm, height (*h*) ≥ 130 cm) and regeneration (*50 ≤ h ≤ 129 cm*) were performed. Measurements occurred between 1992 to 2004. Further details concerning data collection are available in the reference manual (OMNRF, 2016).
The Group Selection dataset (n = 155) comprised circular 0.04 ha plots established across 9 sites within Algonquin Park (45° 17'-35’ N, 78° 16'-29’ W), within stands 20 – 30 ha in size. All trees $D \geq 10.0$ cm were measured and recorded for $D$ and species identity within each 0.04 ha plot. Nested 25 m$^2$ sapling and 4.0 m$^2$ regeneration plots were established within each 0.04 ha overstory plot (Fig. B2). Saplings (2.5 $\leq D \leq 9.9$ cm) were recorded for species identity and $D$. Regeneration was recorded as counts by species for advanced regeneration ($D < 2.5$ cm, $h \geq 130$ cm) and low regeneration ($50 \leq h \leq 129$ cm). Measurements were taken in 2006, prior to group selection harvesting.

The Beech Bark Disease (BBD) dataset (n = 130) comprised circular 0.1 ha plots established across 26 blocks of plots within the French Severn and Bancroft Minden forest management units (FMUs) (45° 7'-19’ N, 78° 44'-49’ W). Each block contained five 0.1 ha large overstory plots. Within these plots, trees with $D \geq 17.0$ cm were recorded for $D$ and species identity. Within the 0.1 ha plot, a 0.04 ha sub-plot was established, within which trees with $8.0 \leq D \leq 16.9$ cm were measured for $D$ and species identity. Nested within the 0.1 ha plot were eight regeneration plots, divided into three size classes: large (16 m$^2$ plot; 2.0 $\leq D \leq 7.9$ cm), medium (8 m$^2$ plot; $D < 2.0$ cm, $h \geq 130$ cm), and small regeneration (4 m$^2$ plot; $20 \leq h \leq 129$ cm) (Fig. B3). Large regeneration stems were measured for species identity and $D$, while medium and small regeneration was recorded as counts by species. Measurements were made in 2016, prior to regeneration treatments.

The largest dataset, Silvicultural Effectiveness Monitoring (SEM), included 888 plots established across 46 stands within the French Severn FMU and Algonquin Park. Trees with $D \geq 10$ cm were selected using a 2 basal area factor prism, and selected trees were subsequently measured and recorded for species identity and $D$. Within each plot, a fixed-area plot of 16 m$^2$ was established to measure species identity and $D$ of saplings (2.5 $\leq D \leq 9.9$ cm) and regeneration ($D < 2.5$ cm, $h \geq 130$ cm). Measurements were conducted in 2010, between 16-22 years after single-tree selection harvesting had occurred.

The portion of the Increased Utilization of Biomass Project dataset used included 15 PSPs established across three sites within Haliburton Forest and Wildlife Reserve (45° 14'-15’ N, 78° 31'-33’ W), a privately owned and commercially managed forest. In each circular, 0.25 ha PSP, all trees with $D \geq 8.0$ cm were recorded for species identity and $D$. Five 50 m$^2$ sapling plots were established per PSP, wherein all trees $2.0 \leq D \leq 7.9$ cm were recorded for species
identity and $D$. Three 4.0 m$^2$ regeneration plots were set up per sapling plot, in which large ($D < 2.0 \text{ cm}, h > 130 \text{ cm}$), medium ($30 \leq h \leq 130 \text{ cm}$) and small regeneration ($h < 30 \text{ cm}, \text{ age} > 1 \text{ year}$) were recorded in a count by species (Fig. B4). Measurements were recorded prior to harvest in 2009.

For the purposes of this study, three size classes were developed: overstory trees, saplings, and regeneration. For understory trees, ‘sapling’ refers to trees with $2.0 \leq D \leq 7.9$ cm, while ‘regeneration’ refers to trees with $D < 2.0$ or $2.5$ cm and $h \geq 130$ cm (Table A1). Overstory trees include those stems with $D \geq 10.0$ cm for most plots (those within the SEM dataset), and $D \geq 8.0$ cm for the remaining plots.

