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Effects of multiaged silvicultural systems on reserve tree growth 19 years after establishment across multiple species in the Acadian forest in Maine, USA

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Draft

Abstract

This study investigated the growth response of mature, isolated reserve trees ($n = 528$) in two multiaged silvicultural systems in the Acadian Forest Ecosystem Research Project (AFERP). The absolute and percent increase in basal area increment (BAI; $\text{cm}^2 \text{yr}^{-1}$) was assessed for the five predominant reserve tree species in AFERP: *Acer rubrum*, *Picea rubens*, *Pinus strobus*, *Thuja occidentalis*, and *Tsuga canadensis*. Absolute growth was significantly greater in the large-gap treatment (23.7 ± 1.1 ; mean $\pm$ SE) than in the small-gap treatment (16.3 ± 0.9). The percent growth increase was greater in the small-gap treatment ($187.6\% \pm 15.8$) than the large-gap treatment ($143.4\% \pm 19.3$) and both treatments had greater percent increases than the unharvested control ($9.6\% \pm 5.2$). Species differed in their response to treatment. *Pinus strobus* had the greatest absolute increase (large-gap: 52.5), while *Tsuga canadensis* (large-gap: $270\% \pm 71.6$) and *Acer rubrum* (small-gap: $262\% \pm 42.4$) had the greatest percent increases. Growth responses typically diminished with increasing tree size and pre-treatment growth rate; however, reserve trees showed greater growth responses than their paired analogues in the control across all initial tree sizes and prior growth rates. The results suggest these silvicultural systems accelerate the development of large trees.

Keywords: basal area increment, ecological forestry, restoration of large-diameter size-classes, retention forestry, retention tree

1. Introduction

The majority of the world's forests are managed as multifunctional forests, providing human commodities and other goods and services (FAO, 2010; Gustafsson et al., 2012). This management has partly contributed to the global decline of large, old trees and large diameter coarse woody debris (CWD; FAO, 2010; Lindenmayer et al., 2012a). Timber management based on the agricultural model often leads to the homogenization and reduced age of forested landscapes, which supports less plant and animal diversity than late-successional or unmanaged forests (Bauhus et al., 2009; Puettman et al., 2009; Fedrowitz et al., 2014). Given that the global area of strict forestland reserves is limited economically and socially, conservation and restoration of large, live trees must occur in managed forests (Gustafsson et al., 2012).

Concerns over the homogenization of the forest landscape as a result of high-yield commodity production has caused a paradigm shift in the way some natural forests are managed (Franklin 1989; Seymour and Hunter, 1999). Land managers are now more commonly implementing multiaged silvicultural prescriptions in response to demand for increased structural heterogeneity (D'Amato et al., 2015), ecological considerations in harvesting strategies (Bauhus et al., 2009; Klingsporn et al., 2012), and the restoration of late-successional features (Gustafsson et al., 2012; Fedrowitz et al., 2014). The retention of diverse species and ages in aggregated or dispersed configurations is often used as a strategy to accomplish these goals (Lindenmayer et al., 2012b).

The structures selected for retention are often large or old trees, or trees with particular attributes, such as cavities, that may promote biodiversity (Hunter, 1990; Gustafsson et al., 2010). In silviculture, such retention trees are termed "reserves" (or reserve trees), defined as any tree, pole-sized or larger, that is left unharvested after the conclusion of the regeneration period,

typically to enhance biodiversity, improve aesthetics, or grow to biological maturity (Helms 1998, p 153). Previous studies have shown that these trees can withstand the increased wind stress and exposure (Lohmander and Helles, 1987; Bladon et al. 2007), in general, experiencing high overall survival rates (Carter et al. 2017). Less is known, however, about the growth response of mature reserve trees, already positioned in the canopy, following the reduction in lateral competition resulting from harvest.

As silvicultural practices incorporate more diversity into harvested landscapes, much of the predictability in management outcomes based on the even-aged, agricultural model begins to weaken (Puettmann et al., 2009; O'Hara, 2014). While tree response to reduced competition has been well documented in suppressed trees and in even-aged stands, less is known about the response of diverse cohorts retained in uneven-aged stands (Bigging and Dobbertin, 1995). These responses have implications for growth projection models (O'Hara, 2014), the recruitment rate of late-successional features (Keeton, 2006), carbon storage and sequestration (Nunery and Keeton, 2010) and overall replicability of silvicultural prescriptions (Puettmann et al., 2009; O'Hara, 2014).

Previous studies have investigated the influence of several factors on the growth of trees within even- and uneven-aged silvicultural systems or natural gaps. In such studies, variables are often measured at the stand-level, which is largely a legacy of growth projection models originating from even-aged management practices (Puettmann et al., 2009). Such studies have found the disturbance severity and spatial configuration of the harvested area has been shown to influence growth responses (McDowell et al., 2003; Wiser et al., 2004). Stand-level variables, however, may be less influential in predicting growth response to harvest in more structurally complex

systems than tree-level variables (Bigging and Dobbertin, 1995). Specifically, Puettmann et al. (2009) found strong evidence in support of the relative dominance hypothesis (D'Amato and Puettmann, 2004) with the pre-harvest competitive neighborhood being highly influential on growth responses to harvest. Similarly at the tree-level, Jones and Thomas (2004) found evidence that growth responses differ by species, shade tolerance, tree size, tree age and spatial location.

With rare exception, mature trees have been shown to respond positively to light and heavy (25% to 82% BA removal) thinnings (Williamson, 1982; McDowell et al. 2003; Latham and Tappeniner, 2002; Mäkinen and Isomäki, 2004, Bevilacqua et al. 2005), shelterwoods (Youngblood, 1991; Walter and Maguire, 2004), seed tree harvests (1.2 tree ha⁻¹; Walter and Maguire, 2004) and uneven-aged treatments (Thorpe et al. 2007; Jones et al. 2009; Supplementary Table 1 (hereafter referred to as "Table S1")). However, there is a paucity of published studies with long-term response (15+ years) data. Furthermore, we found no published studies on growth responses of isolated, mature reserve trees retained in multiaged systems. Given that mature trees may take over a decade to respond to treatment (Latham and Tappeiner 2002), it is critical that mature tree responses in multiaged system be studied and over long periods.

In this study we capitalize on a long-term (19 years), replicated experiment, namely the Acadian Forest Ecosystem Research Program (AFERP), designed to test ecological forestry concepts. Established in 1994, the AFERP experiment includes two multiaged silviculture systems with reserve trees (Seymour et al., 2006), and includes a range of tree species and gap sizes. Informed by the natural gap-dynamics disturbance regime typical of the region (Fraver et al., 2009), it was

postulated that such systems could sustain productivity for commodity harvests, restore structural complexity diminished by even-aged harvesting practices, and promote biodiversity (Holling, 1973; Seymour and Hunter, 1999; North and Keeton, 2008). These silvicultural systems target the retention and restoration of late-successional features – e.g. large, old trees - to maintain biodiversity while managing for economically viable wood production (Bauhus et al., 2009; Lindenmayer et al., 2012b; Fedrowitz et al., 2014). These keystone features (Manning et al., 2006) serve as a “coarse-filter” approach to sustaining viable habitat for threatened species, supplying ecosystem services, and maintaining structural diversity and overstory connectivity on managed landscapes (Hunter, 1990).

