THE INFLUENCE OF STAND STOCKING LEVEL ON THE GROWTH AND
STRUCTURE OF MANAGED OLD-GROWTH NORTHERN HARDWOODS


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# CHAPTER 1

# THESIS INTRODUCTION

Silvicultural systems that maintain a continuous cover of trees in multiple age classes (three or more) in a forest stand while providing a continuous supply of timber at regular intervals are defined as uneven-aged systems (Helms 1998). Selection systems are uneven-aged management systems that harvest individual or small groups of trees to allow regeneration of replacement trees and recruitment of smaller trees into the overstory by releasing them from competition of the larger trees that surround them (Nyland 2007). Interest in the use of uneven-aged management using selection systems has waxed and waned in popularity among forest managers over the last century, but has recently seen a resurgence of interest in its application. This interest stems from the idea that uneven-aged management, by leaving the majority of the trees in a stand at each cutting, may have additional habitat and biological diversity benefits while at the same time providing a continuous fiber supply and being more aesthetically appealing to the public than even-aged harvests (O'Hara 2002, Nyland 2007).

Application of, and subsequent scientific examination of uneven-aged forest management began as early as the 19th century in Europe and was brought to North America by the early 20th century (O'Hara 2002). By the 1920s, partial harvesting methods including single-tree selection in uneven-aged forests were being examined in the Lake States as a means to ensure sustained yield following a period of relatively unregulated and exploitative forest harvesting across much of North America. Although it was generally known at this time that uneven-aged systems could be maintained indefinitely, the amount of volume that could be removed and the frequency at which this could be done were still unknown for a variety of forest types. Early results from short-

term experiments in the Upper Peninsula of Michigan indicated that sustained yield was possible in primarily shade tolerant northern hardwoods using single-tree selection (Eyre and Zilgitt 1953). These results were later used to develop marking guides for uneven-aged northern hardwoods that would be utilized for more than half a decade (Arbogast 1957, Nyland 2007). Soon after the publication of these early results, an experiment was established in what was then old-growth forest to test specifically the effects of different cutting cycles (frequency of harvest) and residual stocking levels (intensity of harvest) that would maximize the amount of board foot volume extracted from this forest type using single-tree selection. This Cutting Cycles and Stocking Levels experiment established from 1952 to 1954 at the Dukes Experimental Forest (then the Upper Peninsula Experimental Forest) near Marquette Michigan, was re-examined recently and is the focus of this thesis. The goal of this re-examination was to examine the long-term effects of these treatments on traditional forest management objectives related to growth and productivity, as well their influence on more recent objectives concerned with the conservation of biodiversity and restoration of late-successional forest structure.

Chapter 2 investigates the effects of different residual stocking levels on the structural complexity and tree species composition of the forest stands. This chapter utilizes the long-term compositional and diameter data along with recent field evaluations of biological and structural attributes within the treatment stands and an adjacent old-growth stand, which is used as a benchmark for unmanaged, old forest conditions.

Chapter 3 investigates the long-term effects of selection harvests on stand growth, tree growth, and tree quality. Examination of the detailed data collected over the last half century in the stands provides a unique opportunity to expand upon previous

investigations into the effects of thinning on production in forest stands, while also examining what effect single-tree selection at different residual densities might have on the quality of trees being produced.

Utilization of the long-term data available from the Cutting Cycles and Stocking Levels experiment is an extremely valuable tool for understanding the effects of forest management on stands of relatively long-lived species. Although the experiment was established in previously unmanaged forest, which may be a unique and uncommon condition today, this re-examination still provides a unique opportunity to contribute to our understanding of the long-term response of a number of variables of interest to the effects of forest management. Assimilating and re-examining the data in the context of contemporary silvicultural goals will provide insight into the appropriateness of selection systems for their achievement and will add to the knowledge base available to forest managers for making decisions regarding the use of uneven-aged approaches in a variety of settings.

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CHAPTER 2

THE INFLUENCE OF CUTTING CYCLE AND STOCKING LEVEL ON THE

STRUCTURE AND COMPOSITION OF MANAGED OLD-GROWTH

NORTHERN HARDWOODS

**Introduction**

Ecologically important old-growth forests have largely disappeared from the

landscapes of eastern North America over the past three centuries (Frelich 1995, Davis

1996). As a result, there is increased emphasis on management approaches that sustain or

foster the development of structurally complex, older forest conditions, or that create old-

growth or late-successional structural attributes in managed stands, including standing

dead trees (snags) and large downed woody debris (DWD) (Franklin 1989, McGee et al.

1999, Seymour and Hunter 1999, Lindenmayer and Franklin 2002, Franklin et al. 2007).

In many regions, this represents a departure from commonly accepted systems

used to manage forests.  For example, the northern hardwood forests of the Great Lakes

region of North America have commonly been managed using a system of single-tree

selection that results in a well-regulated, uneven-aged forest at the stand level (Leak

1964, Crow et al. 1981).  Silvicultural guidelines developed in the early to middle 20$^{th}$

century for managing these forests recommended removal of defective, dead, and dying

trees, as well as "less desirable" tree species (Arbogast 1957).

These management recommendations have proven effective in improving stand

growth and stocking of commercially desired species.  However, they also have resulted

in the deliberate removal of potential biological legacies, such as cavity trees, snags, large

decadent trees, and downed woody debris (McElhinny et al. 2005, Franklin et al. 2007,

Kenefic and Nyland 2007).  The result is that they have likely lessened stand structural

complexity (i.e., the overall abundance of and variation in structural attributes) in stands

that were initially complex or delayed development of this complexity in initially

simplified stands.  As such, an evaluation of the impacts of these treatments on stand

structural attributes, including DWD and snag abundance, density of large diameter trees, and stand diameter distributions, is critical for updating current management guidelines to address objectives related to the retention of late-successional, complex forest structure.

Uneven-aged forest management is often used in northern hardwoods as a method to keep continuous forest cover on the land, while at the same time providing regular supplies of raw materials at relatively short intervals (Eyre and Zillgitt 1953). Uneven-aged management of northern hardwoods has proven to be a successful tool for providing a sustained yield of board foot timber (Crow et al. 1981, Nyland 1998). Most of the literature on managing this forest type calls for regulation of diameter distributions to a negative exponential shape in order to maintain an adequate number of trees surviving into progressively higher diameter classes (Meyer 1952, Arbogast 1957, Nyland 2007). Historically, little consideration has been given to how these uneven-aged management approaches affect other structural attributes of stands. Importantly, a well-regulated forest may provide a sustained timber yield at adequate intervals, but it may lack certain structural characteristics such as live trees at the largest end of the diameter distribution and adequate levels of large dead wood on the ground and standing dead trees; characteristics of unmanaged old-growth stands (Kenefic and Nyland 2007).

In contrast to managed stands, old-growth northern hardwoods are generally composed of a mixture of mid-tolerant and tolerant tree species with a few dominant large crowned trees and many smaller trees leading to a multi-storied canopy (Crow et al. 2002). Other structures characterizing old-growth northern hardwood forests include large accumulations of downed woody debris, high densities of standing dead trees with cavities, high numbers of live trees > 50 cm in diameter with the presence of some trees >

8

70 cm, and a spatially complex horizontal distribution of trees (Goodburn and Lorimer 1998, McGee et al. 1999).  These structures are developed through an intricate regime of spatially and temporally heterogeneous small to meso-scale gap disturbances, such as branch falls or the death and fall of single trees or groups of trees (Runkle 1982, Hanson and Lorimer 2007).  In addition, the infrequent nature of stand-replacing disturbance in these systems also allows for the development of larger trees and subsequent large dead wood inputs (Canham and Loucks 1984).

Several studies have examined structural characteristics in old-growth northern hardwoods in the Lake States, but few have compared the differences in structural characteristics between old-growth and managed northern hardwoods (Tyrrell and Crow 1994b, McGee et al. 1999, Crow et al. 2002).  In addition, those studies comparing managed northern hardwoods and old-growth northern hardwoods have had little control over the specifics of the treatments, often simply labeling managed stands into broad categories, e.g., uneven-aged.  Moreover, these studies can suffer from inconsistent treatment over long periods of time (Goodburn and Lorimer 1999, Schwartz et al. 2005). For example, studies examining changes in live-tree diameter distributions in managed and unmanaged stands have most often been limited to stand simulations, measurements from a single point in time, or a small range of treatments (Lorimer and Frelich 1984, Leak 1996, Goodburn and Lorimer 1999, Leak 2002).  In addition, the lack of detail on management history in work comparing deadwood levels between managed and unmanaged systems has limited our ability to assess how different harvesting intensities over long periods might affect the distribution and abundance of DWD in managed northern hardwood systems (McGee et al. 1999, Angers et al. 2005).

As forest management paradigms have expanded to include more ecological goals over the past two decades, a valuable source of information on the long-term effects of forest management on stand structure and growth have been have been long-term silvicultural trials.  For example, Curtis and Marshall (1993) applied data from long-term growing stock trials in Douglas-fir to show that rotation lengths could be extended beyond those traditionally used with this species to increase the abundance of several forest attributes related to non-timber values, without subsequent losses in timber yields (Curtis 1994).  Similarly, examining long-term data from uneven-aged management experiments may provide insight into how current practices can be modified to better meet stand structural and compositional goals desired today.

With this need in mind, the overall objective of this study was to examine the long-term effects of stocking levels and cutting cycles on the structure and composition of northern hardwood forests managed using single-tree selection systems.  More specifically, I utilized a long-term replicated experiment spanning 57 years to examine the effects of uneven-aged management on species composition, live-tree size distributions, and the abundance of downed woody debris and snags present in managed stands.  Because the stands at the onset of this study were classified as "old growth", this experiment provides a unique opportunity to document how long-term management using single-tree selection affects the degree of structural complexity maintained over time within stands that presumably were quite complex at the onset of treatment implementation.  Such an evaluation can provide critical insights into the degree of stand structural complexity that can be maintained within forests being managed using traditional single-tree selection guidelines.

**Methods**

*Study area*

      The study was conducted in three *Acer saccharum* (sugar maple) dominated stands at the Dukes Experimental Forest, part of the Hiawatha National Forest in the Upper Peninsula of Michigan, USA.  The experimental forest is located 12-14 km south of the shore of Lake Superior at an elevation of approximately 330 m.  Micro-topography is dominated by pit-mounds which originate from past windthrow events (Beatty 1981, Putz 1983, Beatty 1984).  Soils at the study site consist of silt loams, sandy loams, and fine sandy loams, with a friable fragipan between 40 and 70 cm in depth underlying most of the area (NRCS 2009).  Site index ranges from 18 to 21 m at 50 years for sugar maple (Crow et al. 1981).  The entire area used in the study was unmanaged, old-growth northern hardwoods prior to the establishment of the experiment.   Some evidence of the removal of *Pinus strobus* (white pine) by European settlers has been suggested, but the area was largely undisturbed by humans prior to the inception of the study in 1952 (Woods 2000).  Prior to manipulation, live stem stand composition consisted of approximately 70-80 percent *Acer saccharum*, 10 percent *Betula alleghaniensis* (yellow birch), < 10 percent *Fagus grandifolia* (American beech) and < 10 percent other species, including *Acer rubrum* (red maple)*, Ostrya virginiana* (ironwood)*, Abies balsamea* (balsam fir)*, Tillia americana* (basswood)*, Tsuga canadensis* (hemlock)*,* and *Ulmus americana* (American elm).

*Study design and history*

The Cutting Cycles and Stocking Levels Experiment at the Dukes Experimental

Forest was established in 1952 in a randomized complete block design. Three blocks of

ten treatments were established to compare the specific effects of single-tree selection in

old-growth northern hardwoods using differing residual stocking levels and cutting

cycles. The treatment combinations included three levels of cutting cycles (5, 10, and 15

years) combined with three levels of residual stocking 11.5, 16.1, and 20.7 $m^2\ ha^{-1}$ of

residual basal area in trees greater than 24 cm in diameter. One additional treatment of a

20-year cutting cycle at 6.9 $m^2\ ha^{-1}$ of residual basal area (in trees > 24 cm) was also

established in each replication, but is not used in this portion of the study. Each treatment

unit is 4 to 6 ha in size and contains 6 to 17, 0.08 ha permanent circular plots. All trees

on the plots greater than 11 cm in diameter were inventoried for diameter and species

prior to the establishment of treatments and every five years thereafter until 1972-74,

when the study was closed (Table 1). On the permanent plots, trees were assigned a

permanent number and mapped so that diameter growth, ingrowth, and mortality could be

tracked. Renewed interests in the long-term effects of the study treatments spurred re-

measurement and remapping of all the trees on the plots in 2002-2004. Additionally, a

subset of 5 of the 0.08 ha permanent circular plots per treatment were randomly selected

in 2008 for measurement of additional stand structural attributes. One additional harvest

was conducted to the appropriate stocking levels in one of the treatment blocks in 1986

although no significant replication effects or treatment*replication interactions were

detected due to this disparity (Table 1). Also in 2008, 5 additional 0.08 ha permanent

circular plots of the same design as those in the long-term study were established in the

uncut hardwood section of the Dukes Research and Natural Area (RNA). The close
proximity of this relatively undisturbed old-growth forest within the same forest type as
the treatment forest prior to cutting makes it an ideal benchmark for comparison to the
treated stands.