Information on past harvest dates and systems was obtained from provincial harvest shapefiles. Any plots for which harvesting occurred the same year as measurement (without evidence that measurement had occurred prior to harvest, as in the Group Selection dataset), were removed. Plots with no record of harvest were recorded as ‘unharvested’, and given a time since harvest (TSH) value of 30 years, as selective harvest was common within tolerant hardwood forests 30-40 years ago, prior to use of selection and shelterwood cuts (Jones & Thomas, 2004). Unharvested plots were coded with a harvest intensity of 0, while selection and shelterwood cut plots were coded as 25 and 50, respectively, based on basal area removal.

**Statistical Analysis**

For beech regeneration and saplings, the calculated response variable was stem density (stems ha$^{-1}$). Calculations were averaged at the plot level, based on nesting of plots for saplings and regeneration within overstory plots. Stem density was also calculated for other abundant regenerating species (sugar maple and red maple), as a means of determining whether observed relationships with independent variables were unique to beech. This was not possible for intolerant hardwood species, as there were insufficient observations of regeneration and saplings. Overstory was calculated as basal area per hectare. Where sub-plots existed within plots for overstory measurements, basal area calculations were averaged at the plot level.

Hypotheses, based on prior work, were that: (1) Stands with higher total basal area and higher beech basal area would have higher densities of beech regeneration, but sapling density would be higher among stands with lower total basal area and higher beech basal area; and (2) Due to the predominant practice of selection silviculture in tolerant hardwood stands, past management would be positively associated with beech regeneration and sapling densities.
determine the relationships between stem density of understory beech and: (1) Stand composition; and (2) Past management within Ontario’s tolerant hardwood forests, and the utility of those relationships in predicting where beech thickets occur, principal components regression (PCR) was used (Massy, 1965). Where there are many predictor variables, multicollinearity can reduce the ability of regression methods to produce stable and meaningful coefficient estimates (Fekedulegn, et al., 2002). Multivariate techniques can ameliorate such issues in statistical interpretation, in addition to providing a robust analysis where clearly modeled relationships between dependent and independent (predictor) variables are absent (Frank, et al., 1962).

Within PCR, an ordination technique (eg. correspondence analysis (CA) or principal components analysis (PCA)) is first performed, with the principal component (PC) scores from ordination then used as independent variables for regression. Detrended correspondence analysis (DCA) was conducted using all putative predictor variables (Table 2), to determine the ordination technique to be performed (i.e. CA or PCA). Short gradient lengths (< 3) suggested that linear relationships likely underlay the variable patterns, and PCA was selected as the appropriate ordination technique (Jongman, et al., 1995). Due to differences in scale between predictor variables, PCA was performed using a correlation matrix (Jolliffe, 2002). However, as this biases the analysis towards grouping sites in ordination space that share the absence of a species, all rare species (those present in only 1 plot) were first removed (Legendre & Gallagher, 2001). Following removal of rare species, a total of 26 overstory species remained (Table 2).

Dependent variables (sapling and regeneration density) were tested for relationship with the first four PCs using a linear mixed model (LMM; PROC MIXED: SAS). The first four PCs were chosen for regression analysis based on their explanation of 26.7% of the total variance, and the rationale that PCs with smaller eigenvalues are less informative and more likely to suffer from issues of multicollinearity (Fekedulegn, et al., 2002). Random intercepts and coefficients for site were incorporated to account for between-site differences due to the broad geographic area of the study, and lack of environmental variable controls (eg. soil moisture, productivity). During model fitting, regression analysis was first conducted with ecodistrict incorporated as a categorical fixed factor to account for site conditions. Ecodistrict was significant as a categorical predictor (p < 0.05) for all dependent variables, but Akaike’s Information Criterion (AIC) scores indicated that model fit was greatly improved when site was incorporated as a random effect.
To meet parametric test assumptions of normality and homoscedasticity, sapling and regeneration densities were logarithmically transformed to a base of 10. Following regression analysis, non-parametric analysis of variance (ANOVA; Kruskal-Wallis test) and pairwise post hoc t-tests (Wilcoxon Rank-Sum test) were conducted to interpret effects associated with significant interactions for categorical variables (PROC NPAR1WAY: SAS), while Spearman
correlation tests were used to interpret effects associated with continuous variables. To examine the relationships between understory beech density and regeneration densities of other shade-tolerant species, Spearman correlation tests were conducted.