Specifically, in Maine, the capacity of ecological forestry to promote late-successional features has particular relevance as the last four centuries of anthropogenic influence has altered the Acadian forest by favoring generalist and disturbance-associated species, reducing tree size and age, and decreasing structural complexity (Loo and Ives, 2003). Intense harvesting has led to live-tree diameter-class distributions being heavily skewed toward smaller size-classes compared to the size-class distribution pre-settlement (Lorimer and White, 2003). The statewide US Forest Service Forest Inventory and Analysis found that for trees at least 12 cm in DBH, only 7.2% are 33-53 cm in DBH and less than 0.5% are larger than 53 cm in DBH (McCaskill et al., 2010). Maine forests are also known to be lacking large diameter classes of snags, cavity trees, and logs (Rowland et al., 2005).

Here we explore the effect of treatments on dispersed reserve tree growth over a 7 to 19-year period in two, spatially distinct, multiaged silvicultural systems. Our specific objectives were to:

- (i) assess the overall effect of treatments on the growth of mature reserve trees;
- (ii) compare

growth responses among species of varying shade tolerances; and (iii) investigate the influence of various stand- and tree-level variables on the growth of reserve trees. Overall, the results of this study were intended to inform the retention practices of dispersed reserve trees in multiaged systems to maximize their growth responses, thereby accelerating the rate in which large-diameter size-classes are restored.

2. Methods

2.1 Study Site

The AFERP is located in the PEF of central Maine, USA (44_510N, 68_370N). The PEF is 1,618 ha and part of the Acadian Forest Region: a transitional ecotone between the northern boreal, spruce-fir forest type, and southern broadleaf forests with a cool, humid climate. The mean annual temperature is 7.1 C°, with approximately half of the 106 cm of precipitation falling in 156 days from May through October (Aresenault et al. 2011). The soils are derived from glacial till and range from well-drained loams, stony loams and sandy loam ridges, to poorly drained loams and silt loam flat areas (Saunders and Wagner, 2008; Aresenault et al., 2011).

2.2 Project Background and Treatment Descriptions

The silvicultural prescriptions in AFERP consist of two multiaged, natural-disturbance-based silvicultural systems. There are nine, approximately 10 ha research blocks (i.e. research areas; hereafter “RAs”) to which treatments were randomly assigned; six are treated while three serve as unmanaged controls. Three RAs are treated with an irregular group shelterwood with reserves in which 20% of the total area in the RA is harvested every 10 years (hereafter “large-gap treatment”) for 5 cutting cycles. The remaining three blocks were treated with a group selection treatment in which 10% of the total area -- half that of the large-gap treatment -- in the RA is harvested every 10 years (hereafter “small-gap treatment”) for 10 cutting cycles. The large-gap

treatment was designed to encourage natural regeneration of tree species of intermediate shade tolerance and to maintain stands of mid-successional status. The small-gap treatment was designed to encourage shade-tolerant species and accelerate development of late-successional stands.

Prior to treatment, the stands that comprise the RAs were fairly homogeneous. There were no significant differences in basal area (BA) ($37.6 \pm 1.1 \text{ m}^2 \text{ ha}^{-1}$, mean $\pm$ SD), density (2404 ± 138 trees ha^{-1}), or volume ($283.6 \pm 10.4 \text{ m}^3 \text{ ha}^{-1}$) among RAs prior to treatment. Compositionally, *Abies balsamea*, *Acer rubrum* (red maple), and *Tsuga canadensis* (eastern hemlock) were present at the greatest densities (Arsenault et al. 2011). When possible, initial gap harvests were centered on areas of sufficient understory stocking of naturally regenerating desired species. Occasionally these areas were the product of small, pre-existing natural gaps formed by single-tree mortalities.

Both the large- and small-gap treatments are applied using a 10-year cutting cycle. Gaps are only expanded, however, once a 10-year regeneration period has elapsed in the large-gap treatment and a 20-year regeneration period has elapsed in the small-gap treatment. At the time of this study, both treatments had undergone two entries. Gaps in the large-gap treatment had received a single expansion and the small-gap treatment had two entries of gap-creation without expansion. Initial gaps in the large-gap treatment were $0.17 \text{ ha} \pm 0.04$ (mean $\pm$ SD). After expansion, these gaps were $0.63 \text{ ha} \pm 0.02$. In the small-gap treatment, where gap expansions had yet to occur at the time of this study, gaps were $0.12 \text{ ha} \pm 0.01$ in the first and second entry.

In both of these treatments, retention exists in three conditions: unharvested (i.e. yet-to-be harvested) matrix, permanent reserve trees in gaps, and temporary “overwood” trees (defined

later) in gaps that can be harvested in future entries. The latter two conditions are retained in a dispersed configuration throughout the harvested gaps. The permanent reserve trees represent the only retention of the three aforementioned conditions that are to remain after the entirety of the given RA has been harvested. These trees are therefore the focus of this study.

Within the treated RAs, the permanent, reserve tree retention target was $3.7 \text{ m}^2 \text{ ha}^{-1}$ or 10% of the stand BA prior to treatment. These trees were intended to be retained permanently as dispersed reserve trees, distributed throughout the gaps as they are created. Reserve trees were selected to have the following characteristics: (1) possessing cavities and wildlife value, (2) locally uncommon tree species, (3) relatively large size, and (4) the potential for high timber value under a long rotation. All of the reserve trees are permanently tagged when selected and are re-measured on a 5-year interval.

Within the treated RAs, an additional 1-8% of the initial stand BA was retained as temporary “overwood”. In contrast to reserve trees, overwood trees are those that are retained either to grow into merchantable size-classes (e.g. immature growing stock) or as additional overstory cover in areas of low seedling density (e.g. low advance-regeneration stocking).

2.3 Data Collection

In the summer of 2014, all reserve trees ($n=787$) within the six treated RAs were re-inventoried. Species, diameter at breast height (DBH; cm), total height (m), lowest-live-crown (height to lowest live whorl; LLC; m), condition (live, declining, or dead), and spatial data using a Trimble GeoXH with sub-meter precision were recorded. Therefore, tree-level variables consisted of species, age (method of determining age described later), crown ratio, slenderness, volume, and cavity presence. Crown ratio was calculated by subtracting LLC from height and dividing the

total by height. Slenderness was calculated by dividing height by DBH (Petty and Swain, 1985). DBH and height measurements were converted to volume using equations from Honer et al. (1967) to provide a single metric for tree size and reduce collinearity in the variables in the tree-level analysis. Among the subset of reserve tree species sampled in this study, 11 total reserve trees possessed cavities and 17 were noted as ‘declining in health’ with all others being found in good condition. Permanent plot data from the control RAs were used to locate “paired analogues” (defined later) to use as comparisons to reserve trees. For more information on the treatments and field procedures, see Carter et al. (2017).

2.3.1 Tree Growth Data

Of the 787 reserve trees within the treated areas, the five predominant species (n=528), red maple, red spruce (*Picea rubens*), white pine (*Pinus strobus*), white cedar (*Thuja occidentalis*), and eastern hemlock were cored at breast height to determine growth patterns. Cores were also extracted from conspecific trees that were of similar size prior to the onset of harvesting (henceforth referred to as ‘paired analogues’) of each species across all three untreated RAs (n=191). Paired analogues were selected by stratifying previous permanent plot inventory data from the control in the AFERP database by species and five cm diameter-classes. Analogues were then randomly selected from the stratified data. Reserve trees that were not cored were still included in the retained basal area calculation, as were overwood trees.

The cores were mounted to grooved pieces of lath and sanded with progressively fine-grained sandpaper. The cores were measured using a Velmex sliding-stage measuring device interfaced with the MeasureJ2X software program. Tree-ring series were cross-dated by species using the marker-year method (Yamaguchi, 1991), accounting for missing rings when possible, with

statistical confirmation from the COFECHA program (Holmes, 1983). Age at breast height of trees with off-center cores were estimated using pith locators: transparencies with concentric circles equal in width and curvature to the last measured increment (Applequist, 1958).