*Field measurements*

At each of the 0.08 ha subset plots and 0.08 ha RNA plots established in 2008,
downed woody debris (DWD), snags, tree species composition, and tree regeneration
were measured. All DWD pieces and snags with minimum small end diameter of 10 cm
and minimum length of 1.5 m were inventoried on the plots. A piece was considered a
snag if lean was less than 45 degrees from vertical and DWD if more than 45 degrees.
Pieces extending beyond the plot boundary were measured to the edge of the plot. Total
length was recorded for each piece of DWD, and diameter at each end was recorded
assuming a circular cross-sectional shape. An intense storm in 2002 (Woods 2004) may
have created an artificially high DWD volume in the RNA plots, but not in other areas
on the RNA, so an additional survey of DWD using the line intercept method (Van
Wagner 1968, Harmon and Sexton 1996) was completed for the RNA to increase the
accuracy of my estimates of downed DWD. I used 4 randomly oriented 100 meter
transects to cover the hardwood area of the RNA in this additional survey. Each piece of
DWD was tallied at its intercept with the transect line and its diameter recorded as the
average of two caliper measurements. Species and decay class were determined for these
pieces as on all other plots as described below. On all of the circular plots, diameters
were measured on all snags > 10 cm, as well as total height. Decay classes (1 through 4)

were assigned to all DWD based on the methods described in Fraver et al. (2002).

Species was determined in the field for decay class 1 and 2.  The degree of decay for

decay class 3 and 4 pieces often prevented field identification of species, so species was

categorized as hardwood or softwood for these pieces.  Volume of downed DWD in the

treatments was estimated using the formula for volume of a frustum:

$$V = ((1/3)\pi L) \times (D_1^2 + D_2^2 + D_1 D_2)$$

where $V$ is volume (m$^3$), $L$ is length (m), $D_1$ is the small end diameter (m) of the piece,

and $D_2$ is the large end diameter (m) of the piece.  The volume of decay class 4 pieces of

DWD in the treatments were multiplied by 0.575 to account for the collapsed elliptical

shape that was generally encountered in these pieces (Fraver et al. 2002).  Volume of

downed DWD in the RNA was calculated using the line intercept formula:

$$V = (\pi^2 \ \Sigma d^2)/8L$$

where $V$ is volume (m$^3$), $L$ is total length of all transects (m), and $d$ is the average

diameter of two caliper measurements taken of the piece at the intercept point (Van

Wagner 1968).  Snag volume was calculated using a formula based on snag

fragmentation utilizing basal area and height of individual snags (Tyrrell and Crow

1994a).  Volumes of snags and DWD were averaged within the nine treatments and

among the three replications to determine the total pooled mean volume for each

treatment.  Large end diameter of DWD was extracted from the data collected and

analyzed using the same procedure to produce a pooled average for the different

treatments.  The proportion of the volume of DWD in each decay class was also

computed using the same method of pooling the nine treatment averages.

Tree species information was collected for each tree on all of the treatment plots in 1952, 1957, 1962, 1967, 1973, and 2002 by U.S. Forest Service personnel. This data was analyzed using the same methods used for the other stand structural attributes, i.e. tallies were totaled to a per hectare basis and averaged within the nine treatments and among the three replications to determine the total pooled proportion of each species for each treatment at each point in time throughout the study. After initial analysis, computation of the overall pooled percent change in density of the two most important species, *Acer saccharum* and *Betula alleghaniensis* was conducted.

Mortality of trees was also recorded at each point in time. For each stocking level, a pooled mortality was computed within treatments and among replications for all nine treatment stands as the percent of the basal area per hectare per year.

In 2008, I tallied the advance regeneration of all trees by species between 2.5 and 11 cm diameter at breast height (DBH) on two randomly selected quarters of the subset 0.08 ha plots and RNA plots. Trees less than 2.5 cm in diameter but greater than 1 m in height were tallied by species on two 2 m radius nested plots within the abovementioned quarters. Trees less than 1 m in height but greater than 0.5 m high and trees less than 0.5 m high were also tallied separately by species. Tallies were totaled to a per hectare basis and averaged to within the nine treatments and among the three replications to determine the total pooled mean density of regeneration for each treatment.

*Statistical analyses*

The effects of residual stocking level and cutting cycle on snag density and volume; DWD volumes, decay class, and large end diameter; species composition; and

regeneration densities were evaluated for all of the study treatments. Initial ANOVA

analyses indicated no significant cutting cycle effect, so I chose to focus solely on

stocking level effects. Correspondingly, the following ANOVA model was used:

$$Y_{ij} = \mu + R_i + T_j + RT_{ij} + E_{ij}$$

where $Y$ is the sample average for the treatment, $\mu$ is the overall mean, $R_i$ is the effect of

the $i$th replication, $T_j$ is the effect of the $j$th treatment, $RT_{ij}$ is the interaction between the

$i$th replication and the $j$th treatment, and $E_{ij}$ is the random error. Tukey-Kramer multiple

comparison tests were run to determine where specific significant differences existed

between treatments (SAS version 9.1, SAS Institute Inc., 2004).

Gradients in variation of stand structural attributes (DWD attributes, snag

attributes, regeneration, tree size, and tree species composition) among treatments and the

RNA, were examined using non-metric multi-dimensional scaling (NMS). NMS was

used to graphically examine the differences in structural attributes of the treated and

untreated stands using relaxed assumptions of normality and linear relationships to

environmental variables (McCune and Grace 2002). Structural attributes were arranged

along environmental gradients in n-dimensional space using PC-ORD Version 5.

Sørensen distances, a non-parametric comparison statistic, were used in the NMS to

compare the similarity of all 28 sample units from the 2008 sampling (27 treatments and

the RNA) in a distance matrix. PC-ORD determines the optimal solution for the NMS

through a "step-down" through the number of dimensions in a solution, starting at

maximum of six dimensions in this case, to a final and optimal solution that used only

two dimensions. The step down procedure used 250 runs of real data and 250 runs of

randomized (Monte Carlo) data to obtain the optimum dimensionality. The data were

then re-run in 3-dimentional space, reducing model stress until the final instability in the NMS was effectively zero.  The NMS was then examined visually in 2-dimensions using the two axes that explained the greatest percentage of the ordination.  The final NMS axis scores were compared with the structural attributes of the treatments using Kendall's $\tau$ statistic (SAS version 9.1, SAS Institute Inc., 2004).

Following NMS analysis, I used multi-response permutation procedures (MRPP) to conduct multivariate comparisons in structural attributes between the different stocking level treatments (McCune and Grace 2002).  MRPP is a nonparametric procedure that compliments NMS well by testing the hypothesis that there are no differences between the treatment groups.  I used a Sørensen proportional distance measure when running the MRPP to be consistent with the distance measure used in the ordination.

Diameter distributions are a well known and valuable tool for the description of stand structure and development in forest systems (Goff and West 1975, Leak 1996).  Investigators interested in the regulation of uneven-aged northern hardwoods as a means to supply timber at relatively short intervals have used both rotated sigmoid and negative exponential distributions as models for regulating the flow of merchantable timber from stands (de Liocourt 1898, Adams and Ek 1974, Nyland 2007).   In order to better understand the structure of the forest in the study, I created diameter distributions using 5 cm diameter classes for all treatments at all data points in the treated portion of the study using tree diameter data collected from the permanent circular plots.  A similar distribution was created for the RNA using the 2008 data.  Regressions of the base 10 logarithm of trees per hectare on DBH, $DBH^2$, and $DBH^3$ were evaluated for significant models.  The most significant model was selected by using highest adjusted $R^2$ and

lowest root mean square (RMSE) error per Janowiack et al. (2008). This method allows for the assignment of a distribution shape based on the order of signs of regression coefficients. Possible distribution shapes included rotated sigmoid, increasing q, negative exponential, concave, and unimodal (Janowiak et al. 2008). Models of treatments were compared for distribution shape and change in shape of that distribution over time.

**Results**

*Long-term stand development*

Changes in species composition in the managed stands were observed across all treatments over the entire study period. In particular, I observed a decline in the percentage abundance of the density of *B. alleghaniensis* in all treatments, and a similar increase in the abundance of the density of *A. saccharum* (Table 2). Significant differences between treatments were only detected in the change in *B. alleghaniensis* density. In particular, the 11.5 $m^2$ $ha^{-1}$ treatment had a significantly greater reduction in density of *B. alleghaniensis* over the course of the study than in the other two stocking levels (Table 2).

Mortality was calculated as a percentage of stand basal area for all measurement periods in the treatments then converted to an annual rate. No significant differences ($p < 0.05$) were detected among treatments. Mortality ranged from 0.27% to 0.45% BA $ha^{-1}$ $year^{-1}$ (Table 3). Mortality for the RNA could not be computed directly because of my single data point for this area in 2008.

Development of diameter distributions could be observed for the treated stands throughout the length of the study. A single distribution was created for the RNA in

2008. This distribution, along with the initial (1952) stand distributions for the treated stands were all found to have an increasing q distribution shape for trees > 15 cm DBH (Fig. 1, Table 4). The 11.5 m$^2$ ha$^{-1}$ treatments shifted to a concave distribution form after the initial treatment in 1952, and remained concave until the 2002 re-measurement when they showed a negative exponential form (Fig. 1, Table 4). The 16.1 m$^2$ ha$^{-1}$ treatments shifted to a negative exponential distribution after the initial cut and retained that shape until returning to an increasing q distribution shape by 2002. The 20.7 m$^2$ ha$^{-1}$ treatments continued to have increasing q distribution shapes throughout the study, although decreasing density in the smaller diameter classes was observed through the active treatment periods in these treatments (Fig. 1, Table 4).

*Stand structural responses*

Stem densities of trees greater than or equal to 11 cm in diameter were highest in the low stocking treatments, and lowest in the high stocking treatments in 2008 (Table 3). In contrast, the highest stocking treatments had significantly higher densities of large diameter trees (DBH > 50 cm and 70 cm) compared to the lowest stocking level treatment and similar densities as the 16.1 m$^2$ ha$^{-1}$ treatment (Table 3). Stem density in the RNA was considerable lower overall, but with higher numbers of trees occurring in the large diameter classes than in the low stocking level treatments (Table 3).

There was a general trend in current DWD volumes with higher volumes found in treatments managed with higher stocking levels and lower volumes in treatments managed with lower stocking levels (Fig. 2). In particular, the 11.5 m$^2$ ha$^{-1}$ (p = 0.05) and the 16.1 m$^2$ ha$^{-1}$ (p = 0.10) treatments both had significantly lower volumes of DWD

than the 20.7 $m^2$ $ha^{-1}$ treatment.  The volume of DWD in the RNA (97.0 $m^3$ $ha^{-1}$) was

higher than those found in the managed treatments (Fig. 2).   As with DWD volumes,

average large end diameter of DWD pieces was smallest in the 11.5 $m^2$ $ha^{-1}$ stocking

treatment (Table 3).  The average DWD large end diameters in the 11.5 $m^2$ $ha^{-1}$ treatment

were similar to those found in the RNA (Table 3); however, it is likely that greater DWD

large end diameters existed in the RNA, as the diameters I collected from this area were

from randomly intercepted portions of the DWD piece rather than the ends of the pieces.

The lack of trends in relative proportions of downed DWD volume by decay class (Table

3)  suggest that DWD inputs within among  the treatments were quite heterogeneous

spatially and temporally (assuming decay rate is constant).

The number of snags across treatments ranged from $8 \pm 1.5$ to $10 \pm 1.6$ snags per

hectare (Fig. 3) and there was no statistical difference in the number of snags among

treatments when not considering the size of the snags (Fig. 3).  The RNA contained 12

snags per hectare, which was slightly higher although similar to the levels observed in the

treated stands.  I divided snags into two size classes (> 30 cm and < 30 cm) in an attempt

to quantify differences in the number of snags in each size class.  Trends in snag size

were apparent and significant differences were detected between the 11.5 $m^2$ $ha^{-1}$ and

20.7 $m^2$ $ha^{-1}$ treatments for both size classes (Fig. 3).  Snags > 30 cm occurred more often

in treatments with higher stocking levels, while small snags (< 30 cm) occurred less

frequently in these stands.  In contrast to snag density, significant differences existed

among treatments in terms of snag basal area (Fig. 4a) and snag volume (Fig. 4b).

Overall, snag basal area and snag volume generally increased with increasing stocking

level in the managed stands. In particular, the 20.7 $m^2$ $ha^{-1}$ treatment had significantly

greater basal area and volume in snags than the treatments with lower stocking levels. Greater volumes and basal area of snags were observed in the RNA compared to the treatments, and were most closely approximated by treatments managed with higher stocking levels (Figs. 4a and b).