**Results**

*Patterns of Overstory Variation in Tolerant Hardwood Plots*

The main patterns of variation between tolerant hardwood plots in the GLSL forest region (the first and second component axes) were determined to represent stand history (based on high correlations of this axis with years since harvest, harvest intensity, and total basal area) and stand composition, along a gradient from plots with high sugar maple basal areas to plots with a mixed overstory (Fig. 2). Stand history was determined to represent a gradient from more recent and intense disturbance, to less recent disturbance with corresponding increased total basal area. Along the second component gradient, plots with higher beech basal areas had lower sugar maple components in the overstory, and tended to be mixed in overstory composition.

*Figure 2. Axes 1 and 2 from a principal components analysis on tree species basal areas, total basal area, harvest intensity, and years since harvest for 1,334 plots in the Great Lakes - St. Lawrence forest region.* The first component axis (x axis) was interpreted as being representative of stand history, based on correlation with total basal area, years since harvest, and harvest intensity. The second component axis (y axis) was interpreted as representing a gradient from sugar maple-leading to mixed composition stands. All species labels represent the basal area for that species, with three species of interest (American beech, sugar maple, red maple).
red maple, and sugar maple) being delineated in full. Other species acronyms include: AB (Fraxinus nigra), AG (F. pensylvanica), AW (F. americana), BD (Tilia americana), BF (Abies balsamea), BW (Betula papyrifera), BY (B. alleghaniensis), CB (Prunus serotina), CE (Thuja occidentalis), CP (Prunus pensylvanica), EW (Ulmus americana), HE (Tsuga canadensis), IW (Ostrya virginiana), MP (Acer pennsylvanicum), MS (A. saccharinum), OR (Quercus rubra), PL (Populus grandidentata), PR (Pinus resinosa), PT (Populus tremuloides), PW (Pinus strobus), SB (Picea mariana), SR (Picea rubens) and SW (Picea glauca).

Relationship Between Past Management and Beech Understory Densities

LMM results indicated that logarithmically transformed beech regeneration (n = 507, p < 0.0001) and sapling (n = 454, p < 0.0001) densities were significantly and negatively associated with the first component axis (Table 3; 4). This suggests an association of higher beech sapling and regeneration densities with more recent and intense logging disturbance. The association was stronger for beech sapling densities than regeneration densities, based on the larger regression coefficient estimate for saplings (-0.123) compared to regeneration (-0.073). For regeneration, log-transformed sugar maple (n = 824, p = 0.012) density, but not red maple (n = 81, p = 0.233) stem density, was also significantly associated with the first principal component (PC1) (Table 3). Based on regression coefficient estimates, response was greatest for beech regeneration. For saplings, log-transformed sugar maple (n = 659, p < 0.0001) and red maple (n = 94, p = 0.0006) stem densities were significantly and negatively associated with PC1. Estimated regression coefficient for red maple (-0.124) was greater than for sugar maple (-0.097) or beech (-0.123).

Table 3. Regression coefficients and significance values (p-values) for fixed factors from a linear mixed model analysis of logarithmically transformed regeneration stem density by species. Independent factors included the intercept and principal components (PC) 1 to 4. For each independent factor, regression coefficients and significance values are provided by dependent variable (i.e. stem density of study species). P-values are provided within brackets except for intercepts, due to the use of random intercepts in the linear mixed model, and significant p-values are bolded. Species examined included American beech (Fagus grandifolia), sugar maple (Acer saccharum), and red maple (Acer rubrum).