Tree-ring series from increment cores were converted to basal area increment (BAI) in R v. 3.2.1 (Biondi 1999; Biondi and Qaadan, 2008; R Project, 2015). BAI was assessed on a per-tree basis to determine if reserve trees experienced a growth response to the treatments. Growth responses were measured using the mean post-treatment BAI (hereafter referred to as the ‘absolute growth increase’) and the percent growth increase (Henry and Swan, 1974):

$$\text{Percent growth increase} = ((A - B)/B) * 100$$

In this equation, A is the mean post-treatment BAI and B is 10-year mean pre-treatment BAI.

2.3.2 Spatial and Gap-Level Data

To capture any effect the group selection and expanding-gap systems had on reserve tree growth, retention basal areas and gap areas were calculated, as were metrics related to proximity to gap edge. Retained basal area (BA) was calculated by summing the total retained BA (overwood and reserve trees) and dividing by the area of the gap or expansion in which the trees were retained. This metric was included to test the effect of retained BA on individual tree growth, as protection from windstress or as potential competitors. Competition among retained trees was not expected in this study given the relative isolation in which they were retained. The retained BA associated with a given reserve tree was specific to the gap or gap expansion in which the reserve tree was retained. Gap edge was defined by the stems of trees on the edge of gaps. Gap area was used in tree-level analyses. The gap area associated with a given reserve tree described the growing

conditions of the tree upon initial release from lateral competition. In other words, trees in initial gaps that were expanded in a second entry were assigned the gap area of the initial entry. Reserve trees in the gap expansions, however, were assigned the total area of the expanded gap. Growth responses of reserve trees to their locations within gaps was then further described using three predictors: (1) nearest distance to original gap edge (i.e. reserve trees in unexpanded gaps (small-gap system only) and gaps prior to expansion (large-gap system only)), (2) nearest distance to expanded gap edge (i.e. reserve trees in the expanded gaps (large-gap system only)), and (3) nearest distance to original gap edge from expansion (large-gap system only) (for an illustrated depiction of these metrics, see Carter et al. (2017)). This final metric characterizes the degree of partial exposure experienced by reserve trees prior to gap expansions and any potential influence partial exposure may have had on growth. These metrics were determined using ArcGIS v. 10.2. Exposure variables therefore consisted of treatment, retained BA ($\text{m}^2 \text{ ha}^{-1}$), gap area (ha), distance to the nearest original gap edge (m), distance to the nearest expanded gap edge (m), and distance to the nearest original gap edge from expansion (m).

2.4. Analysis

2.4.1. Treatment and Species-Level Growth Responses

The design and compositional differences among treatments and species were assessed in ANOVAs. A treatment and species interaction was tested and post-hoc comparisons were made using the least squares means (LS means) function in the lsmeans package (Lenth, 2016) in R v. 3.2.1 (R Project, 2015). The differences in the absolute growth increase among treatments (small-gap, large-gap, and control) and species were assessed using a mixed-effects ANCOVA with pre-treatment BAI as the covariate and entry year nested within RA as the random effects. Pre-

treatment BAI could not be included as a covariate in the analysis of the percent increase because of its inclusion in the percent increase formula. Pre- and post-expansion growth rates of reserve trees in expanded gaps were compared using a repeated measures ANOVA for evidence of a second pulse of accelerated growth. Post-hoc pairwise comparisons were conducted using the LS means.

The differences in the percent growth increase among treatments (small-gap, large-gap, and control) and species were assessed using a mixed-effects ANCOVA with pre-treatment DBH as the covariate and entry year nested within RA as the random effects. Post-hoc pairwise comparisons were conducted using the LS means.

2.4.2. Tree-level Variables

To assess tree-level growth responses to treatments, model construction was conducted in five steps: (1) First, the importance of variables in predicting the absolute and percent growth increases were quantified using the relaimpo package in R (Gromping, 2006). This was done by partitioning the total variance explained (R^2) in a multiple linear regression by averaging sums of squares over all sequential orderings of the predictor variables. Due to the relatively small sample size across conditions and species, 95% bootstrap confidence intervals were calculated using 1000 replications sampled from the original data (Anning and McCarthy, 2013). (2) Predictors with high R^2 values were incorporated into linear mixed-effects models. To account for the nested nature and staggered implementation of the experiment and test for the effect of treatment and species, mixed-effects models were constructed for species-pooled and each species, respectively. Entry year nested within RA were assigned as random effects. (3) Due to the relatively small sample sizes for some species in this study, models were compared using the

Akaike information criterion with a small-sample bias correction (AIC_c) using the AIC_c function in the 'AICcmodavg' library in R (Burnham and Anderson, 2002; Mazerolle, 2015). This function was used to determine which model form was best supported by the data, as well as the most parsimonious within a set of models. (4) Finally, to assess model performance, marginal and conditional R^2 values were calculated using the $r.squaredGLMM$ function in R (Barton, 2015). Marginal R^2 values represent the variance explained by fixed factors, and conditional R^2 values represent the variance explained by fixed and random factors. The absolute and percent growth increases were tested for all species pooled, plus red maple, red spruce, white pine, white cedar and eastern hemlock, individually. Non-significant variables ($p > 0.1$) were not incorporated into the final models.

3. Results

3.1 Description of Treatments and Reserve Trees

3.1.1 Treatments

While similar attributes were targeted for retention among reserve trees, retention was not intended to be experimentally similar between the small- and large-gap treatments. The treatments and their design and compositional differences are summarized in Table 1. The initial and second entry gap sizes were greater in the large-gap treatment (initial: 0.17 ± 0.04 ha; second entry: 0.63 ± 0.02 ha) than the small-gap treatment (initial and second entry: 0.12 ± 0.01 ha). Among the treatments, the control had the greatest retained BA with equivalent first and second entry retained BA quantities in the small- and large-gap treatments. Retention within gaps was higher than the intended target of $3.7 \text{ m}^2 \text{ ha}^{-1}$. Trees in the large-gap treatment were generally larger, with pre- and post-treatment DBHs being greater in the large-gap treatment (35.3 ± 0.9

cm; 38.1 ± 0.9 cm) than the small-gap treatment (29.1 ± 0.8 cm; 31.8 ± 0.9 cm) and control (27.8 ± 1.0 cm; 28.8 ± 0.9 cm). Similarly, tree heights and volumes were higher in the large-gap treatment (20.2 ± 0.3 m; 1.45 ± 0.1 m³) than the small-gap treatment (18.9 ± 0.4 m; 0.82 ± 0.1 m³). Crown ratios were also greater in the large-gap treatment (0.55 ± 0.01) than the small-gap treatment (0.52 ± 0.01). Reserve trees in the small-gap also tended to be more slender (0.64 ± 0.01) than the large-gap (0.57 ± 0.01). Ages did not differ among the small- (91.3 ± 2.2 years) and large-gap (89.4 ± 1.9 years) treatments, but they both were less than the age of trees in the control (101.1 ± 2.4 years). Reserve trees in the large-gap treatment also tended to have greater retained BA among entries in their gaps (10.4 ± 0.3 m² ha⁻¹) than the small-gap treatment (8.4 ± 0.7 m² ha⁻¹). The pre-treatment BAI and first and second entry post-treatment BAIs were greater in the large-gap treatment (13.9 ± 0.8 cm² yr⁻¹; 17.9 ± 1.3 cm² yr⁻¹; 24.2 ± 1.2 cm² yr⁻¹) than the small-gap treatment (9.9 ± 0.9 cm² yr⁻¹; 11.9 ± 1.4 cm² yr⁻¹; 17.6 ± 0.9 cm² yr⁻¹) and the control (9.7 ± 0.7 cm² yr⁻¹; 8.2 ± 0.7 cm² yr⁻¹; 10.4 ± 0.9 cm² yr⁻¹).