There were no statistical differences in regeneration densities among treatments (Table 3). It is worth noting that although I could not elucidate a statistical difference, the RNA had the greatest number of large (2.5-11 cm) regenerating trees and the smallest number of small (< 0.5 m tall) seedlings. The large standard errors observed in the treatments highlight the extreme variability observed on the plots in terms of seedling and sapling densities.

NMS ordination of the structural attributes was best-explained by a 3-dimentional solution that explained 94.7 percent of the variation in the structural data. The ordination had a final stress of 7.85 and very low instability (< 0.00001), which is within the accepted range for this type of analysis (McCune and Grace 2002). The first two axes explained a majority of the variation (80.4%; Fig. 5). There was a clear gradient in stands managed at the different stocking levels in the NMS, where stands managed at lower stocking (11.5 $m^2$ $ha^{-1}$ and 16.1 $m^2$ $ha^{-1}$) were grouped furthest from the RNA benchmark, and stands managed at high (20.7 $m^2$ $ha^{-1}$) stocking levels were grouped closely to the RNA (Fig. 5). MRPP analysis confirmed that there were significant differences in structural characteristics among treatment groups (A = 0.14; p = 0.05). The ordination results indicate that stands managed at higher stocking levels more closely approximated the structural conditions found in similar unmanaged forests (i.e., the RNA).

Many of the stand structural attributes associated with old forest conditions (e.g., high snag and DWD volumes, high densities of large trees) were positively correlated with NMS axis 1 and/or negatively with NMS axis 2 (Table 4).  All structural attributes were found to be significantly correlated (p = 0.05) with at least one axis of the NMS, although attributes related to the presence of large snags had the highest correlations ( $r \geq$ 0.6) with NMS axis 1 (Table 4).

**Discussion**

*Effects of treatments on species composition*

My results indicate that in all treatments, the abundance of *B. alleghaniensis* decreased sharply, with a corresponding increase in *A. saccharum* (Table 2).  These findings are consistent with other studies, which found that the abundance of mid-tolerant trees was reduced in the presence of heavy *A. saccharum* competition (Leak and Sendak 2002, Webster and Lorimer 2005, Neuendorff et al. 2007).  *B. alleghaniensis* requires relatively large canopy openings to establish (Woods 2000) and single-tree selection, even to low stocking levels, likely does not permit gaps of sufficient size to allow this mid- tolerant species to establish or recruit to larger sizes (Webster and Lorimer 2005). As such, the application of single-tree selection systems in the management of uneven-aged northern hardwoods may limit our ability to achieve ecological objectives such as a diversity of overstory tree species (Lindenmayer and Franklin 2002).

*Effects of treatments on structural attributes*

Managed stands that were subject to lower intensity harvest disturbance most closely approximated conditions found in the old-growth stand. In particular, the abundance and size of snags, the volume of DWD, and the variation in tree diameters in the 20.7 $m^2ha^{-1}$ treatment were most similar to values in the old-growth stand. Stands managed at 11.5$m^2$ $ha^{-1}$ had less structural similarity (less DWD, fewer large snags and large living trees) to the old-growth stand while having greater numbers of small diameter living trees.

Intensity of harvesting disturbance had the greatest impact on the abundance of DWD and snags in my stands. In addition, my data suggests that harvesting disturbance at regular intervals causes an overall reduction in the number of large and medium sized trees in the stand, further reducing the future recruitment of large snags, DWD volume, and DWD piece size (Table 5, Fig. 2, Table 6). Work in northern hardwoods in Quebec indicated that longer return intervals would contribute to the recruitment of large snags and DWD because of the reduction in mortality and mean tree diameter that likely occurs with frequent harvesting disturbance (Angers et al. 2005). More frequent harvesting likely results in removal of a greater percentage of dying trees from a stand, decreasing the abundance of the very type of trees most likely to contribute to the downed and standing dead wood pool. Loss of these trees also may decrease the abundance of other structures such as tip-up mounds and tree cavities. In the context of this study, the higher removal rates associated with the lower stocking level treatments likely removed a greater proportion of the old-growth structural elements present at the onset of this study relative to the higher stocking levels.

The volume of DWD in the old-growth strand (97.0 $m^3$ $ha^{-1}$) was similar to those found in other eastern old-growth northern hardwoods (Goodburn and Lorimer 1998, McGee et al. 1999). DWD volume in my managed stands generally decreased with increasing intensity of harvest (Fig. 2). This trend supports the hypothesis proposed by Vanderwel et al. (2008) that harvesting residues may be unimportant after more than 20 years, and that intense harvesting may result in long-term DWD losses for northern hardwood stands managed under traditional selection system guidelines. The reduction in DWD inputs in managed stands over time may result from decreased mortality (Vanderwel et al. 2008). I observed a reduction in overall mortality in managed stands (2-6% BA per decade compared with the 9% BA per decade reported by Woods (2004)). The density of snags in my study was fairly constant (8-13 per hectare) across all treatments and the RNA (Fig. 4). This range of densities is significantly less than Goodburn and Lorimer (1998) who found as many as 39 snags per hectare; however, other studies have found similar densities to those in the stands I examined (Keeton 2006, Kenefic and Nyland 2007). Despite the relatively low density of snags across treatments and the RNA, I saw clear trends in the volume and basal area of snags in relation to harvesting disturbance. An overall reduction in mortality in the managed stands and a deliberate removal of snag producing trees and trees in larger diameter classes likely reduced the number of larger diameter snags in the more heavily disturbed stands (Kenefic and Nyland 2007).

*Effects of treatments on diameter distributions*

My findings indicate there is considerable variation in the effect of single-tree selection on live-tree diameter distributions, depending on harvest intensity. In the stands receiving low intensity harvests ($20.7m^2$ ha$^{-1}$ residual stocking), I observed no quantitative change in distribution shape over time. Distributions in this treatment had an increasing q structure in all the measurement periods. Other studies have also observed the increasing q structure in northern hardwoods, but this structure tends to be far less common than rotated sigmoid and negative exponential distributions (Leak 1964, Goodburn and Lorimer 1999, Schwartz et al. 2005, Neuendorff et al. 2007, Janowiak et al. 2008). Rotated sigmoid diameter distributions in hardwood stands have been attributed to recovery of stands previously exhibiting negative exponential distributions from recent disturbance (Schmelz and Lindsey 1965). Disturbance in the $20.7m^2$ ha$^{-1}$ treatments apparently was not intense enough to affect the distribution shape over the 57 years of this study. In particular, this treatment has generated diameter distributions that most closely approximated the diameter distributions found in the treatment stands prior to cutting and presently found in the RNA old-growth stand. It is reasonable to conclude from this that disturbance in the $20.7 \ m^2$ treatment was similar in intensity to the natural wind disturbance regime that the old-growth stand has experienced over the last few hundred years (Woods 2004).

Increased intensity of disturbance resulted in concomitant changes in the distribution forms observed. For example, harvesting to $11.6 \ m^2$ ha$^{-1}$ quickly resulted in a change to a concave or negative exponential distribution. Both negative exponential and concave distributions in these stands (Table 4, Fig. 1) had a constant average q value

that is typical of what might be called a "well-regulated" managed uneven-aged forest (Meyer 1952, Goodburn and Lorimer 1999). As management continued, these more intensively disturbed stands continued to develop toward this regulated condition, with more trees in the smaller diameter classes, and fewer trees in the middle and larger diameter classes, relative to their starting distribution (Fig. 1). Although a negative exponential distribution may satisfy the classical definition of a balanced stand, there is considerable evidence that forests that exhibit this condition may not completely satisfy ecological forestry objectives for northern hardwood forests (O'Hara 1998, Keeton 2006). Rotated sigmoid and increasing q distributions allow greater allocation of basal area to larger diameter classes, which may in turn lead to the increased recruitment of structures dependent on large trees such as large snags, DWD, and tip-up mounds (Keeton 2006).

*Implications for management*

The use of single-tree selection guidelines for northern hardwoods created in the middle 20th century have proven appropriate where the silvicultural goal is to maintain a simple regulated structure that provides an adequate volume of timber at regular intervals (Arbogast 1957, Crow et al. 1981). Management using this regime provides timber, while also maintaining a continuous forest canopy that may be more aesthetically appealing than an even-aged management system, and may superficially approximate wind-driven natural disturbance dynamics in this forest type (Frelich and Lorimer 1991, Nyland 2007).

My findings indicate that this approach does require modification to more adequately achieve stand structural objectives suggested by an ecological forestry

paradigm (Franklin et al. 2007), which is inclusive of more complex and heterogeneous stand structures. For instance, traditional single-tree selection management guides (Meyer 1952, Eyre and Zillgitt 1953, Arbogast 1957) attempt to optimize growing space and increase overall sawlog quality (Crow et al. 1981). This is accomplished by preferentially removing defective and poor quality trees; however, from an ecological perspective, retention of "defective" trees may no longer be considered as wasted growing capacity (Seymour and Hunter 1999, Lindenmayer and Franklin 2002, Franklin et al. 2007) because of their importance as wildlife habitat and as a source of snags and DWD.

With modification, selection systems can provide unique opportunities to minimize the ecological distance between managed and unmanaged stands. Given that over 60% of the stand basal area is generally retained in selection systems, there should be sufficient basal area to foster the development of large diameter trees, including decadent individuals, DWD, and snags. If landowner/manager goals are to incorporate ecological principles and promote the development of old-growth attributes, a high degree of flexibility exists in the allocation of growing space for commercially desirable trees, as well as for the recruitment of ecologically important structures.

Managing for diameter distributions other than negative exponential can facilitate meeting ecological objectives. For example, simulation studies of northern hardwoods have shown that old-growth structural characteristics are more likely to be achieved by managing for a rotated sigmoid diameter distribution, with a very high or no maximum diameter and retaining high stand basal areas (Keeton 2006). Data from my study suggests that other stand distributions, such as an increasing q, may also work toward

achieving this goal, so long as enough growing space is allocated to the middle and large

diameter classes and enough very large trees (trees >70cm) are left in the stand.

Maintaining high residual stocking will also help achieve structural objectives.

For example, I observed higher density of trees greater than 24 cm diameter in stands

managed at 20.7 m$^2$ ha$^{-1}$, compared to those managed at lower stocking levels. While

managing at a high stocking level does not guarantee the development of late

successional stand structural conditions, my findings indicate that intensively harvested

stands (i.e., lower stocking levels) tended to have a lower degree of stand structural

complexity as compared to stands managed less intensively. If the management goal is

to more closely approximate the structure found in old-growth northern hardwoods, while

also actively managing for timber, higher target stocking levels, such as 20.7 m$^2$ ha$^{-1}$, may

prove most effective.

There are still challenges to overcome in the application of ecological forestry

principles to the management of uneven-aged northern hardwoods. For example, if an

increase in abundance *B. alleghaniensis* is desirable, single-tree selection will not

accomplish this goal. Other approaches utilizing intense localized disturbance to

replicate larger wind events may be necessary to accomplish this goal when it is

appropriate (Woods 2000, Hanson and Lorimer 2007, Neuendorff et al. 2007). Despite

this, managers who find the application of single-tree selection in maple-dominated

forests desirable may be able to reduce the ecological and stand structural differences

from old-growth northern hardwoods by adapting traditional guidelines using the

recommendations outlined above.

**Chapter 2 References**

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# CHAPTER 2


# TABLES

**Table 1.** Treatment history for the applicable portion of the original stocking levels and cutting cycles experiment at the Dukes Experimental Forest, MI.

| Treatment | | | | | | |
|---|---|---|---|---|---|---|
| **Stocking Level** $(m^2 \ ha^{-1})$ | **Cutting Cycle (years)** | **Establishment Cut†** | **2nd Cut** | **3rd Cut** | **4th Cut** | **5th Cut*** |
| 11.5 | 5 | 1952-54 | 1957-59 | 1962-64 | 1967-69 | 1973-74 |
| 11.5 | 10 | 1952-54 | | 1962-64 | 1967-69 | 1973-74 |
| 11.5 | 15 | 1952-54 | | | 1967-69 | |
| 16.1 | 5 | 1952-54 | 1957-59 | 1962-64 | 1967-69 | 1973-74 |
| 16.1 | 10 | 1952-54 | | 1962-64 | 1967-69 | 1973-74 |
| 16.1 | 15 | 1952-54 | | | 1967-69 | |
| 20.7 | 5 | 1952-54 | 1957-59 | 1962-64 | 1967-69 | 1973-74 |
| 20.7 | 10 | 1952-54 | | 1962-64 | 1967-69 | 1973-74 |
| 20.7 | 15 | 1952-54 | | | 1967-69 | |

† Replications were harvested sequentially in consecutive years, i.e. Replication A was first cut in 1952, Replication B in 1953, and Replication C in 1954.