<table>
<thead>
<tr>
<th>Independent Factor</th>
<th>American beech</th>
<th>Sugar maple</th>
<th>Red maple</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.076</td>
<td>3.349</td>
<td>2.884</td>
</tr>
<tr>
<td>PC1</td>
<td>-0.073</td>
<td>-0.033</td>
<td>0.030</td>
</tr>
<tr>
<td></td>
<td>(&lt; 0.0001)</td>
<td>(0.012)</td>
<td>(0.233)</td>
</tr>
<tr>
<td>PC2</td>
<td>-0.061</td>
<td>0.081</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>(&lt; 0.0001)</td>
<td>(&lt;0.0001)</td>
<td>(0.796)</td>
</tr>
<tr>
<td>PC3</td>
<td>-0.019</td>
<td>-0.051</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td>(0.126)</td>
<td>(0.004)</td>
<td>(0.444)</td>
</tr>
<tr>
<td>PC4</td>
<td>0.020</td>
<td>-0.055</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>(0.097)</td>
<td>(0.0001)</td>
<td>(0.420)</td>
</tr>
</tbody>
</table>
Table 4. Regression coefficients and significance values (p-values) for fixed factors from a linear mixed model analysis of logarithmically transformed sapling stem density by species. Independent factors included the intercept and principal components 1 to 4 (i.e. PC1 to PC4). For each independent factor, regression coefficients and significance values are provided by dependent variable in the model (i.e. stem density of the given species). P-values are provided within brackets except in the case of the intercepts, due to the use of random intercepts in the linear mixed model. Significant p-values are bolded. Species stem densities analyzed included American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*).

| Independent Factor | Coefficient and Significance (p-values) |  |  
|--------------------|-------------------------------------|---|---|
|                    | *American beech* | *Sugar maple* | *Red maple* |
| Intercept          | 2.721               | 2.744               | 2.18       |
| PC1                | -0.123 (< 0.0001)   | -0.097 (< 0.0001)   | -0.124     |
| PC2                | -0.096 (<0.0001)    | 0.007 (0.565)       | -0.125     |
| PC3                | -0.007 (0.622)      | -0.018 (0.269)      | 0.066      |
| PC4                | 0.014 (0.303)       | -0.044 (0.0009)     | -0.017     |

Results of non-parametric ANOVA tests for effect of management on beech stem densities indicated a significantly higher mean score for regeneration density within recently harvested plots compared to unharvested plots, for both regeneration (n = 1,271; p < 0.0001) and saplings (n = 1,215; p < 0.0001). When harvested plots were examined for effects of harvesting based on categories of years since harvest (1-10, 11-20, and 21-30), mean score for beech regeneration density was significantly higher in the 1-10 years since harvest category compared to the 11-20 (n = 971; p < 0.0001) and 21-30 (p = 0.0001) years since harvest periods, while the mean regeneration density score for the 11-20 years since harvest group did not significantly differ from the 21-30 group (p = 0.671). For beech sapling density, mean score for stem density was significantly higher in the 1-10 group than in the 11-20 (n = 971; p < 0.0001) and 21-30 (p = 0.0006) years since harvest groups. Mean score was also significantly higher 21-30 years post-harvest compared to the 11-20 years post-harvest period (p = 0.031). This indicates that the highest stem densities for both beech regeneration and saplings were within 10 years following harvest, with higher stem densities also observed 21-30 years post-harvest for beech saplings. There were too few plots where shelterwood harvesting had occurred (n = 7) to compare the effects of selection and shelterwood harvesting on understory beech stem density (Table 1).
Spearman correlation tests for association between beech stem density and total basal area indicated a weak, negative significant correlation with beech sapling density ($r_s = -0.081$, $p = 0.005$), but a non-significant relationship with beech regeneration density ($p = 0.068$).

**Relationship Between Stand Composition and Beech Understory Densities**

LMM results indicated that log-transformed beech regeneration stem densities ($n = 507$, $p < 0.0001$) and sapling stem densities ($n = 454$, $p < 0.0001$) were significantly and negatively associated with the second component axis (Table 3; 4). This suggests that beech understory density is higher in stands where sugar maple is a large component of the overstory, and a more mixed species composition exists. Such stands also have higher overstory beech basal area and have more recently undergone harvest disturbance (Fig. 2). Based on regression coefficients, the relationship of log-transformed beech sapling density (-0.096) with the second principal component (PC2) was greater than that of log-transformed beech regeneration (-0.061). For regeneration, a significant and positive relationship was observed for log-transformed sugar maple stem density ($n = 824$, $p < 0.0001$), but the association for red maple was non-significant ($n = 81$, $p = 0.796$) (Table 3). The magnitude of the regression coefficient for sugar maple (0.081) was larger than for beech (-0.061) stem density. For saplings, a significant negative association with PC2 was observed for red maple ($n = 94$, $p = 0.006$), but not sugar maple ($n = 659$, $p = 0.565$) (Table 4). The estimated regression coefficient for red maple (-0.125) was greater than for beech (-0.096) sapling density.