3.1.2. Species

Species' attribute and growing condition differences are summarized in Table 2. With a few exceptions, the interaction of treatment and species was not significant. In the case of gap area, neither treatment nor species was significant. White pine had the greatest pre-treatment DBH among species, while white pine, followed by eastern hemlock, had the two greatest post-treatment DBHs. Red maple, red spruce, and white cedar were all statistically similar in these variables. White pine also had the greatest height while white cedar had the lowest height among species. White pine in the large-gap, followed by white pine in the small-gap, had the two greatest volumes among species and treatments (4.1 ± 0.3 m³; 2.8 ± 0.3 m³). Shade tolerant white cedar and hemlock had the greatest crown ratios among species. Red maple and hemlock were

the oldest species in the study. Slenderness among species was in the following order: red maple, then red spruce and hemlock, followed by the most tapered species, white pine and white cedar. Retained BA varied greatly among treatment and species with hemlock in the large-gap treatment having the greatest retained BA associated with its gaps ($12.5 \pm 0.5 \text{ m}^2 \text{ ha}^{-1}$) and red maple in both the small- and large-gap treatments (6.6 ± 0.3 ; $8 \pm 0.4 \text{ m}^2 \text{ ha}^{-1}$) and red spruce in the small-gap treatment ($7.3 \pm 0.5 \text{ m}^2 \text{ ha}^{-1}$) having the lowest retained BA. Red maple had the greatest distance to first entry gap edge among species.

3.2 Treatment and Species-Level Growth Responses

3.2.1 Absolute Growth Increase

The absolute growth increase ($\text{cm}^2 \text{ yr}^{-1}$) was greater in the large-gap treatment (23.7 ± 1.1) than the small-gap (16.3 ± 0.9) and control treatments (8.9 ± 0.7) (Table 1; Figure 1). In testing for a second pulse of growth acceleration in trees retained in expanded gaps, reserve trees in expanded gaps had a significantly higher post-expansion BAI ($22.9 \pm 1.6 \text{ cm}^2 \text{ yr}^{-1}$) than their post-initial-gap-creation BAI ($17.9 \pm 1.3 \text{ cm}^2 \text{ yr}^{-1}$; $t: -5.79$; $p < 0.0001$). Species differed in their response to treatment, with white pine (large-gap: $52.5 \pm 2.4 \text{ cm}^2 \text{ yr}^{-1}$) having the greatest absolute growth increase. The post-treatment BAI of white pine in the control was greater than all other species' post-treatment BAIs except hemlock in the large-gap.

Species with high pre-treatment BAIs, tended to have high post-treatment BAIs (Figure 2). With the exception of white pine in the large-gap treatment, all species showed a dramatically increasing absolute growth increase with increasing pre-treatment BAI (Figure 2; $F: 2.2$; $p: 0.2$). The steeper the slope of the line in Figure 2, the greater the response given the species pre-treatment BAI. As the line begins to flatten, the closer the species within a given treatment

begins to approach its pre-treatment BAI; as in the case of white pine reserve trees in the large-gap treatment. With the white pine in the large-gap removed from the mixed-effects ANCOVA, the treatment and species interaction remained significant ($F: 4.95; p < 0.0001$). While pre-treatment BAI was significant in predicting post-treatment BAI, age was not significant as a covariate ($F: 0.39; p: 0.93$; Figure 3).

3.2.2 Percent Growth Increase

The percent growth increase was greater in the small-gap treatment ($187.6\% \pm 15.8$; mean $\pm$ SE) than the large gap treatment ($143.4\% \pm 19.3$) and both treatments had significantly greater percent growth increases than the unharvested control ($9.6\% \pm 5.2$) (Table 1). Species differed in their response to treatment, with eastern hemlock (small-gap: $213.9\% \pm 23.9$, large-gap: $270\% \pm 71.6$) and red maple (small-gap: $262.4\% \pm 42.4$) having the greatest percent growth increases; Table 2). Red spruce (small-gap: $146.4\% \pm 28.9$; large-gap: $110.4\% \pm 14.7$) and white cedar (small-gap: $131\% \pm 21.5$; large-gap: $133.8\% \pm 18.8$) more than doubled their pre-treatment BAI. White pine had the lowest percent increase (small-gap: $71.7\% \pm 16.3$; large-gap: 81.6 ± 10.6) among the species but still showed a substantial response. All treatment and species responses were greater than those in the control.

With the exception of red maple in the large-gap treatment, all species showed a decreasing percent growth increase with increasing pre-treatment DBH ($F: 3.2; p: 0.01$; Figure 4). With the red maple removed from the mixed-effects ANCOVA, the three-way interaction term of treatment, species, and pre-treatment DBH is no longer significant ($F: 0.15; p: 0.93$). The percent growth increase was greater for all species relative to their conspecific control (Table 2; Figure 4). While pre-treatment DBH was significant in predicting percent increase, age was not a

significant predictor (Figure 5).

3.3 Tree-level Growth Responses

The models predicting the absolute increase outperformed those predicting the percent increase in terms of R^2 (Table 3). Species varied greatly in their respective proportional set of explanatory variables that best predicted absolute and percent growth increases (Tables 3 and 4). In general, metrics associated with tree-size (pre-treatment BAI, volume, and slenderness) were most influential in predicting the absolute increase. The percent growth increase, on the other hand, in general showed greater sensitivity to release-related metrics (distance to first entry edge, treatment, and crown ratio) and a negative relationship with large-size related metrics (age and volume). With species pooled, the fixed factors of species, pre-treatment BAI, slenderness, and volume explained 76% of the variance in absolute increase. For the percent increase, the fixed factors of species, volume, and distance to first entry edge explained 18% of the variance.

3.3.1 Absolute Growth Increase

With the exception of age in white pine (negative correlation) and crown ratio (positive correlation) in red spruce, pre-treatment BAI, volume, and slenderness were most often in the highest supported models in explaining the variance of the absolute increase among species (Table 3). When significant, pre-treatment BAI and volume were positively correlated with the absolute increase, while slenderness (increasing values for slenderness equate to increasingly spindly trees) was negatively correlated with the absolute increase. Red maple had the greatest R^2 with 61% of the variance explained by the fixed factors, followed by eastern hemlock (59%), white pine (50%), red spruce (47%) and white cedar (34%).

3.3.2 Percent Growth Increase

With the exception of the effects of treatment in red maple, crown ratio in red spruce, and age in white pine, the explanatory variables of volume and distance to first entry edge were most often in the highest supported models in explaining the variance of the percent growth increase among species (Table 3). When significant ($p < 0.1$), volume was negatively correlated with the percent growth increase. Similarly, when significant, distance to first entry edge was positively correlated with the percent growth increase, with the exception of white pine, in which case it was negatively correlated (Table 4). White pine had the greatest R^2 with 46% of the variance explained by the fixed factors, followed by red spruce (20%), eastern hemlock (14%), red maple (11%), and white cedar (7%).

4. Discussion

This study showed positive growth of reserve trees in response to multiaged silvicultural prescriptions over a 19-year period. Few studies have investigated the growth response of mature (age 75+ years) residual trees in multiaged systems (e.g. Walter and Maguire, 2004; Jones et al., 2009; Puettmann et al., 2009). Furthermore, we could not find any studies of such systems covering a longer duration than this study. Of the studies investigating mature reserve tree growth, our results were largely in agreement with their findings, with overall positive growth responses to treatment (Table S1).