* Only replication A of each treatment was fully harvested in 1973, some tree removals occurred in parts of replication B during 1974, and no harvesting occurred in replication C in 1975.

*** Replication A was also harvested (to the appropriate stocking levels) in 1986, no significant replication effects or treatment*replication interactions were detected (see Table 6 for type 3 fixed effects and associated p-values for ANOVAs).

**Table 2.** Mean proportion of the density of the two most important tree species (*A. saccharum* and *B. alleghaniensis*) in each stocking level.  Proportions are presented for the initial pre-treatment stand conditions (1952) and the last complete census period (2002).  The percent change in species composition over this period is also presented. Standard errors are in parenthesis. Note: treatments marked with an * were significantly different at p = 0.05, treatments marked with † were significantly different at p = 0.10, but not p = 0.05, n = 9.

| | 1952 | | 2002 | | % Change | |
|---|---|---|---|---|---|---|
| **Stocking level (m² ha⁻¹)** | *% Acer. sacch.* | *% Betula alleg.* | *% Acer sacch.* | *% Betula alleg.* | *Acer sacch.* | *Betula alleg.* |
| 11.5 | 79.4 (3.6) | 10.4 (1.1) | 83.0 (4.7) | 3.3 (0.8) | 4.4(1.8) | -69.6(4.6)* |
| 16.1 | 78.6 (3.3) | 9.7 (0.9) | 82.3 (3.9) | 4.8 (0.8) | 4.8(2.0) | -48.9(7.7)* |
| 20.7 | 75.0 (3.7) | 11.7 (0.5) | 77.9 (5.0) | 5.8 (0.8) | 3.5(3.5) | -49.3(6.1)† |

**Table 3.** Average annual mortality rates (1952-2004), large end diameter of downed woody debris (DWD) pieces, proportion of DWD volumes within each decay class, density of trees, and the density (stems ha^{-1}) of seedlings and saplings by size class for the treatments in 2008, at the Dukes Experimental Forest, MI.  For DWD diameter, the RNA value represents the average line intercept diameter, not the large end diameter of the piece.  Numbers in parentheses represent standard errors, n = 9.  Treatments with the same letter within each variable were not statistically different at p = 0.05.

| | Stocking level (m$^2$ ha$^{-1}$) | | | |
|---|---|---|---|---|
| **Variable** | 11.5 | 16.1 | 20.7 | RNA |
| Average annual mortality (% basal area ha$^{-1}$ year$^{-1}$) | 0.27 (0.03)*a* | 0.34 (0.06)*a* | 0.45 (0.10)*a* | 0.27 (0.03) |
| DWD average large end diameter (cm) | 21.3 (0.8)*a* | 23.7 (1.6)*ab* | 26.4 (0.5)*b* | 28 |
| Proportion of DWD by decay class | | | | |
| Decay class 1 | 30.8 (7.6)*a* | 23.9 (10.3)*a* | 26.0 (7.5)*a* | 21.4 |
| Decay class 2 | 25.8 (4.8)*a* | 27.6 (8.8)*a* | 35.6 (5.1)*a* | 27.1 |
| Decay class 3 | 18.3 (4.9)*a* | 22.6 (7.0)*a* | 21.9 (5.2)*a* | 24.3 |
| Decay class 4 | 25.2 (10.1)*a* | 25.8 (8.9)*a* | 16.6 (7.4)*a* | 27.0 |

**Table 3.** (continued)

| Variable | Stocking level ($m^2$ $ha^{-1}$) | | | |
| --- | --- | --- | --- | --- |
| | 11.5 | 16.1 | 20.7 | RNA |
| Stem density (trees $ha^{-1}$) | | | | |
| Trees $\geq$ 11 cm | 347 (11)*a* | 315 (14)*ab* | 307 (8)*b* | 260 |
| Trees $\geq$ 50 cm | 38 (3)*a* | 46 (3)*ab* | 56 (1)*b* | 64 |
| Trees $\geq$ 70 cm | 5 (1)*a* | 8 (2)*ab* | 11(1)*b* | 10 |
| Density (stems $ha^{-1}$) of seedlings and saplings by size class | | | | |
| 2.5-11cm DBH, > 1m tall | 341 (55)*a* | 468 (65)*a* | 512 (40)*a* | 628 |
| < 2.5cm DBH, > 1m tall | 566 (217)*a* | 3430 (1850)*a* | 1630 (774)*a* | 4780 |
| 0.5-1m tall | 2330 (1240)*a* | 2890 (1060)*a* | 3890 (1260)*a* | 4000 |
| 0-0.5m tall | 375000 (58600)*a* | 329000 (77200)*a* | 466000 (52000)*a* | 133000 |

**Table 4.** Quantitative distribution shapes at the Dukes Experimental Forest, MI
following Janowiak (2008). Letters indicate quantitative distribution shape. IQ =
increasing q, CO = concave, and NE = negative exponential.

| Stocking level | Distribution Shape | | | | | |
|:---:|:---:|:---:|:---:|:---:|:---:|:---:|
| $(\mathbf{m^2\ ha^{-1}})$ | 1952 | 1957 | 1962 | 1967 | 1973 | 2002 |
| 11.5 | IQ | CO | CO | CO | CO | NE |
| 16.1 | IQ | NE | NE | NE | NE | IQ |
| 20.7 | IQ | IQ | IQ | IQ | IQ | IQ |
| RNA | n/a | n/a | n/a | n/a | n/a | IQ† |

† The RNA had an increasing q distribution shape in 2008. No data is available for the
RNA in other time periods.

**Table 5.** Summary of correlations (Kendall's τ statistic) between stand structural attributes and the first and second NMS axes. Correlations coefficients in bold indicate a significant correlation with the NMS axis score (n = 28, p = 0.05).

| Structural Attribute | Axis 1 | Axis 2 |
|---|---|---|
| DWD volume | **0.376** | **-0.402** |
| Number of snags | **0.465** | -0.054 |
| Snag volume | **0.862** | **-0.370** |
| Snag basal area | **0.847** | **-0.333** |
| Snags ≥ 30 cm | **0.640** | **-0.359** |
| Snags < 30 cm | -0.149 | **0.490** |
| Coefficient of variation of DBH | **0.291** | **-0.370** |
| Number of regenerating trees | -0.032 | **-0.503** |
| Live trees ≥ 50 cm | **0.442** | **-0.601** |
| Live trees ≥ 70 cm | 0.241 | **-0.567** |
| DWD size | **0.302** | **-0.370** |

**Table 6.** Summary of type 3 fixed effects, including source of variation, degrees of freedom for both numerator and denominator, F-values and probability values for the percent change in species composition for *A. saccharum* and *B. alleghaniensis* (1952-2002), stem density, DWD volume, DWD large end diameter, the number of snags, the number of snags by size class, snag basal area, snag volume, regeneration densities, average annual mortality, and proportion of DWD by decay class for the treatments in 2008 at the Dukes Experimental Forest, MI.

| | | Source of variation | | |
|---|---|---|---|---|
| | | Stocking Level | Replication | Stocking x Rep. |
| Degrees of freedom | | | | |
| | d.f. numerator | 2 | 2 | 4 |
| | d.f. denominator | 18 | 18 | 18 |

**Table 6.** (continued)

| | | Source of variation | | |
| --- | --- | --- | --- | --- |
| | | Stocking Level | Replication | Stocking x Rep. |
| Percent change in species composition | | | | |
| Acer saccharum | | | | |
| | F-statistic | 0.07 | 1.29 | 1.60 |
| | P-value | 0.929 | 0.299 | 0.218 |
| Betula alleghaniensis | | | | |
| | F-statistic | 4.39 | 1.48 | 2.15 |
| | P-value | 0.028 | 0.254 | 0.117 |

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**Table 6.** (continued)

| | | Source of variation | | |
| --- | --- | --- | --- | --- |
| | | Stocking Level | Replication | Stocking x Rep. |
| Stem density | | | | |
| trees ≥ 11 cm | | | | |
| | *F-statistic* | 3.93 | 2.86 | 0.64 |
| | *P-value* | 0.038 | 0.083 | 0.639 |
| trees ≥ 50 cm | | | | |
| | *F-statistic* | 14.83 | 2.71 | 0.50 |
| | *P-value* | 0.001 | 0.094 | 0.738 |
| trees ≥ 70 cm | | | | |
| | *F-statistic* | 5.81 | 0.91 | 2.41 |
| | *P-value* | 0.011 | 0.422 | 0.087 |

**Table 6.** (continued)

| | | Source of variation | | |
|---|---|---|---|---|
| | | Stocking Level | Replication | Stocking x Rep. |
| DWD volume | | | | |
| | *F-statistic* | 5.05 | 2.00 | 2.06 |
| | *P-value* | 0.018 | 0.164 | 0.129 |
| | | | | |
| DWD large end diameter | | | | |
| | *F-statistic* | 4.83 | 0.31 | 0.40 |
| | *P-value* | 0.021 | 0.740 | 0.808 |
| | | | | |
| Snag density | | | | |
| | *F-statistic* | 0.39 | 1.19 | 0.65 |
| | *P-value* | 0.685 | 0.327 | 0.637 |

**Table 6.** (continued)

| | | Source of variation | | |
|---|---|---|---|---|
| | | Stocking Level | Replication | Stocking x Rep. |
| Snag density by size | | | | |
| snags > 30 cm | | | | |
| | *F-statistic* | 4.70 | 0.81 | 0.77 |
| | *P-value* | 0.023 | 0.459 | 0.561 |
| snags < 30 cm | | | | |
| | *F-statistic* | 4.75 | 1.54 | 1.21 |
| | *P-value* | 0.022 | 0.242 | 0.339 |
| Snag basal area | | | | |
| | *F-statistic* | 10.01 | 0.95 | 0.88 |
| | *P-value* | 0.001 | 0.406 | 0.494 |

**Table 6.** (continued)

| | | Source of variation | | |
|---|---|---|---|---|
| | | Stocking Level | Replication | Stocking x Rep. |
| Snag volume | | | | |
| | *F-statistic* | 13.55 | 1.43 | 1.83 |
| | *P-value* | 0.001 | 0.264 | 0.167 |
| Regeneration density | | | | |
| 2.5-11cm DBH, > 1m tall | | | | |
| | *F-statistic* | 2.57 | 0.48 | 1.08 |
| | *P-value* | 0.105 | 0.626 | 0.394 |
| < 2.5cm DBH, > 1m tall | | | | |
| | *F-statistic* | 1.84 | 2.84 | 1.20 |
| | *P-value* | 0.187 | 0.085 | 0.343 |
| | | | | |

**Table 6.** (continued)

| | | Source of variation | | |
|---|---|---|---|---|
| | | Stocking Level | Replication | Stocking x Rep. |
| Regeneration density (continued) | | | | |
| 0.5-1m tall | | | | |
| | *F-statistic* | 0.43 | 0.11 | 1.36 |
| | *P-value* | 0.655 | 0.900 | 0.287 |
| 0-0.5m tall | | | | |
| | *F-statistic* | 1.21 | 0.36 | 1.34 |
| | *P-value* | 0.322 | 0.704 | 0.293 |
| | | | | |
| Average annual mortality in % BA | | | | |
| | *F-statistic* | 1.63 | 0.53 | 1.39 |
| | *P-value* | 0.223 | 0.600 | 0.278 |

**Table 6.** (continued)

| | | Source of variation | | |
|---|---|---|---|---|
| | | Stocking Level | Replication | Stocking x Rep. |
| Proportion of DWD by decay | | | | |
| Decay 1 | | | | |
| | *F-statistic* | 0.17 | 1.70 | 0.77 |
| | *P-value* | 0.845 | 0.210 | 0.558 |
| Decay 2 | | | | |
| | *F-statistic* | 0.81 | 0.29 | 2.98 |
| | *P-value* | 0.460 | 0.751 | 0.048 |
| Decay 3 | | | | |
| | *F-statistic* | 0.13 | 0.01 | 0.16 |
| | *P-value* | 0.883 | 0.987 | 0.958 |

**Table 6.** (continued)

| | | Source of variation | | |
|---|---|---|---|---|
| | | Stocking Level | Replication | Stocking x Rep. |
| Proportion of DWD by decay (cont.) | | | | |
| Decay 4 | | | | |
| | *F-statistic* | 0.37 | 2.04 | 1.02 |
| | *P-value* | 0.695 | 0.159 | 0.423 |