Results of non-parametric ANOVA tests for difference of beech stem densities between sugar maple-leading and non-sugar maple-dominated plots indicated that mean score for beech regeneration stem density was significantly higher ($n = 1,271$; $p < 0.0001$) among plots where sugar maple was not dominant in the overstory. In contrast, mean score for beech sapling density did not significantly differ between plots based on sugar maple dominance ($n = 1,215$; $p = 0.070$) (Fig. 3). However, both sapling ($p < 0.0001$) and regeneration ($p < 0.0001$) densities were significantly lower among plots with monospecific sugar maple canopies ($n = 159$). 161 plots had monospecific overstories, with the two non-sugar maple plots comprised of beech and red oak. There was a significant positive correlation between overstory beech basal area and beech regeneration density ($r_s = 0.600$, $p < 0.0001$), and a slightly weaker correlation between beech basal area and beech sapling density ($r_s = 0.449$, $p < 0.0001$).
Figure 3. Mean stem density of American beech regeneration and saplings among sugar maple (MH)-dominant and non-MH-dominant plots. Error bars indicate standard deviations from the mean. Significant differences from Wilcoxon two-sample tests, which used mean scores rather than absolute values, are indicated by shared lowercase letters (a). Significance (p < 0.05) here indicates significant differences in distribution location between MH-dominant and non-MH-dominant plots.

**Relationship Between Beech Understory Densities and Regeneration of Other Species**

Results of Spearman correlations for beech regeneration and sapling densities with stem densities of other regenerating species indicated that beech regeneration density was significantly negatively correlated with sugar maple ($r_s = -0.255, p < 0.0001$), red maple ($r_s = -0.105, p < 0.0001$) and yellow birch ($r_s = -0.114, p < 0.0001$) regeneration stem densities (Table 5). Beech sapling stem density was also significantly negatively correlated with sugar maple ($r_s = -0.329, p < 0.0001$), red maple ($r_s = -0.130, p < 0.0001$) and yellow birch ($r_s = -0.170, p < 0.0001$) stem densities, with higher correlation coefficients than beech regeneration. A similar effect was observed when examining correlations with sugar maple saplings, which were abundant across sites, for red maple ($r_s = -0.060, p = 0.036$) and yellow birch ($r_s = -0.138, p < 0.0001$), but correlation coefficients were lower than for beech sapling stem densities, indicating weaker monotonic relationships.
Table 5. Spearman correlation results for correlation tests between beech regeneration density, beech sapling density and sugar maple sapling density, and regeneration densities of study species. Results are provided by Spearman correlation values ($r_s$) and significance values (p-values) for correlation tests. The key association of interest was between beech (*Fagus grandifolia*) regeneration and sapling densities and regeneration densities of sugar maple (*Acer saccharum*), red maple (*A. rubrum*) and yellow birch (*Betula alleghaniensis*). Sugar maple sapling density was included as a means of comparing suppressive effects of beech on regeneration densities.

<table>
<thead>
<tr>
<th>r$_s$ and Significance (p-values)</th>
<th>Sugar maple</th>
<th>Red maple</th>
<th>Yellow birch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beech regeneration density</td>
<td>-0.255</td>
<td>-0.105</td>
<td>-0.114</td>
</tr>
<tr>
<td>($&lt; 0.0001$)</td>
<td>($&lt; 0.0001$)</td>
<td>($&lt; 0.0001$)</td>
<td></td>
</tr>
<tr>
<td>Beech sapling density</td>
<td>-0.329</td>
<td>-0.130</td>
<td>-0.170</td>
</tr>
<tr>
<td>($&lt; 0.0001$)</td>
<td>($&lt; 0.0001$)</td>
<td>($&lt; 0.0001$)</td>
<td></td>
</tr>
<tr>
<td>Sugar maple sapling density</td>
<td>0.318</td>
<td>-0.060</td>
<td>-0.138</td>
</tr>
<tr>
<td>($&lt; 0.0001$)</td>
<td>($0.036$)</td>
<td>($&lt; 0.0001$)</td>
<td></td>
</tr>
</tbody>
</table>