In absolute terms, white pine was capable of amassing large gains in basal area, more than double that of the next highest species, eastern hemlock. It is important to consider these differences in absolute gains that are otherwise lost when describing growth responses in relative

terms, particularly in multiaged systems where the autecology of residual trees can differ dramatically. Regression analyses of the absolute increase yielded, almost exclusively, size-related relationships that would have been true in the absence of treatment. That is, large trees are capable of greater absolute gains than small trees.

In general, the consensus from previous studies is that growth responses vary in magnitude with the severity of the treatment and diminish with increasing tree DBH, age, shade-intolerance, and pre-disturbance canopy class (Thorpe et al., 2007; Jones et al., 2009). In this study, treatments did not reflect the magnitudes of the growth responses as the small-gap treatment had a greater percent growth increase than the large-gap treatment. However, increasing distance to the gap edge did generally result in greater percent increases. We attribute the lack of a consistent treatment effect to the compositional and volume dissimilarities in the retained trees between treatments; mostly the disparity in white pine retention between the large- (n=76) and small-gap (n=23) treatments.

This study has elucidated the growth responses of reserve trees to under-studied but increasingly utilized silvicultural systems. Additionally, this study provides evidence that the large- and small-gap systems, in addition to being economically viable systems (Saunders and Arseneault, 2013), are capable of accelerating the restoration of large-diameter classes and maintaining structural and biological diversity via high survival (92%; Carter et al., 2017) and increased growth.

4.1 Treatment-Level Growth Responses

The absolute and percent growth rates in the treatments were both significantly greater than the

control. The small- and large-gap treatments varied compositionally in their retention, which made direct comparisons of growth responses as a result of treatment difficult. The retained BA was not experimentally varied, nor selected to be compositionally similar. Therefore treatment-level comparisons likely differed, at least in part, due to these compositional dissimilarities, i.e. tree-size and species, and not necessarily the treatments per se. This is best exemplified with the small-gap treatment experiencing a higher percent increase than the large-gap treatment, while maintaining a lower absolute increase than the large-gap treatment. This treatment difference reinforces the results found in growth responses at the tree-level: (1) gap area and retained basal area did not result in significantly different growth rates; (2) the small-gap system was composed of, on average, smaller trees than the large-gap system; and (3) the small-gap system had less large white pine, which had considerably greater average size and higher growth rates prior to harvest likely due to its emergent status in the canopy. The lack of a direct treatment effect in this study demonstrates why tree-level analyses are critical in multiaged systems. Comparing these two treatments also suggested that, because gap size and retained basal area (i.e. treatment severity) had little effect on growth response, both treatments, regardless of the gap size, equally reduced lateral competition, resulting in similar growth responses of conspecific trees of similar attributes. This finding, in addition to the greater growth rates of trees in the treated RAs compared to the control, suggests that if restoring large-diameter size-classes by accelerating growth is a silvicultural goal, dispersed, rather than aggregated, retention should be used.

The growth rate of reserve trees in expanded gaps yielded a significant absolute increase post-expansion, though a significant percent growth increase was not found. This is partial evidence of a second pulse of growth acceleration as result of gap expansion. While interesting, more

detailed analyses would be required to determine if this growth response is independent of a time-lag in response to the original gap entry, however.

4.2 Species-Level Growth Responses

All species responded with increased growth as a result of treatment, though at a slightly decreasing rate with increasing pre-treatment BAI in the case of the absolute increase and pre-treatment DBH in the case of the percent increase. Comparably sized, conspecific trees had greater absolute and percent growth increases than their paired analogues in the control, however. This suggests that growth acceleration, even for large trees which are commonly thought to not respond to treatment (Walter and Maguire, 2004), is possible in these systems. Similarly, the lack of a significant age effect on the absolute and percent growth increases, except in white pine (which is likely related to its canopy status more than a physiological, age-related decline), suggests that these tree species are capable of responding positively to treatment despite advanced ages and pre-treatment canopy-ascension.

The comparably high percent growth increase of eastern hemlock is likely due to its ability to persist under low light conditions. This high shade tolerance likely allows it to respond more dramatically to increased light levels post-treatment when compared to species of lesser shade tolerances. Similar results were found by Jones et al. (2009) in which shade-tolerant species demonstrated greater responses to treatment than mid-tolerant and intolerant species. White pine had the greatest absolute increase among species but was the least responsive species in terms of percent increase, likely as the result of its emergent canopy position and innately high growth rate prior to treatment. These traits resulted in overall high growth rates both pre- and post-treatment, resulting in a low percent growth increase. Red maple in the small-gap treatment had

the second greatest percent growth increase of any species. This response could be attributed to the small size of red maple in this system and the degree to which it was released compared to the other species (red maple had the greatest average distance to first entry edge among species). Red spruce and white cedar also responded positively to treatment; however, their respective growth responses were lower than that of the other species. These species were often shorter and more tapered and thus likely less capable of intercepting the newly available light post-harvest.

4.3. Tree-Level Growth Responses

The results show that both relatively large (24+ cm DBH) and relatively old (75+ years at breast height) reserve trees exhibit positive growth responses to the treatments but, as the highest supported models show, at a decreasing magnitude with size. Age was surprisingly not significant in predicting growth among many of the species using either the absolute or percent increase. This suggests that their capacity to respond to treatment in these systems is more related to resource availability than age-related vigor.

Exposure positively influenced percent increases, with the exception of white pine. This finding suggests that growth had been constrained by resource limitations and that growth acceleration of mature trees, approximately 80% to 260% greater than trees in untreated conditions, can be achieved by reducing lateral competition. When significant, distance to first entry edge was positively correlated with greater percent growth increase. White pine, however, demonstrated the opposite relationship, with a negative relationship with distance to first entry edge. The majority of white pine reserve trees were in an emergent canopy position at the time of harvest, so increased wind stress or thinning shock (Kozlowski et al., 1991) are unlikely causes of this pattern. Because many gaps were initially located in patches of advance regeneration that

presumably established from canopy mortality prior to the experiment, it is possible that white pines near centers of such gaps had already begun to respond, where trees nearer gap edges had not, thus producing a more pronounced response near gap edges.

Species varied greatly in their respective sets of explanatory variables that best predicted percent growth increases. These differences likely reflect the species' ecology or resource limitation that either enabled or prohibited responses to treatment. In general, all trees retained closer to gap edges were likely inhibited by competition as the percent growth increase was positively correlated with distance from first entry edge, which is in agreement with the findings of York et al. (2010). Similarly, comparing the growth rates of retained trees after the first entry to the growth rates of the same trees post-expansion did result in the presence of a significant second pulse of accelerated absolute growth. White cedar maintained the lowest average volume of all species (0.46 m^3) and increased distance to the first entry edge was the most important in predicting a positive growth response of the explanatory variables tested. This finding suggests that centering gaps on desired species of lower canopy position and advanced age, such as white cedar, in order to compensate for insufficient light interception, may be the optimum strategy for maximizing growth response for relatively short trees in these systems.

Finally, we should emphasize that the primary objective of these silvicultural prescriptions is not to produce such growth responses, but to foster regeneration of relatively shade-tolerant species while leaving structural legacies. The positive reserve tree growth response demonstrated here, coupled with their high 19-year survival (92%; Carter et al., 2017), can thus be viewed as an important additional benefit – in terms of both stand structure and productivity – to the multiaged silvicultural systems described here.