# CHAPTER 2


# FIGURES

**Figure. 1.** Diameter distributions for all treatments and measurement periods at the Dukes Experimental Forest, MI. Curves represent the best fitted regressions using adjusted $r^2$ and RMSE following Janowiak et al. (2008).
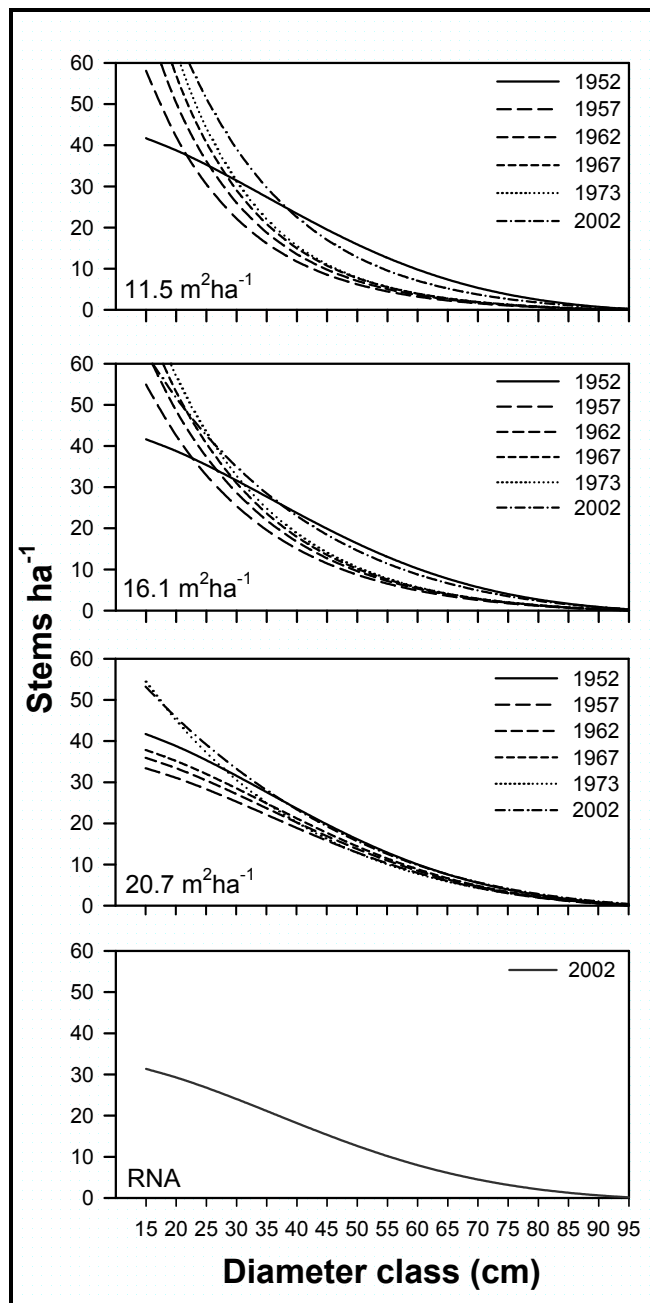
**Figure. 2.** Volume of downed woody debris by treatment at the Dukes Experimental Forest, MI. Error bars represent standard errors, n = 9. Columns with the same letters were not significantly different, p = 0.05.
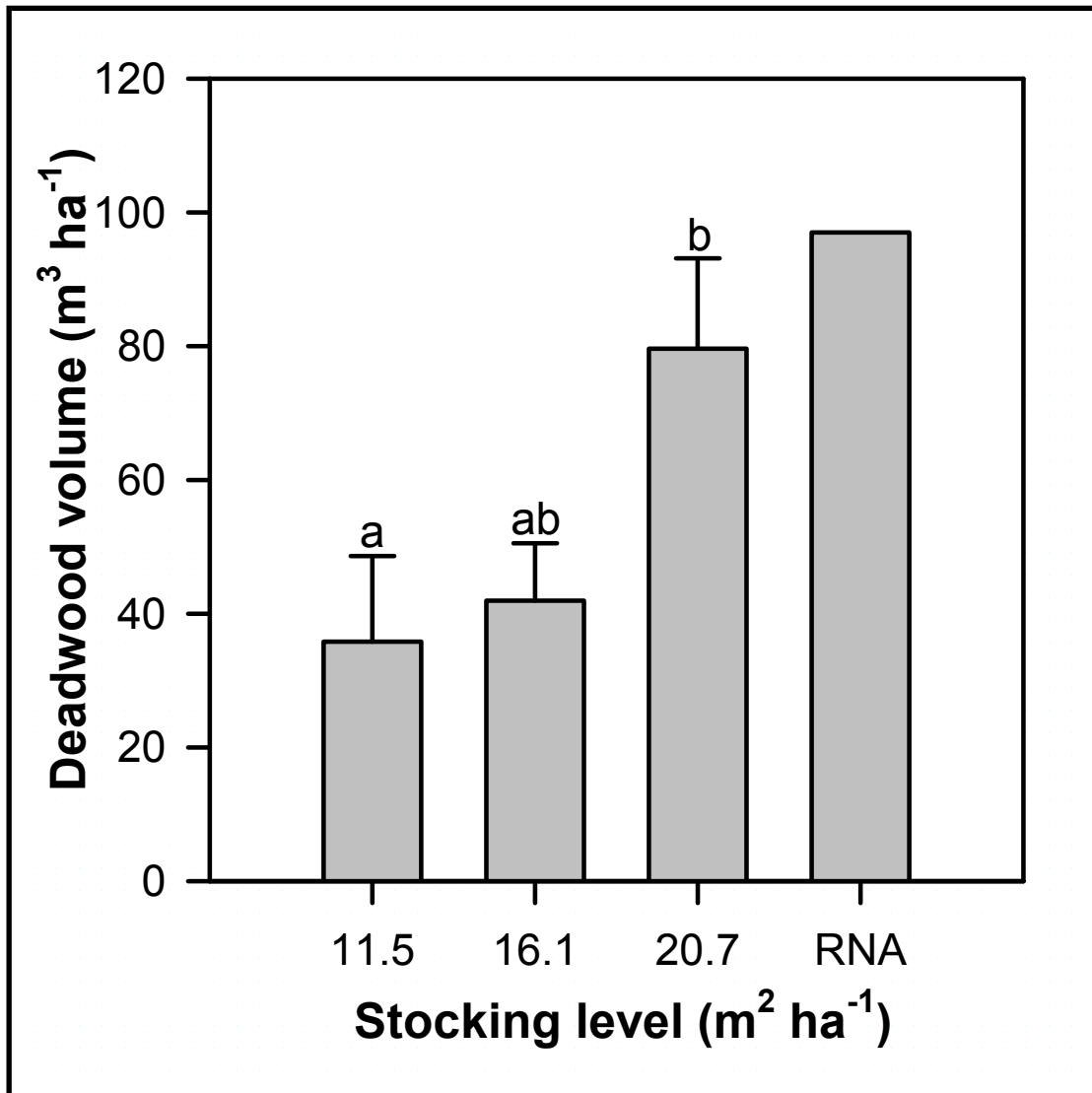
**Figure. 3.** Number of large (≥ 30 cm DBH) and small (< 30 cm DBH) snags across treatments within the Dukes Experimental Forest, MI in 2008. Error bars represent standard errors, n = 9. Columns for each size class with the same letters were not significantly different, p = 0.05. The total number of snags between treatments were not significantly different, p = 0.05.
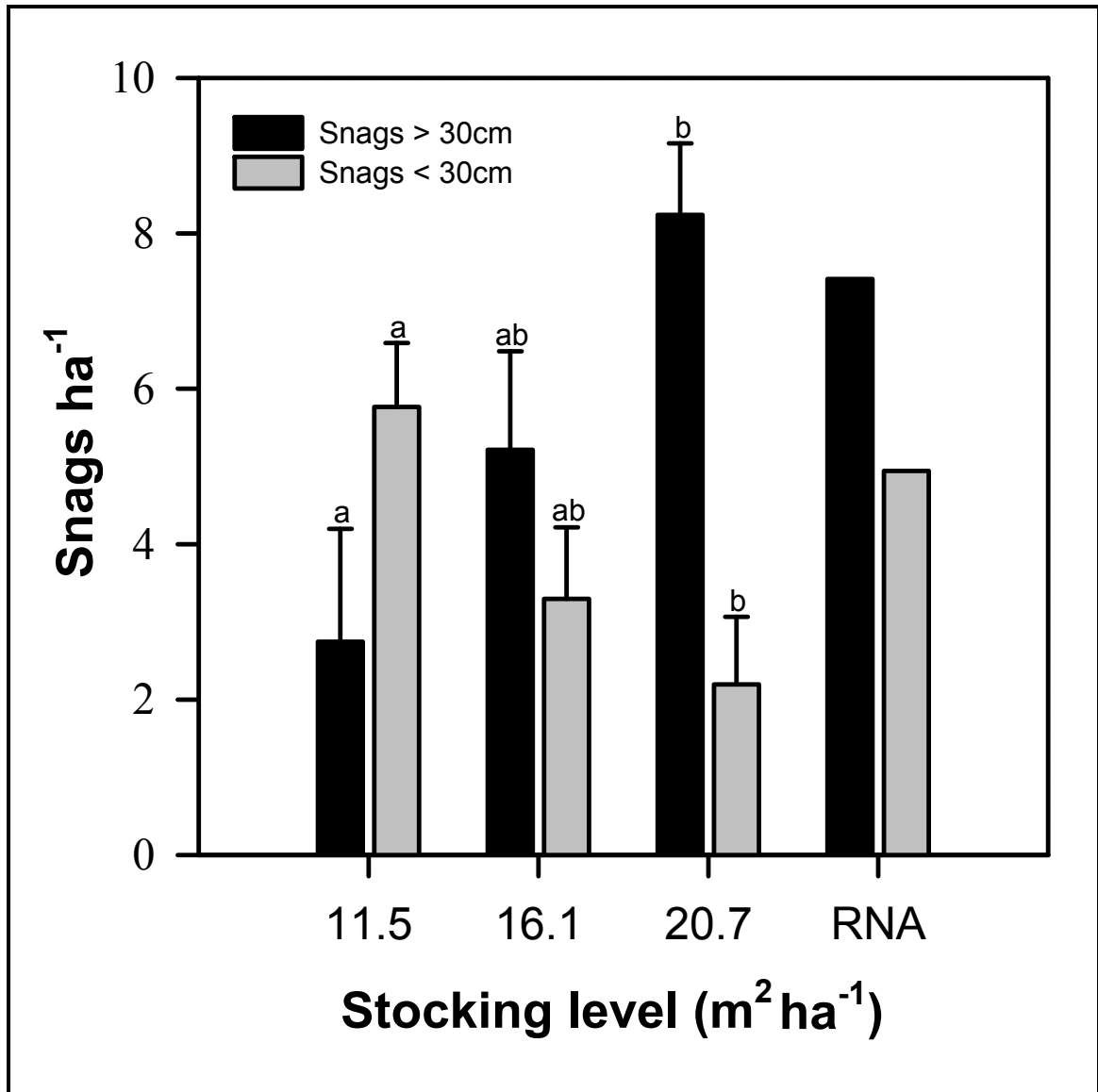
**Figure. 4.** (a) Basal area and (b) volume of snags across treatments at the Dukes

Experimental Forest, MI in 2008. Error bars represent standard errors, n = 9. Columns