**Discussion**

Significant, negative correlations between beech regeneration and sapling densities and regeneration densities of sugar maple, red maple and yellow birch suggest that high densities of understory beech in Ontario’s tolerant hardwood forests may inhibit regeneration of more desirable timber species, as observed at other locations impacted by BBD (Cale, et al., 2017; Collin, et al., 2017). Correlations were weak to moderate, but stronger than the monotonic relationships observed between sugar maple sapling density and regeneration density of red maple. For beech sapling density, the correlation with yellow birch was also stronger than the relationship between yellow birch and sugar maple sapling density. Beech scale insect has only recently (within the past 20 years) been identified in many counties in Ontario, and the inhibitory influence of beech understory densities on regeneration of other shade-tolerant species may increase over time, with the propagation of thickets (Cale, et al., 2017).

An understanding of the occurrence of beech thickets therefore holds management significance in Ontario. The results of this study indicate that beech regeneration density in tolerant hardwood forests is significantly influenced by: (1) Prior management, with a positive association with more recent and intense logging disturbance; and (2) Stand composition, having a negative association with increasing sugar maple dominance in the overstory. This is consistent with recent findings that beech-dominance in the understory is more likely under mixed
hardwood canopies (Bose, et al., 2017). Additionally, a strong monotonic relationship was observed between overstory beech basal area and beech regeneration density, and beech basal area was higher among mixed composition stands. This supports results from prior studies in the northeastern United States, where beech regeneration density was found to be higher among both BBD-impacted and BBD-absent stands with higher beech basal areas (Bose, et al., 2017; Ramage & Mangana, 2017). As beech regeneration density is greatest where beech is a larger component of the overstory, and canopy beech provide an inoculum source for younger stems, it may be anticipated that many regenerating beech stems will eventually succumb to BBD (Houston, 1975; Houston, 2005).

Beech sapling density was also significantly influenced by prior management and stand composition, having a positive association with more recent and intense logging disturbance, and with mixed overstory composition. No significant difference was observed in mean scores of beech sapling density between sugar maple-leading and non-sugar maple-leading plots, but sapling density was significantly lower in plots with monospecific sugar maple canopies. This may be attributable to the correlation between beech saplings and overstory beech; among old-growth *Fagus-Acer* forests in Quebec subject to frequent natural disturbance, beech saplings were largely restricted to sites where beech formed a large proportion of the overstory (Arii & Lechowicz, 2002). Similarly, among sugar maple-dominated stands in Quebec, higher relative beech sapling densities were associated with overstory beech (Nolet, et al., 2008). A study across hemlock-northern hardwood forests in the northeastern United States also observed that canopies with higher sugar maple influence favoured beech sapling growth over other species (Woods, 1984), which may account for findings that beech sapling density is not significantly lower at plots where sugar maple is dominant. In contrast, Poulson and Platt (1996) observed that beech saplings were larger than sugar maple under monospecific patches of overstory sugar maple, but such patches consisted of only 3 to 4 canopy trees.

Comparing effects of past logging disturbance between beech saplings and beech regeneration, a larger regression coefficient for PC1 (stand history) in the beech sapling density model suggests that sapling response to logging disturbance is greater. This may indicate that root suckering response to harvest is lower than beech sapling growth response to increased light availability post-harvest (Nyland, et al., 2006; Canham, 1990), but the model does exclude...
smaller regeneration classes. A larger regression coefficient was also observed for PC2 (stand composition) in the beech sapling density model. Given that beech regeneration density was significantly lower in sugar maple-dominant plots, in addition to monospecific sugar maple plots, the source of this difference may be the stronger association of beech sapling density with harvest disturbance and stand basal area. Mixed composition plots with higher beech basal areas tended to be more recently harvested, and consequently had lower total basal areas (Fig. 2).