It is critical to evaluate the capacity of the trees retained in multiaged systems to respond to treatment in order to inform growth projection models (Puettmann et al., 2009), for replicability (O'Hara, 2014), and to determine the efficacy of treatments in restoring large-diameter size-classes (Keeton, 2006). The growth responses of mature trees found in this study suggest that these prescriptions accelerate the restoration of large-diameter size-classes of living trees compared to the control; which is analogous to an ecological reserve or the interior of large aggregated retention patches.

4.4. Growth Metrics

Few studies quantify growth responses in terms of BAI, as was done here. More often, DBH, basal area ratio, or radial increment are used to quantify growth responses. All of which result in differing relative growth responses for the same individual. Thus, in order to fully understand growth responses, especially among differently sized trees of various species, it is important to consider multiple measures of growth as they all have associated strengths and weaknesses.

One of the shortfalls of using the percent increase, particularly in multiaged silvicultural systems where tree sizes and species autecology inherently differ, is its oversensitivity to the responses of small and slow growing trees and insensitivity to the responses of large and fast-growing trees (Fraver and White, 2005). Another shortfall of this method is that pre-treatment growth can no longer be appropriately used as a predictor without potentially confounding the findings by having the pre-treatment growth metric on both sides of the equation for the model. Using post-treatment BAI as the response, however, allows for the inclusion of pre-treatment BAI as a predictor. Anning et al. (2013) also used this method when characterizing the growth of mature trees in experimental blocks treated with prescribed fires. Pre-treatment growth is a logical

covariate when constructing models of this type as it is often highly influential. The use of only the average post-treatment BAI does not allow for a measure of relative magnitude of the growth response, however, which is a convenient and easily interpretable – though occasionally spurious, for reasons previously mentioned – metric. However, post-treatment BAI as a response variable ostensibly demonstrates an over-sensitivity to large trees as small trees are constrained to lesser gains in basal area.

5. Management Implications

The factors influencing tree growth response varied dramatically among species, making generalized management recommendations difficult. However, the results do suggest that one can expect reserve trees to respond positively to treatment even at an advanced age and size, though at a decreasing rate. While the diversity of variables most strongly influencing species' growth responses may pose issues for management and growth projections, this is the positive consequence of promoting complex stand structures. Such complex stands promote greater functional diversity and, thus, resilience to variable future conditions (Elmqvist et al., 2003; Lebourgeois et al., 2013, Brang et al., 2015).

Though selecting species that tend to have greater growth responses would increase overall responses of retained trees, consistently selecting only these species would compromise the objective of retaining a diversity of reserve trees of varying size and wildlife value. Therefore, deliberate location and spatial configuration of harvest gaps that selectively benefits trees of interest – centering gaps on old, overtopped trees and retaining white pine with emergent canopies near northern edges of gaps, for example – would assist in maximizing the growth response of a diverse class of reserve trees. By maximizing these growth rates, large-diameter

size-classes would more quickly be achieved as well as their associated benefits to structural complexity and biodiversity.

Although this study focused on growth responses, we recognize that additional reserve tree attributes, such as reproductive success and biodiversity maintenance, are equally worthy of consideration. We recommend that future studies of reserve trees focus on the link between growth and these additional ecological attributes. Similarly, future studies of reserve tree growth would benefit from defining pre- and post-treatment neighborhoods (i.e., mapped locations of neighboring trees) to create competition-based growth projections suitable for multiaged silvicultural prescriptions such as those in this study.

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Table 1. Summary of variables measured for each treatment with mean and $\pm$ SE in parentheses. Letters denote significant least square mean differences at 95% level of confidence among different letters within each row.

Variable	Small-Gap Treatment	Large-Gap Treatment	Control
Sample Size -- 1 st Entry Gaps	17	26	--
First Entry Gap Area (ha)	0.12 (0.01) ^b	0.17 (0.04) ^a	--
Sample Size -- 2 nd Entry Gap	26	21	--
Second Entry Gap Area (ha)	0.12(0.01) ^b	0.63(0.02) ^a	--
First Entry Retained Basal Area (m ² ha ⁻¹)	8.6(0.2) ^b	10.6(0.3) ^b	37.6(1.1) ^a
Second Entry Retained Basal Area (m ² ha ⁻¹)	8.1.(0.2) ^b	10.1(0.5) ^b	37.6(1.1) ^a
Sample Size -- Trees	198	330	191
Pre-Treatment DBH (cm)	29.1(0.8) ^b	35.3(0.9) ^a	27.8(1) ^b
DBH (cm)	31.8(0.9) ^b	38.1 (0.9) ^a	28.8(0.9) ^b
HT (m)	18.9(0.4) ^b	20.2(0.3) ^a	--
Volume (m ³)	0.82(0.1) ^b	1.45(0.1) ^a	--
Crown Ratio	0.52(0.01) ^b	0.55(0.01) ^a	--
Age (yrs)	91.3(2.2) ^b	89.4(1.9) ^b	101.1(2.4) ^a
Slenderness	0.64(0.01) ^a	0.57(0.01) ^b	--
Retained BA (m ² ha ⁻¹)	8.4(0.3) ^b	10.4(0.3) ^a	--
Distance to First Entry Gap Edge (m)	6.5(0.3) ^a	6.4(0.2) ^a	--
Distance to Expanded Gap Edge (m)	--	12.3(0.5)	--
Distance to First Entry Gap Edge from Expansion	--	10.6(1.5)	--
BAI Pre (cm ² yr ⁻¹) (10-yr Avg)	9.9(0.9) ^b	13.9(0.8) ^a	9.7(0.7) ^b
First Entry BAI Post (cm ² yr ⁻¹)	11.9(1.4) ^b	17.9(1.3) ^a	8.2(0.7) ^b
Second Entry BAI Post (cm ² yr ⁻¹)	17.6(0.9) ^b	24.2(1.2) ^a	10.4(0.9) ^c
Original Gap Post-Expansion BAI	--	22.9(1.6)	--
Expansion-Only Post-Expansion BAI	--	25.9(1.5)	--
BAI Post (cm ² yr ⁻¹ ; Absolute Growth Increase)	16.6(0.9) ^b	24.4(1.1) ^a	8.9(0.7) ^c
Percent Growth Increase (%)	187.6(15.8) ^a	143.4(19.3) ^a	9.6(5.2) ^b

Figure 1. Time-series of average basal area increment (BAI; cm²) by treatment with species pooled. Harvests began in 1995. Second entries and gap-expansions began in 2005

Figure 2. Three-way interaction plots of treatment, species and pre-treatment BAI predicting the absolute growth increase.

Figure 3. Three-way interaction plots of treatment, species, and age predicting the absolute growth increase with 95% confidence bands.

Table 2. Mean ($\pm$ SE in parentheses) of tree-level variables in the three treatments: small-gap (SG), large-gap (LG), and control (C). Data are from the end of the growth period (2014) and are specific to the reserve trees. Letters denote significant least square means differences at 95% level of confidence among different letters within each row.