with the same letters were not significantly different, p = 0.05.
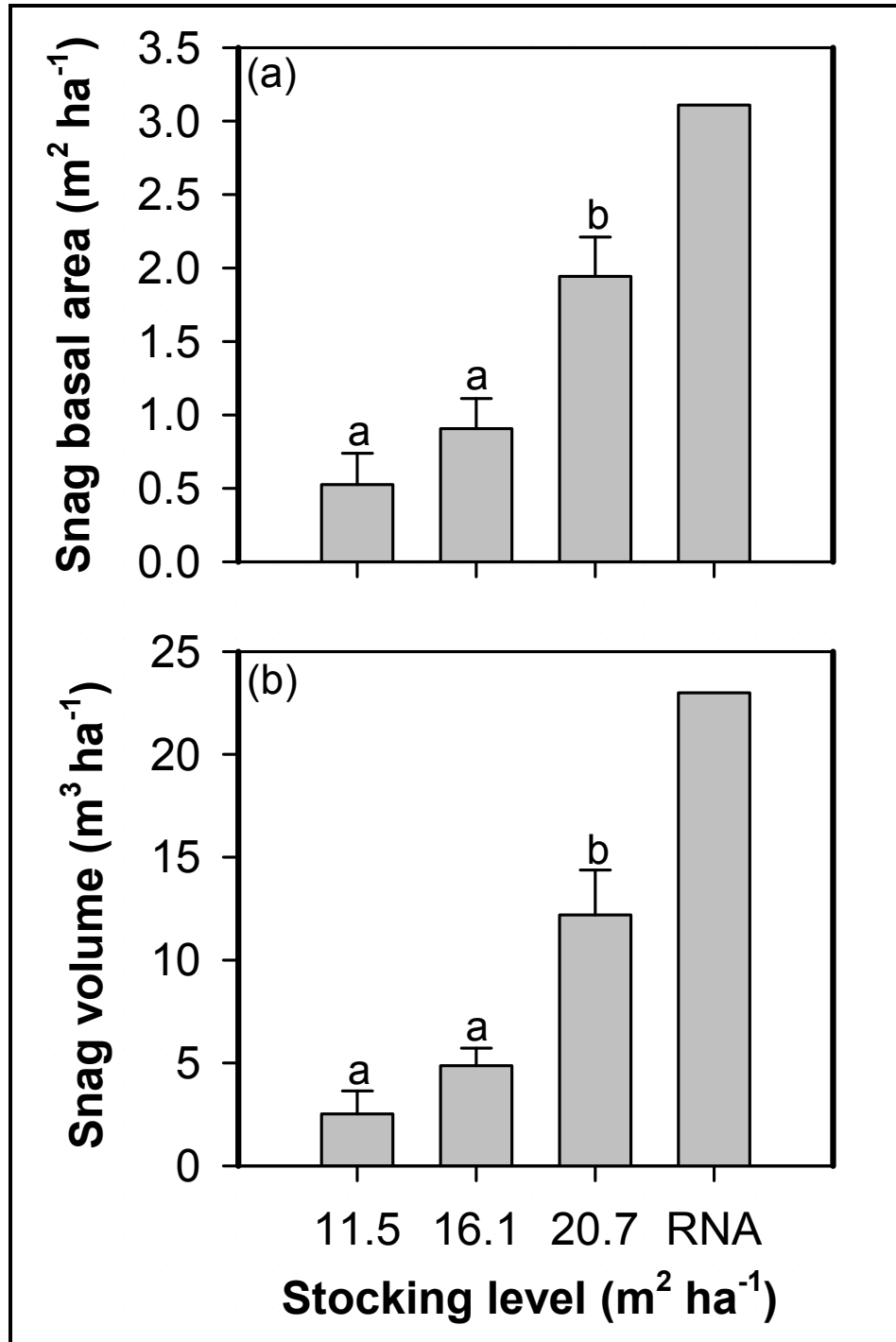
**Figure. 5.** Nonmetric multidimentional scaling (NMS) ordination of treatment stands and an old-growth forest (RNA) benchmark in 2008. The percentage of the ordination explained by each axis is given in parentheses. Stands (treatments and RNA) are indicated by the legend symbols. Vector length represents the explanatory power of stand stocking level in explaining the variation in stand structure among treatments stands and the RNA.
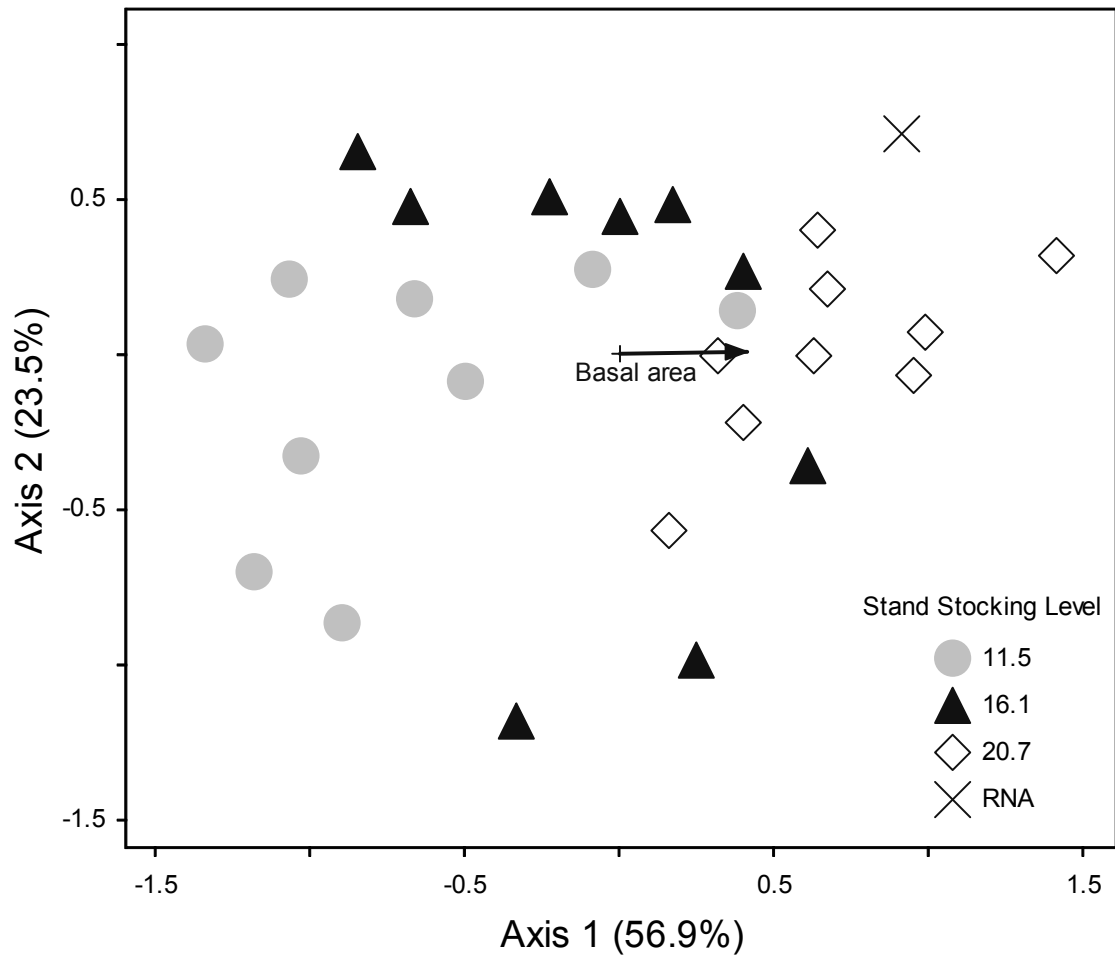
**CHAPTER 3**

**RELATIONSHIPS BETWEEN GROWTH, QUALITY, AND STOCKING**

**WITHIN MANAGED OLD-GROWTH NORTHERN HARDWOODS**

**Introduction**

Selection-based silvicultural systems are a widely implemented approach to the

management of forests around the globe (e.g. Knuchel 1953, Assman 1970; O'Hara

1996; Nyland 2007). A central component to the successful implementation of selection

systems is an understanding of the long-term effects of different cutting strategies on tree

growth and quality development (Nyland 1998). In particular, the quality of trees

produced in stands managed using uneven-aged systems strongly influences the

economic value of the extractable timber products and is therefore an important aspect of

the economic viability of this management approach (Niese et al. 1995). As such,

management regimes that improve tree quality have been suggested as a means to

provide additional potential income to landowners, while also increasing the standing

value of the forest on a given property (Nyland 2003). Tree growth also has an important

influence on tree quality (Strong et al. 1995), and the impacts of cutting strategies (e.g.,

cutting cycle, stocking level) on growth of residual trees is a fundamental component of

management regimes designed to improve product yield. Nonetheless, important

tradeoffs exist between the growth and quality of individual trees and the overall

production of a forest stand (Long 1985).

Traditionally, one of the fundamental aims of selection silviculture has been the

improvement of tree quality (Eyre and Zillgitt 1953; Arbogast 1957; Blum and Filip

1963; Tubbs 1977; Guldin and Fitzpatrick 1991). A number of tree quality improvement

goals are included in guidelines for selecting residual crop trees in selection stands

(Arbogast 1957; Trimble Jr. 1974; Nyland 2007), including the removal of dying or

defective trees, the retention of a substantial volume of large vigorous crop trees, and the

removal of low value or high risk species. Despite the emphasis on tree quality development in selection silviculture guidelines, few studies have rigorously evaluated the long-term influence of single-tree selection using different stand stocking levels on tree quality. Studies of hardwood tree grade have often been limited to studies of second-growth forests that have been converted to uneven-aged stands, or stands managed using diameter-limit cutting (Erdmann 1986; Strong et al. 1995; Leak and Sendak 2002). Moreover, those studies that have examined these factors have been limited to short-term experiments, second-growth stands, and/or small treatment areas leaving key knowledge gaps regarding how different stocking levels affect the residual quality of uneven-aged stands (Godman and Books 1971; Sonderman and Rast 1987; Strong et al. 1995). Due to the extended time periods over which uneven-aged stands are managed, evaluations of quality development in long-term silvicultural experiments may provide useful insights into factors affecting quality development in stands managed using selection systems.

Many selection system management guides are based on relatively short-term field experiments and have resulted in stand structural targets thought to produce optimum sustained yields (Pearson 1942; Eyre and Zillgitt 1953; Arbogast 1957; Leak et al. 1969; Baker et al. 1996). In most cases, these guides have been based on a reverse-J shaped target distribution shape and have allocated growing space among diameter classes by utilizing stocking control through application of the BDq approach (Meyer 1943, see review in O'Hara and Gersonde (2004)). Several theoretical and simulation studies have highlighted that structures based on the allocation of basal area to diameter classes can produce optimum yields in stands managed using selection systems (Adams and Ek 1974; Hansen and Nyland 1987); however, few long-term empirical evaluations

of growth and productivity based on stocking control through residual density management in selection systems exist.

Several hypotheses have been proposed to explain the relationships between gross production and stocking levels within forest stands (Langsaeter 1941; Assman 1970; Smith et al. 1997). In most cases, these relationships between stocking level and stand production have been evaluated in even-aged stands (e.g., Curtis and Marshall 1993, Gilmore et al. 2005, Pretzsch 2005, D'Amato et al. 2010); however, principles between growing space occupancy and stand-level productivity are readily transferable to uneven-aged stand structures. For example, O'Hara (1996) found that physiological constraints on the growth of multi-aged ponderosa pine were similar to those found in even-aged forests, demonstrating that the biological maximum in growth and productivity is related to stand occupancy, regardless of stand age or structure.

O'Hara and Gersonde (2004) outlined several approaches for controlling stocking in uneven-aged forest stands that have been demonstrated or proposed with varying degrees of success. The commonly applied BDq, or Q-factor approach, has been applied frequently and uses a strict but simple approach to regulating basal area stocking by defining a strict target (reverse J) diameter distribution to ensure a continual supply of both timber and growing stock in each cohort (Meyer 1952, Nyland 2007). The plenter system has been used extensively in central Europe and builds on the BDq approach but allows for more flexibility in the actual stand structure, with the goal of having a constant volume output at each cutting (O'Hara and Gersonde 2004; Schütz 2001). Leaf area allocation using a leaf area index (LAI) has been hypothesized as a method of stocking control in uneven-aged forests (O'Hara 1996). O'Hara and Gersonde (2004) emphasize

that all stocking control systems in uneven-aged stands are tools to design sustainable structures, and that these structure depend on the silvicultural objective.  An evaluation of stocking level relationships using long-term data from selection experiments in the context of these approaches may help us to further refine our understanding regarding growing stock relationships in uneven-aged stands.

To better understand how single-tree selection affects tree growth and quality, I utilized the results of a long-term silvicultural study in the Upper Peninsula of Michigan, USA that examined single-tree selection harvests in managed old-growth northern hardwoods over a 57-year period.  This study provided a unique opportunity to assess the long-term effects of single-tree selection on the growth and quality of primary northern hardwoods across several residual stocking levels.  The objectives of this study were (1) to evaluate the effects of 57 years of single-tree selection on tree quality development within primary northern hardwoods and (2) to examine the relationships between residual stocking levels and growth rates in these stands, including tradeoffs between stand level and individual tree growth.  Based on the findings of work done in second-growth northern hardwood stands (Strong et al. 1995), I hypothesized that stands managed with lower residual basal areas would have higher average tree grade than stands managed at higher residual basal areas.  I further hypothesized that although average annual tree basal area growth would be greatest for stands managed at lower residual stand densities, stand-level basal area growth would be constant over a range of residual densities consistent with the predictions put forth by Langsaeter (1941) and translated by Smith et al. (1997).

**Materials and Methods**

*Study sites and treatments*

The study was established in 1952 at the Dukes Experimental Forest in the Upper Peninsula of Michigan, USA and was designed to examine the optimum stocking levels and cutting cycles for the production of high quality sawtimber using single-tree selection (Crow et al. 1981). Study treatments were established in a randomized complete block design within a sugar maple-dominated forest with limited history of human disturbance prior to the establishment of the experiment. Three blocks of ten treatment stands were established to compare the specific effects of single-tree selection in old-growth stands using different residual stocking levels and cutting cycles. The treatment combinations included three cutting cycles (5, 10, and 15 years) combined with three residual stocking levels of 11.5, 16.1, and 20.7 $m^2$ $ha^{-1}$ of residual basal area in trees greater than 24 centimeters in diameter. One additional treatment of a 20-year cutting cycle at 6.9 $m^2$ $ha^{-1}$ of residual basal area (in trees > 24 cm) was also established in each replication. Each treatment unit is 4 to 6 hectares in size and contains 6 to 17 0.08 hectare permanent circular plots. Detailed descriptions of the study sites and treatment histories were given in chapter 2 of this thesis.