**Uniqueness of Beech Understory Response to Stand Gradients**

Significant relationships between sapling and regeneration densities and past logging disturbance seen in beech were also observed for sugar maple and red maple. Beech regeneration density response to past logging disturbance was greater than that of sugar maple, based on the magnitudes of the regression coefficients for PC1. This may be attributed to the ability of beech to propagate profusely via root suckering in response to canopy and surface disturbance from logging, whereas root suckering is not common to sugar maple or red maple, which are more likely to reproduce asexually through stump sprouting (Nyland, et al., 2006; Babeux & Mauffette, 1994).

In contrast, the regression coefficient for PC1 was higher for beech sapling density than sugar maple, but slightly lower for LMM analysis of red maple. That harvest disturbance did not appear to favour beech sapling density over both species was surprising, given the greater sensitivity of beech to light levels following partial disturbances compared to other tolerant hardwoods (Canham, 1990). However, understory densities of beech relative to sugar maple have been linked to resource availability, with competitive advantages for beech existing on nutrient-poor sites, and beech saplings being restricted to sites with higher moisture (Nolet, et al., 2008; Finzi & Canham, 2000; Arii & Lechowicz, 2002). On base-poor soils in Quebec, beech and sugar maple sapling radial growth did not significantly differ at clearcut sites, despite the expected growth advantage for sugar maple at higher light levels (Bannon, et al., 2015). Relationships between site characteristics and response to light availability following harvest may also exist between beech and red maple, such as at higher soil moisture, where red maple saplings are expected to have a growth advantage over beech (Kobe, 2006). It is possible that abiotic factors not captured in this study contribute to the competitive advantages of beech relative to other tolerant hardwood species following partial disturbance, in Ontario.
In terms of the effect of stand composition (PC2) on regenerating species, a greater regression coefficient for PC2 was observed in LMM analysis for sugar maple stem density compared to beech, likely due to the stronger association of sugar maple with PC2 (Fig. 2). Additionally, despite the competitive advantage for beech regeneration under dense canopies due to its high shade tolerance (Canham, 1990), no significant correlation was observed between beech regeneration density and stand basal area. However, beech regeneration densities have also been positively associated with lower basal area following canopy disturbance in logged stands (Petrillo & Witter, 2005), which may have confounded results in this study. Similarly, the regression coefficient for PC2 was lower for LMM analysis of beech sapling densities than red maple, which may be due to the stronger association of red maple in the overstory with PC2 compared to beech (Fig. 2).

**Beech Densities Following Time Since Harvest**

Further examination of the effect of management through non-parametric ANOVA tests indicated that mean beech regeneration and sapling density scores were higher among harvested sites, and that mean beech regeneration and sapling density scores were highest 1-10 years post-harvest, decreasing in the 11-20 years post-harvest period. For saplings, beech sapling density was also higher 21-30 years post-harvest, compared to the 11-20 years since harvest period. Cyclical changes in relative abundance and dominance of beech regeneration were observed in BBD-impacted stands in New Brunswick, with beech relative abundance peaking 16-30 years post-harvest, and being absent >30 years since harvest. These changes were attributed to the rapid cycle of sprouting and death due to the severity of BBD in this region (Salmon, et al., 2016). In comparison, this study of tolerant hardwood stands within Ontario observed a peak in beech understory abundance 1-10 years following harvest. However, as BBD progresses, decreased root sprouting capability has been observed among cankered beech, relative to resistant or less severely infected canopy beech (Houston, 2001). This may explain the later peak in beech understory abundance observed by Salmon et al. (2016), where BBD intensity is considered severe.
Management Recommendations

Results indicate that managers can expect to encounter abundant beech regeneration in recently disturbed stands with mixed overstories where sugar maple is non-dominant, while abundant beech saplings may be found in recently disturbed stands with mixed overstories, even where sugar maple is the dominant canopy species. Should second entries be made to previously harvested stands, managers should be advised that treatment of beech regeneration and saplings may be necessary. To limit propagation of beech in the understory, it is recommended that harvesting in Ontario’s tolerant hardwood forests occur in stands where sugar maple is the leading overstory species, and beech basal area is low. Though results suggest that logging disturbance increases the abundance of beech saplings and regeneration, past research has indicated that pre-logging stand composition also contributes to beech regeneration dominance post-harvest (Bohn & Nyland, 2003). Due to the strong monotonic relationship between beech sapling and regeneration densities and beech overstory basal area, it is anticipated that avoidance of harvest in stands with high beech basal area will limit beech proliferation in the understory.