Variable	Red Maple			Red Spruce			White Pine			White Cedar			Eastern Hemlock		
	SG n=57	LG n=51	C n=35	SG n=34	LG n=93	C n=31	SG n=23	LG n=76	C n=39	SG n=29	LG n=36	C n=33	SG n=55	LG n=74	C n=53
Pre-Treatment DBH	24.8(1) ^b	29.2(1.5) ^b	20.6(1.1) ^b	24.5(1.5) ^b	26(0.9) ^b	21.9(1.4) ^b	50.1(2.7) ^a	56.7(1.7) ^a	47.3(1.9) ^a	27.3(1.2) ^b	29(1.2) ^b	22(1.1) ^b	28.6(1.3) ^b	32.4(1.4) ^b	25(1.7) ^b
DBH (cm)	27.2(1.0) ^c	31.0(1.5) ^c	22.3(1.1) ^c	27.1(1.5) ^c	28.7(0.9) ^c	24.0(1.5) ^c	54.7(2.9) ^a	61.9(1.8) ^a	51.7(2.0) ^a	29.3(1.3) ^c	31.1(1.2) ^c	23.8(1.2) ^c	31.5(1.4) ^b	35.5(1.5) ^b	27.8(1.8) ^b
HT (m)	19.1(0.5) ^b	19.3(0.6) ^b	--	17.5(0.9) ^b	17.7(0.4) ^b	--	26.9(0.7) ^a	28.6(0.5) ^a	--	14.2(0.7) ^c	15.0(0.5) ^c	--	17.5(0.5) ^b	18.3(0.4) ^b	--
Volume (m ³)	0.5(0.04) ^c	0.7(0.1) ^c	--	0.6(0.1) ^c	0.6(0.1) ^c	--	2.8(0.3) ^b	4.1(0.3) ^a	--	0.4(0.04) ^c	0.5(0.1) ^c	--	0.7(0.1) ^c	1.0(0.1) ^c	--
Crown Ratio	0.5(0.02) ^b	0.5(0.02) ^b	--	0.4(0.03) ^b	0.5(0.02) ^b	--	0.5(0.02) ^b	0.5(0.01) ^b	--	0.6(0.03) ^a	0.6(0.03) ^a	--	0.6(0.02) ^a	0.6(0.1) ^a	--
Age (yrs)	96.8(4.6) ^a	88.2(5.4) ^a	97.3(5.6) ^a	76.4(3.8) ^c	76.6(2.2) ^c	87.2(4.6) ^c	101.2(7.3) ^b	98.6(3.8) ^b	122.3(3.6) ^b	99.6(7.7) ^b	113.4(5.3) ^b	113.2(5.6) ^b	90.1(3.1) ^a	89.0(4.8) ^a	93.0(5.3) ^a
Slenderness	0.8(0.02) ^a	0.7(0.02) ^a	--	0.7(0.02) ^b	0.6(0.01) ^b	--	0.5(0.02) ^c	0.5(0.01) ^c	--	0.5(0.03) ^c	0.5(0.02) ^c	--	0.6(0.02) ^b	0.5(0.02) ^b	--
Retained Basal Area (m ² ha ⁻¹)	6.6(0.3) ^c	8.0(0.4) ^c	--	7.3(0.5) ^c	10.7(0.5) ^{ab}	--	8.9(1.2) ^{abc}	9.0(0.5) ^b	--	7.6(0.6) ^{bc}	11.6(0.9) ^{ab}	--	11.2(0.5) ^{ab}	12.5(0.5) ^a	--
Gap Area (ha)	0.14(0.01)	0.40(0.05)	--	0.12(0.01)	0.59(0.04)	--	0.11(0.01)	0.48(0.04)	--	0.08(0.06)	0.55(0.06)	--	0.10(0.04)	0.41(0.03)	--
Distance to First Entry Gap Edge (m)	8.1(0.8) ^a	4.7(0.7) ^a	--	6.0(0.6) ^b	2.4(0.5) ^b	--	5.4(0.8) ^b	2.5(0.5) ^b	--	4.9(0.5) ^b	0.7(0.3) ^b	--	6.6(0.5) ^b	1.6(0.4) ^b	--
Distance to Expanded Gap Edge (m)	--	17.8(1.4)	--	--	11.1(0.8)	--	--	13.6(1.1)	--	--	12.3(1.1)	--	--	8.6(0.6)	--
Distance to First Entry Gap Edge from Expansion (m)	--	3.5(1.2)	--	--	6.0(0.9)	--	--	5.4(0.8)	--	--	9.1(1.8)	--	--	10.0(4.1)	--
BAI Pre (cm ² yr ⁻¹) (10-yr Avg)	4.6(0.4) ^b	10.5(0.9) ^b	4.3(0.5) ^b	6.2(0.9) ^b	7.2(0.5) ^b	4.3(0.5) ^b	28.6(3.2) ^a	34.0(1.8) ^a	27.5(2.6) ^a	5.3(0.4) ^b	6.4(0.4) ^b	4.7(0.5) ^b	6.7(0.6) ^b	9.5(0.8) ^b	7.0(1.0) ^b
BAI Post (cm ² yr ⁻¹ ; Absolute Increase)	12.2(0.9) ^c	15.7(1.5) ^c	3.9(0.5) ^c	11.6(1.1) ^c	11.7(0.7) ^c	3.7(0.5) ^c	40.6(2.6) ^{ab}	52.5(2.4) ^a	22.9(2.3) ^b	10.9(0.8) ^c	13.3(0.7) ^c	4.6(0.5) ^c	17.2(1.5) ^c	23.1(1.1) ^b	7.9(0.8) ^c
Percent Increase (%)	262.4(42.4) ^{ab}	118.1(56.2) ^{ab}	-2.3(6.4) ^{ab}	146.4(28.9) ^b	110.7(14.7) ^b	-3.4(13.6) ^b	71.7(16.3) ^c	81.6(10.6) ^c	-9.7(5.9) ^c	131(21.5) ^b	133.8(18.8) ^b	-0.13(5.7) ^b	213.9(23.9) ^a	270.1(71.6) ^a	44.9(14.5) ^a

Figure 4. Three-way interaction plots of treatment, species and pre-treatment DBH predicting the percent growth increase with 95% confidence bands. The horizontal line indicates no growth response to treatment.

Table 3. Summary table of the highest supported models predicting percent growth increases in reserve trees in the treated RAs. Marginal R^2 values represent the variance explained by fixed factors and conditional R^2 values represent the variance explained by fixed and random factors.

Response	Species	Model (+/- represent direction of relationship)	Marginal R^2	Conditional R^2
Absolute Growth	All	Species + Pre-Treatment BAI – Slenderness + Volume	0.76	0.79
	Red Maple	+ Volume + Pre-Treatment BAI	0.61	0.66
	Red Spruce	+ Pre-Treatment BAI + Crown Ratio	0.47	0.47
	White Pine	+ Pre-Treatment BAI – Age – Distance to First Entry Edge - Slenderness	0.5	0.59
	White Cedar	+ Volume + Pre-Treatment BAI	0.34	0.41
	Eastern Hemlock	+ Pre-Treatment BAI + Volume - Slenderness	0.59	0.65
Percent Growth Increase	All	Species - Volume + Distance to First Entry Edge	0.18	0.26
	Red Maple	Treatment	0.11	0.24
	Red Spruce	+ Crown Ratio – Volume + Distance to First Entry Edge	0.20	0.20
	White Pine	-Volume - Age - Distance to First Entry Edge	0.46	0.52
	White Cedar	+ Distance to First Entry Edge	0.07	0.19
	Eastern Hemlock	+ Distance to First Entry Edge	0.14	0.5

Table 4. Summary of R² (%) of covarites used in linear mixed-effects models and their bootstrapped 95% confidence intervals in parentheses for percent and absolute increase in growth by species.