*Field measurements*

All trees on the plots greater than 11 centimeters in diameter were inventoried for diameter and species prior to the establishment of treatments and every five years thereafter until 1972-74, when the cutting cycles portion of the study was abandoned. An additional stocking level treatment application occurred in 1986 in one replication, but data was not collected at that time. Renewed interests in the long-term effects of the

treatments spurred re-measurement of the plots in 2002-2004. Additionally, a subset of 5 plots per treatment was randomly selected in 2008 for measurement of tree quality (see methods below). Also at that time, 5 additional plots of the same design as those in the treatments were established in the uncut hardwood section of the Dukes Research and Natural Area (RNA). The close proximity of this relatively undisturbed old-growth forest and its nearly identical composition and structure as the treatment forest prior to cutting makes it an ideal benchmark for comparison to the treated stands in terms of tree quality.

Tree quality was assessed using a grading method that evaluates the value of individual hardwood trees, while leaving the trees on the stump. Grading systems developed by the U.S. Forest Service in the 1950s and field guides for evaluation of tree grade serve as useful tools that allow foresters to estimate the value of timber in their stands by examining the external characteristics of the butt logs of the individual trees (Hanks 1976; Vaughan 1966; Miller et al. 1986). In the summer of 2008 I measured tree grade per Miller et al. (1986) on all trees > 11cm on the 5 randomly selected sub-plots in each treatment and the RNA. Evaluation of tree grade is a process that uses a dichotomous key (Miller et al. 1986) to evaluate the quality of a tree's second best face on the best 3.7 meter section of the butt (base) 4.9 meter log section of the tree. The key uses tree diameter size class as the first deduction in grade followed by a series of deductions for surface defects, taper, species and form (Miller et al. 1986). The result is a numerical grade for tree quality - 1 being the highest quality, 2 and 3 progressively lower, and "below grade" trees being the lowest.

*Statistical analysis*

The effects of cutting cycle length and stocking level on mean tree grade, diameter growth, and average annual stand basal area growth were evaluated using mixed model analysis of variance (ANOVA). Initial ANOVA results indicated no significant cutting cycle effects, so I chose to focus solely on stocking level. By eliminating cutting cycle and examining only stocking levels as treatments, the number of sample units were increased from $n = 3$ to $n = 9$ in the 11.5, 16.1, and 20.7 $m^2$ $ha^{-1}$ stocking levels with $n = 3$ in the 6.9 $m^2$ $ha^{-1}$ stocking level treatment. Correspondingly, ANOVAs according to the following model were used:

$$Y_{ij} = \mu + R_i + T_j + RT_{ij} + E_{ij}$$

where $Y$ is the sample average for the treatment, $\mu$ is the overall mean, $R_i$ is the effect of the $i$th replication, $T_j$ is the effect of the $j$th treatment, $RT_{ij}$ is the interaction between the $i$th replication and the $j$th treatment, and $E_{ij}$ is the residual error. The difference in the number of sample units among treatments ($n = 3$ for the 6.9 $m^2$ $ha^{-1}$ treatment and $n = 9$ for the other treatments) resulted in an unbalanced design. Correspondingly, a mixed model analysis with Type III fixed effects was used (SAS version 9.1, SAS Institute Inc., 2004), as this is the preferred method for analyzing data with an unequal number of observations in each sample unit (Shaw and Mitchell-Olds 1993). Tukey-Kramer multiple comparison tests were run to determine where specific significant differences existed between treatments (SAS version 9.1, SAS Institute Inc., 2004). A mixed-model repeated-measures ANOVA was also performed to examine the stand and average tree basal area growth between the different measurement periods. The following model was used in this analysis:

$$Y_{ijk} = \mu + P_i + T_j + PT_{ij} + R_k + E_{ijk}$$

where $Y$ is the sample average for the treatment, $\mu$ is the overall mean, $P_i$ is the effect of the $i$th measurement period, $T_j$ is the effect of the $j$th treatment, $PT_{ij}$ is the interaction between the $i$th measurement period and the $j$th treatment, $R_k$ is the random effect of the $k$th replication, and $E_{ijk}$ is the residual error.

Because tree size is one of the primary determinants of hardwood tree grades (Miller *et al.*1986), the distribution of trees in each grade were examined by diameter class. The diameter classes were chosen to reflect the minimum sizes necessary for a tree to reach a particular grade, i.e. a tree must reach 24.4, 32.0, and 39.6 cm to qualify as a grade 3, 2, and 1 tree, respectively. As such, I analyzed the distributions of trees separately within three corresponding size classes; 24.4 – 31.8 cm, 31.9 – 39.6 cm, and greater than 39.6 cm. This analysis allowed me to examine changes between the distributions of an observed grade in the context of the highest grade possible in a particular size class. Distributions were analyzed using Kolmogorov-Smirnov tests, a non-parametric test that allows for comparisons between two sample distributions (SAS version 9.1, SAS Institute Inc., 2004). Within individual size classes, each treatment distribution was compared iteratively with all the other treatment distributions to detect differences.

Average annual basal area growth was calculated for the entire 50 year period after initial treatment. Residual growth (the total growth for all trees that survived from one measurement period to the next), ingrowth, gross growth (residual + ingrowth), and mortality were calculated for all measured trees by diameter class using the same size classes as the quality analyses mentioned above. The mean annual diameter growth was

also calculated for the entire 50 year period for all treatments by the same diameter classes.

Although mean annual growth rates were analyzed in an ANOVA framework, I felt that an additional analysis of the growth rates in the context of a continuum of stand measurement periods was warranted because of the range of residual stand stocking levels observed at different measurement periods. To explore these relationships between tree and stand growth and stocking levels more thoroughly, I calculated stand density index (SDI) for all twelve individual sample units at each measurement period in the study. SDI has been widely used as a means to assess relative stand density in fully stocked pure even-aged stands (Reineke 1933), but has also been adapted for use in uneven-aged stands (Stage 1968; Long and Daniel 1990; Shaw 2000). I calculated the SDI of all twelve sample units at all measurement periods using the additive method for uneven-aged stands found in Woodall and Fiedler (2005). I then used the highest SDI found in the any of the sample units at any measurement period as the highest known density ($SDI_{max}$) and calculated a standardized stand density index (SSDI); (Pretzsch 2005), which is the ratio of a given stand SDI relative to $SDI_{max}$, to allow for comparisons of periodic growth of trees and stands at different relative densities. Because of the wider range of tree sizes and ages found within uneven-aged versus even-aged stands, I broke down the analysis of growth-growing stock relationships by the diameter-classes mentioned above to determine the relative contribution of each size class to stand-level growth.

**Results**

*Tree quality*

Mean tree grade in 2008 was not significantly different (p = 0.05) among

treatments (Table 1).  Mean tree grade ranged from 2.75 to 2.92 in the treated stands and

was only slightly lower in grade than the unmanaged RNA (2.97; Table 1).  There were

limited differences among treatments and the RNA in the proportion of trees in each

grade, within different diameter classes (Table 2). There were no significant differences

(p = 0.05) among treatments in the 24.4 - 31.8 cm size class (Table 2a), while the

distribution of tree grades in the 32.0-39.6 cm size class differed significantly between

the unmanaged RNA and the managed stands (Table 2b).  In particular, there was a

greater proportion of below grade trees and a lower proportion of grade 3 trees in this size

class in the unmanaged RNA compared to the managed stands (Table 2b).  For trees

greater than 39.6 cm, there were greater proportions of trees in grades 1 and 2 and fewer

grade 3 and below grade trees in the managed stands, relative to the RNA (Table 2c);

however, only the comparison between the RNA and the 6.9 $m^2$ $ha^{-1}$ treatment was

significant (Table 2c).


*Tree and stand growth*

Overall annual diameter growth ranged from 0.22 cm to 0.36 cm per year (Table

3).  Mean annual tree diameter growth differed significantly across stocking level

treatments (Table 3).  For all diameter classes, annual growth was greatest in the 6.9 $m^2$

ha$^{-1}$ and 11.5 m$^2$ ha$^{-1}$ residual stocking level treatments, and decreased as the sawtimber residual stocking level increased (Table 3).  There was no significant difference between the 6.9 m$^2$ ha$^{-1}$ and 11.5 m$^2$ ha$^{-1}$ residual stocking level treatments in any of the diameter classes.  The 20.7 m$^2$ ha$^{-1}$ treatment had significantly less diameter growth than the other treatments in all diameter classes.

As with average individual tree growth, average stand-level basal area growth also differed among stocking level treatments over the period from 1952 to 2002. Residual growth in the smallest two diameter classes was greatest in the 6.9 m$^2$ ha$^{-1}$ and 11.5 m$^2$ ha$^{-1}$ residual stocking level treatments although differences were very slight (Table 4a,b).  Residual growth in the largest trees (trees > 39.6 cm) was greatest in the 16.1 m$^2$ ha$^{-1}$ and 20.7 m$^2$ ha$^{-1}$ residual stocking level treatments (Table 4c).   Ingrowth was greatest in the 6.9 and 11.5 m$^2$ ha$^{-1}$ residual stocking level treatments in the smallest two size classes (Table 4a,b).  Across all size classes, the 20.7 m$^2$ ha$^{-1}$ treatment had significantly lower ingrowth than the other three stocking level treatments (Table 4). Gross growth in the smallest two diameter classes showed significant decreases as stocking level increased (Table 4a,b).  For the largest diameter class, the only significant difference was greater gross growth in the 16.1 m$^2$ ha$^{-1}$ treatment over the other stocking level treatments (Table 4c).  Average annual basal area mortality was similar among all size classes and all treatments (Table 4).  The only significant differences in mortality were related to higher levels of mortality in the largest diameter classes in the highest stocking level treatments (Table 4c).

Results of the repeated-measures ANOVA indicated that patterns in average annual tree and stand basal area growth were related to stocking level and measurement

period (Table 5). A significant interaction between stocking level and treatment period was also detected for average annual stand basal area growth (Table 5); this resulted from a lag in growth response in the 20.7 $m^2$ $ha^{-1}$ treatment compared to the other stocking levels (Figure 1). During the active treatment period from 1957-1972, both individual tree and stand growth showed significant stocking level effects, with growth inversely related to stocking level (Figure 1).

Average annual stand basal area growth varied as a function of relative stand density across all treatments and was generally greatest at stand densities between 40 and 75 percent SSDI (Figure 2). Examinations of these trends by diameter class indicated that percentage of basal area growth accounted for by a given size class varied as a function of stand stocking (Figure 3). In trees 11.4 cm to 24.3 cm there was a decrease in the percent of stand basal area growth as relative density increased, with a very small proportion of the growth being accounted for by this size class at the highest stocking levels (Figure 3a). The 24.4 cm to 39.6 cm tree size class constituted a relatively constant and moderate proportion of total stand growth across stocking levels (Figure 3b), whereas, the proportion of average annual stand basal area growth accounted for by the largest size class (i.e., > 39.6 cm) strongly increased with increasing relative density (Figure 3c).

Individual tree basal area growth generally declined as stand stocking increased (Figure 4). In the smallest trees (11.4 cm - 24.3 cm) there were very low rates of individual tree growth, particularly as relative stand density increased (Figure 4a). A similar trend could also be observed in the 24.4 cm – 39.6 cm diameter size class (Figure 4b) although the total average annual tree growth was slightly higher than those observed

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in the smallest size class (Figure 4a).  Trees in the largest size class had greater growth

rates than either of the smaller size classes at the lowest stocking levels, with growth in

this size class also declining significantly as relative stand density increased (Figure 4c).

**Discussion**

My findings indicate that several applications of single-tree selection over a 50-

year period have had limited effect on tree quality development within previously

unmanaged old-growth northern hardwood systems.  Although some level of change was

apparent in the number of trees moving from lower to higher grades in comparison to the

unmanaged stands, overall mean grade was relatively unaffected by residual stocking

levels.  In contrast, individual and stand-level growth was strongly related to stocking

level and the contrasting relationships observed between individual tree growth, stand-

level growth, and relative density were consistent with the tradeoffs Long (1985) outlined

between these parameters.  Due to the importance of individual tree growth in developing

tree quality within stands managed using single-tree selection, these tradeoffs need to be

considered when assessing the long-term impacts of this management approach on

residual stand quality and growth.


*Quality development*

My hypothesis that stands managed at lower stocking levels would show strong

quality improvement was unsupported by the data (Table 1, Table 2).  In particular, I

expected that the removal of defective trees at each  harvest  would allow smaller crop

trees to develop into larger high quality trees as the treatments progressed; a trend

documented by Strong et al. (1995) in their examination of single-tree selection in

second-growth northern hardwoods in Wisconsin. The failure to find a similar trend within my study is likely due to several factors, including differences in sampling methodology, the initial conditions of stands, and possibly the number of entries into the stands. In particular, Strong et al. (1995) were able to track grade development over time, at two periods during treatment application, whereas I assumed that each stand had a similar distribution of tree grades at the onset of the experiment. In addition, the stands examined in this study were unmanaged, old-growth northern hardwoods at the onset of the experiment, whereas the second-growth sites examined by Strong et al. (1995) were 45-years old when treatment applications began. Correspondingly, the ability to affect quality development within the second-growth stand was likely much greater due to the younger age and high amount of potential crop trees to choose from within these young stands.