Future Research

The current study lacked environmental controls for study site, and was predominantly focused on biotic factors such as species basal areas and stand basal area, in addition to anthropogenic effects from past management. However, given the ability of site incorporated as a random effect in LMM analysis to improve model fit above inclusion of ecodistrict as a fixed factor, abiotic factors likely significantly contribute to density of beech in the understories of tolerant hardwood stands at finer spatial scales. For example, prior work has indicated that variables such as soil moisture, pH and carbon/nitrogen ratios are significant determinants of beech sapling density (Nolet, et al., 2008; Arii & Lechowicz, 2002). The influence of abiotic factors should be incorporated in future attempts to predict beech thicket occurrence in tolerant hardwood forests.
Acknowledgments

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Appendix A. Supplementary Tables and Figures

Table A1. **Standardized size class organization of tree-level measurements by dataset.** Size classes included overstory trees, saplings, and regeneration. Size class boundaries are indicated in centimeters (cm) in diameter at breast height and, for regeneration, cm in height (h). Where data collection methods allowed, data were reorganized to produce similar size intervals for vertical tree classes. Datasets included: (1) Group Selection (n = 155 plots); (2) Beech Bark Disease (BBD) (n = 130); (3) Silvicultural Effectiveness Monitoring (SEM) (n = 888); (4) Increased Utilization of Biomass Project (n = 15); and (5) Growth & Yield Program (n = 146).

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Group Selection</th>
<th>BBD</th>
<th>SEM</th>
<th>Biomass Project</th>
<th>Growth &amp; Yield</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Overstory</em></td>
<td>≥ 8 cm</td>
<td>≥ 8 cm</td>
<td>≥ 10 cm</td>
<td>≥ 8 cm</td>
<td>≥ 8 cm</td>
</tr>
<tr>
<td><em>Saplings</em></td>
<td>2.5 – 7.9 cm</td>
<td>2.0 – 7.9 cm</td>
<td>2.5 – 7.9 cm</td>
<td>2.0 – 7.9 cm</td>
<td>2.5 – 7.9 cm</td>
</tr>
<tr>
<td><em>Regeneration</em></td>
<td>&lt; 2.5 cm, h ≥ 130 cm</td>
<td>&lt; 2.0 cm, h ≥ 130 cm</td>
<td>&lt; 2.5 cm, h ≥ 130 cm</td>
<td>&lt; 2.0 cm, h ≥ 130 cm</td>
<td>&lt; 2.5 cm, h ≥ 130 cm</td>
</tr>
</tbody>
</table>
Appendix B. Study Plot Design

Figure B1. Plot design for Ontario Ministry of Natural Resources and Forestry (OMNRF) Growth and Yield Program A) Permanent sample plots (PSPs) and B) Permanent growth plots (PGPs). Of interest for this study are the growth plots (3 per PSP, 1 per PGP), in which overstory tree measurements were taken, and the vegetation plots (1 per growth plot), in which sapling and regeneration measurements were taken.
Figure B2. Plot design for the Group Selection study, for A) treatment and B) control plots. Overstory tree measurements were obtained within the total plot area, while sapling measurements were obtained from the sapling plots (SPs) and regeneration measurements were taken within regeneration plots (RGPs). Both treatment and control overstory plots contained one nested SP, while treatment plots contained 6 RGPs, and control plots contained only 3 RGPs.
Figure B3. *Plot design for the Beech Bark Disease (BBD) dataset.* Overstory trees were measured within large and small overstory plots, while saplings and regeneration were measured within 8 nested plots within the large overstory plot boundary. Saplings were measured within the bounds of the pink plot circles (Regen2.26), while regeneration was measured within the bounds of the blue (Regen1.60) and yellow (Regen1.13) circles.
Figure B4. Plot design for the Increased Utilization of Biomass Project. Of interest for this study are the: (1) Main plot (pink), in which overstory tree measurements were taken; (2) Sapling plots (blue) in which sapling measurements were made; and (3) Regeneration plots (red), in which regeneration was measured.
Literature Cited


Shannon Kainula