Variable	All Species		Red Maple		Red Spruce		White Pine		White Cedar		Eastern Hemlock	
	%Increase	Absolute	%Increase	Absolute	%Increase	Absolute	%Increase	Absolute	%Increase	Absolute	%Increase	Absolute
Treatment	0.2 (0.2-4.2)	0.8 (0.4-1.5)	16.3 (8.6-33)	2 (1.1-9.6)	0.2 (0.2-4.2)	0.2 (0.2-2.4)	0.2 (0.2-5)	2.2 (0.7-6.3)	0.4 (0.2-5.4)	0.4 (0.1-5.7)	2.9 (0.7-9.4)	3.6 (0.8-9.7)
Species	4 (3.1-11.2)	26.1 (22.3-30.3)	--	--	--	--	--	--	--	--	--	--
Volume (m³)	1.2 (0.6-5.4)	14.9 (12.8-17.7)	0.1 (0.4-5.6)	33.5 (18-44.1)	10.4 (4.9-16.4)	6.2 (2.3-13.1)	15.9 (9.4-21.9)	4 (2.6-7.5)	2.2 (0.3-22.4)	12.9 (0.4-35.2)	0.7 (0.4-7.3)	12.6 (7.4-18.4)
Crown Ratio	0.6 (0.2-3.1)	1.1 (0.4-2.3)	0.3 (0.2-8)	2.1 (0.5-9)	1.7 (0.2-7.8)	9.6 (3.5-18.7)	1.1 (0.4-6.7)	3.1 (0.8-10.8)	1.5 (0.4-19.6)	0.4 (0.5-11.7)	0.2 (0.1-4.8)	4.4 (1-10.7)
Age (yrs)	1.1 (0.5-3.9)	1.6 (1-2.4)	0.3 (0.3-5.4)	5.3 (2.1-12.1)	1.3 (0.4-4.4)	1.4 (0.5-4.7)	20.2 (8.9-33.1)	11.5 (3.2-22.3)	0.2 (0.4-19.2)	2.6 (0.9-17.9)	1.6 (0.9-8.3)	2.1 (0.9-7)
Slenderness	0.1 (0.1-1.4)	7.9 (6.2-9.8)	0.1 (0.5-6.9)	11.8 (5.6-18)	1.3 (0.4-4.4)	6 (2.2-11.1)	5.2 (2.7-11.1)	6.8 (2.4-12.8)	3.1 (0.3-27.4)	3.7 (0.7-30)	0.2 (0.1-3.3)	13.8 (7.3-21.8)
Retained Basal Area (m² ha⁻¹)	0.3 (0.1-2.8)	0.4 (0.2-1.1)	2 (0.3-15)	0.8 (0.4-4.4)	0.4 (0.1-6)	0.3 (0.2-3.9)	2.1 (0.5-9.1)	0.4 (0.3-4.5)	1.4 (0.7-18.2)	0.6 (0.8-13.8)	0.1 (0.1-3.3)	3.3 (0.7-9.5)
Gap Area (ha)	0.4 (0.2-1.5)	0.5 (0.1-0.2)	0.9 (0.6-6.4)	0.6 (0.4-6.2)	0.5 (0.2-5)	0.3 (0.2-3.2)	0.6 (0.4-4)	3.3 (0.9-12)	0.9 (0.9-11.7)	1.7 (0.9-16.5)	0.7 (0.4-4.3)	1.5 (0.4-5.1)
Distance to First Entry Gap Edge (m)	3 (0.9-6.7)	0.3 (0.1-1.1)	4.7 (0.8-23.6)	1.2 (0.4-7.5)	2.9 (0.3-12.8)	1.1 (0.3-6.2)	3.4 (0.5-10.9)	6.1 (2.2-11.8)	5.7 (0.8-26.3)	0.7 (0.7-10.4)	7.4 (2.8-17.5)	0.6 (0.5-3)
Distance to Expanded Gap Edge (m)	0.2 (0.1-1.1)	0.5 (0.1-1.7)	3.2 (1.6-10.7)	1.4 (1.2-7.3)	0.4 (0.2-8)	0.3 (0.2-2.6)	0.7 (0.2-4.7)	1.2 (0.4-6.5)	0.2 (0.4-17.6)	2.5 (0.7-19.5)	4 (1.8-14.9)	1.1 (0.3-4.7)
Distance to First Entry Gap Edge from Expansion (m)	0.1 (0.1-0.6)	0.1 (0.1-1.3)	1 (0.5-6.1)	0.7 (0.6-4.4)	0.2 (0.1-2.2)	0.4 (0.2-5.2)	1.1 (0.3-6.9)	3.1 (0.8-14.7)	0.4 (0.7-21.2)	0.8 (0.7-14.7)	0.6 (0.3-2.7)	0.4 (0.2-2)
BAI Pre (cm² yr⁻¹) (10-yr Avg)	--	24.1 (19.3-28.4)	--	11.8 (3.9-24.8)	--	25 (12.7-35)	--	17.7 (7.7-30.1)	--	13.2 (3.6-32.4)	--	20.5 (12.6-30.1)
Total R²	11.3	78.2	30.2	71.2	20.7	50.8	50.6	59.4	15.5	39.3	18.5	63.3

Comment [AW1]:

Supplementary Table 1. Summary of literature review of release of mature trees

Author	Location	Species	Tree Age	Post-Release Period (yrs)	Treatment	Metric of Measurement	Average Response
Williamson (1982)	Washington, USA	Douglas-fir	110	19	Thinning: 25%-50% BA Removal	Volume	8%-30%
Youngblood (1991)	Alaska, USA	White spruce	174	14	Shelterwood	Ring width	164%
Urban et al. (1994)	Alberta, Canada	White spruce	120	16	Adjacent to new road	Ring width	31%
McDowell et al. (2003)	Oregon, USA	Ponderosa pine	250	7-15	Thinning 61%, 74%, 82% BA removed	Basal area increment	124%, 303%, 109%
Latham and Tappeiner (2002)	Oregon, USA	Douglas-fir	158-650	20-50	Light and moderate thinning	Basal area ratio	10%-68%
		Ponderosa pine					
		Sugar pine					
Walter and Maguire (2004)	Oregon, USA	Douglas-fir	80-125	10	Shelterwood: 75% BA removed	Basal area ratio	14%
					Clearcut: 1.2 trees/ha		31%
Mäkinen and Isomäki, (2004)	Finland	Scots pine	40-124	25	Thinning: ranged from 0% to 42%	Volume	Volume increment decreased
Bevilacqua et al. (2005)	Ontario, Canada	White pine	68.5	23	Thinning: 46% BA removal (compared to control)	Annual diameter increment	Intermediate crown class: 231%; Emergent: 63%; Dominant: 62% (compared to control)
Thorpe et al. (2007)	Ontario, Canada	Black spruce	25-175	12	Partial harvesting	Annual radial growth	Doubled
Jones et al. (2009)	Ontario, Canada	Black cherry	20-50	3-15	Group selection; trees within cutblocks	Basal area increment	-7%
		White spruce					13.5%
		Red maple					5.3%
		Yellow birch					24.6%
		Sugar maple					25%
		Beech					55.1%
		Hemlock					26%
Stan and Daniels (2014)	British Columbia, Canada	Western red cedar	Unknown	4-48	In or adjacent to natural, small gaps	Basal area increment	Canopy: 76%
							Sub-canopy: 64%
		Western hemlock	Unknown				Canopy: 133%
							Sub-canopy: 187%
		Pacific silver fir	Unknown			Canopy: 107%	
						Sub-canopy: 172%	
This study	Maine, USA	Red maple	88	7-19	Expanding-gap; 75% BA removal	Basal area increment	118%
		Red Spruce	77				111%
		White Pine	96				82%
		White cedar	113				134%
		Hemlock	89				270%
		Red Maple	97		Group selection; 80% BA removal		262%
		Red spruce	76				146%
		White pine	101				71.7%
		White cedar	100				131%
		Hemlock	90				214%