Despite the failure to detect any changes in mean grade across different stocking levels, there was some evidence that these treatments have affected the distribution of tree grades within stands (Table 2), particularly when compared to the unmanaged RNA. Early descriptions of old-growth northern hardwoods in the upper Great Lakes region estimated that below grade trees often made up as much as 40 percent of the growing stock within a stand (Eyre and Zillgitt 1953). The percentage of below grade trees above 31.9 cm dbh documented within the unmanaged RNA is consistent with these estimates and it is likely that the removal of poor quality trees in the managed stands reduced the number of below grade trees relative to the RNA. This decrease in below grade trees was most pronounced in the largest size class (trees > 39.5 cm), where a significant reduction in below grade trees and a corresponding increase in grade 1 trees was observed relative

to the unmanaged RNA. This shift in the distribution may be due to the removal of defective trees (Kenefic and Nyland 2007), and the growth of better quality residual trees into the larger size classes over the 50 year study period.

*Tree and stand-level growth responses to stocking level treatments*

As expected, the greatest mean annual diameter growth rates occurred within the lowest stocking level treatments (Assman 1970; Smith et al. 1997; Zhang and Oliver 2006), reflecting the higher levels of resources available to residual trees in these stands. Similarly, I observed a general decline in individual tree basal area growth and increased mortality with increasing stand stocking, consistent with the idea that increased inter-tree competition at higher stand densities cause a decline in individual tree vigor (Drew and Flewelling 1979). In particular, I observed maximum rates of individual tree growth at low to moderate stand densities and decreasing mean individual tree growth as density increased, regardless of size-class examined, except in trees in the 24.4 cm – 39.6 cm diameter class where reduced basal area growth also occurred at very low densities. (Figure 4). By comparison, the trends in stand-level growth demonstrated little variation in stand basal area production across a wide range of stand densities (Figure 2). Only at very low or high stand densities was stand growth at its lowest (Figure 2).

The relationships between stand-level growth and stocking I observed have important implications for tree grade distributions within managed stands of old-growth origin. In particular, there was no significant difference in grade between the stocking level treatments (Table 2), suggesting that stands of this type maintained at stocking levels optimum for stand level production may not exhibit an appreciable difference in

stem quality. Despite the relatively high levels of stand and individual tree growth observed at the lowest two stocking levels (i.e, 6.9 and 11.5 $m^2$ $ha^{-1}$), these are not residual stocking levels typically recommended for managing northern hardwood stands using selection systems. As such, some loss of individual tree growth and quality improvement is likely under the typical, higher densities commonly recommended for use in selection systems (Arbogast (1957) recommends 15 to 17 $m^2$ $ha^{-1}$ in 25 cm and greater trees). Nonetheless, it is important to note the degree to which tree growth declines from 60 to 100 percent of maximum stand density (Figure 4). At these high stand densities, where residual stocking was greatest, individual tree growth declined in all size classes.

Although the approaches presented by Reineke (1933) and Long (1985) for density management were intended for even-aged stands, the data from this study may be useful as a "practical approach" in uneven-aged stands where density management is significantly more complex (Long and Daniel 1990; Nyland 2007), and silvicultural goals may include either maximizing volume production, increasing the value in the residual growing stock (i.e. quality), or even the recruitment and/or retention of structural components such as large diameter trees for future sources of dead wood (Franklin et al. 2007). My study results, as well as those from other recent studies, lend support to the idea that stocking control using Reineke's (1933) SDI approach may be a valid tool in the management of uneven-aged stands, where different silvicultural goals must be balanced to meet a variety of objectives (Long and Daniel 1990; Cochran 1992; Woodall and Fiedler 2005).

Despite the overall decline in individual tree growth documented at higher stocking levels, I observed varying degrees of stand growth in different size classes

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(Figure 3), with the larger trees accounting for a relatively greater proportion of stand-level growth, particularly at higher stocking levels. The differences in relative production patterns observed are likely related to differences in resource availability between large trees and suppressed smaller trees in these stands. Although I did not attempt to quantify growth dominance (*sensu* Binkley 2004), the stands in my study were generally displaying patterns of positive growth dominance in which larger trees exhibit proportionally greater growth than small trees (Binkley 2004; Bradford et al. 2010). Bradford et al. (2010) demonstrated that in even-aged *Pinus resinosa* stands allocation of resources, and thus reduction in growth dominance, was greatest in thinned versus unthinned stands. By comparison, I observed a greater proportion of growth in the largest trees in the highest stocking level stands (Figure 3c), and the most even allocation of growth among size classes in the lowest stocking level stands (Figure 3a, b, c). These differences might be due to the significant crown overlap in shade tolerant trees within uneven-age stand structures that allows for significant layering of both foliage and rooting depth (Curtis 1970; Goodburn and Lorimer 1999; O'Hara and Nagel 2006). Although the largest trees in these stands may be less efficient in terms of resource use on an individual level (Smith and Long 2001; Seymour and Kenefic 2002), the multi-layered nature of uneven-aged stands composed of shade tolerant trees may allow for relatively efficient resource use, even at high stand densities due to the juxtaposition of more efficient smaller trees underneath the largest trees (Bourne 1951; O'Hara and Nagel 2006).

Whether thinning increases total production in forest stands is a continuing debate in the literature that has been explored in considerable depth (Smith et al. 1997; Zeide

2001; Pretzsch 2005). Langsaeter (1941), Mar:Moller (1947), and others assert that optimum production can occur over a wide range of residual stand densities, and therefore moderate thinning simply redistributes resources to the remaining trees. Assman (1970) on the other hand observed that the residual trees in some stands underwent a lag in growth response, which he supposed was a physiological response to being suppressed for such a long period. His observations, which were confirmed by a set of robust experiments in even-aged Douglas-fir by Curtis (1997), highlighted that as stand density increased, total stand volume production similarly increased. Taken together, both views suggest that in order to maximize production, stands should be managed at an optimum stocking level that is generally less than the biological maximum, but more than a minimum critical threshold where total stand production is reduced (Mar:Moller 1947; Assman 1970; Pretzsch 2005). The actual optimum stocking level in Assman's (1970) observations often depended on stand age, site quality and composition; but tended to follow a similar pattern where the optimum growth increment was achieved at some density above a minimum threshold and below maximum stocking. In this study, it appears that optimum growth occurred between 50-80% SSDI (Figure 2, 3). This range of stocking conditions corresponds to the recommendations outlined by Eyre and Zillgitt (1953) and Crow et al. (1981) for this forest type. Specifically, they recommended stocking levels at or near 16.1 $m^2$ $ha^{-1}$, although with appropriate cutting cycle lengths residual stocking levels of 11.5 $m^2$ $ha^{-1}$ and 20.7 $m^2$ $ha^{-1}$ may also be warranted, particularly if other silvicultural goals such as increased stand structural complexity are objectives of management (see Gronewold et al. 2010).

I suggest here that there is a biological maximum in growth and productivity that is related to stand occupancy in uneven-aged stands under a variety of structures. Although there appears to be a range of stand densities which maintain optimum stand growth in this study, it is important to recognize the relative constancy of growth across the range of stocking levels examined. At multiple stand densities, there exists a tradeoff in the relative allocation of growing space and resource availability as illustrated in Figure 3. O'Hara (1996) noted that in uneven-aged stands, growing space, and thus resource availability can be shifted from tree to tree and from cohort to cohort across cutting cycles without sacrificing stand productivity. The trends documented in Figure 3 highlight that different size classes make up similar proportions of growth except at the highest stand densities. When basal area is removed from the stand, growth is shifted towards the smaller diameter classes, confirming that resources may be shifted amongst cohorts (Figure 3). Importantly, as stated previously, a relatively constant level of growth can be maintained at a variety of stand densities as this shift occurs (Figure 2). O'Hara (1996) also suggested that allocation of too much, or even equal allocation of resources to the smaller diameter classes would be wasted in multi-cohort stands as many of the smaller diameter trees would succumb to mortality in a self-thinning process. As demonstrated in Gronewold et al. (2010), multiple stand structures occurred over time in the stands examined in this study; however, analysis of growth trends from these stands (Figure 2; Table 4) suggest that optimum growth was achieved at a variety of residual stocking levels despite the lack of a constant stand structure. The data from this study, taken in this context, supports the idea that equal allocation of resources among diameter classes in uneven-aged stands (i.e. strict control over stand structure using a q-factor) is

not necessary to support sustainable recruitment of trees into higher diameter classes, nor is it necessary to support optimum growth (O'Hara 1996; O'Hara et al. 2001; Webster and Lorimer 2003).

**Conclusions**

As selection systems become a more utilized method of management of forests in North America (O'Hara et al. 2001), the need for an adequate understanding of the expected outcomes, both from an ecological and economic standpoint is becoming increasingly important. Correspondingly, well-monitored long-term experiments such as the one presented here are invaluable for understanding the effectiveness of a particular silvicultural system at meeting diverse forest management objectives. My findings suggest that although tradeoffs can exist between individual tree quality, tree growth, and stand growth, the relatively small range in overall growth at different residual stand densities provides a general flexibility that allows for the achievement of multiple management goals and objectives over time. If increased individual tree growth is the desired outcome then managing at lower residual stocking levels will likely produce the desired results while maintaining a sustainable yield. If other silvicultural goals requiring higher residual stocking levels in stands of similar condition (e.g. increased structural complexity via the presence of large trees, large coarse woody debris, etc) are desired, management at higher stocking levels can still support an acceptable amount of production – the tradeoff being less individual tree growth and less growth in the suppressed cohorts. Furthermore, the findings of this study lend further support to the utility of extending the largely even-aged concepts of density management, leaf area

allocation, and growth dominance to the management of uneven-aged stands using

selection systems (Long 1985; O'Hara 1996; Binkley 2004).

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# CHAPTER 3

# TABLES

**Table 1.**  Mean tree grade in for the various treatments and the RNA (Research and

Natural Area) in 2008 at the Dukes Experimental Forest, MI.  Numbers in parentheses

represent standard errors, n = 3 for the 6.9 m$^2$ ha$^{-1}$ treatment, all other treatments n = 9.

Treatments with the same letter within each variable were not statistically different at p =

0.05.

| Stocking Level (m$^2$ ha$^{-1}$) | Mean Tree Grade 2008 |
|---|---|
| 6.9 | 2.75 (0.07)*a* |
| 11.5 | 2.92 (0.04)*a* |
| 16.1 | 2.89 (0.04)*a* |
| 20.7 | 2.90 (0.04)*a* |
| RNA | 2.97 |

**Table 2.** Distribution of the proportion of trees in each grade by size class (2008) at the Dukes Experimental Forest, MI. Stocking level treatments with the same letters did not have significantly different distributions of tree grades at p = 0.05.

| Diameter class (cm) | Tree grade | Stocking Level (m² ha⁻¹) | | | | |
|---|---|---|---|---|---|---|
| | | 6.9 | 11.5 | 16.1 | 20.7 | RNA |
| (a)24.4 – 31.8 | | *a* | *a* | *a* | *a* | *a* |
| | Grade 1 | n/a | n/a | n/a | n/a | n/a |
| | Grade 2 | n/a | n/a | n/a | n/a | n/a |
| | Grade 3 | 65.6 | 67.9 | 68.5 | 61.1 | 66.6 |
| | Below Grade | 34.4 | 32.1 | 31.5 | 38.9 | 33.3 |
| | | | | | | |
| (b)31.9 – 39.6 | | *a* | *a* | *a* | *a* | *b* |
| | Grade 1 | n/a | n/a | n/a | n/a | n/a |
| | Grade 2 | 35.0 | 27.4 | 26.8 | 22 | 36.4 |
| | Grade 3 | 42.5 | 48.1 | 53.5 | 55 | 18.2 |
| | Below Grade | 22.5 | 24.4 | 19.7 | 22.9 | 45.5 |
| | | | | | | |
| (c)> 39.6 | | *a* | *ab* | *ab* | *ab* | *b* |
| | Grade 1 | 35.3 | 22 | 20.4 | 20.4 | 16.2 |
| | Grade 2 | 22.4 | 24 | 27.2 | 23.8 | 13.5 |
| | Grade 3 | 23.5 | 29.1 | 22.3 | 30.4 | 35.1 |
| | Below Grade | 18.8 | 24.8 | 30.1 | 25.4 | 35.1 |

**Table 3.** Mean annual diameter growth 1952 – 2002 by size class at the Dukes

Experimental Forest, MI. Numbers in parentheses represent standard errors, n = 3 for the

6.9 $m^2$ $ha^{-1}$ treatment, all other treatments n = 9.   Treatments with the same letter within

each variable were not statistically different at p = 0.05.

| Stocking Level ($m^2$ $ha^{-1}$) | Mean annual diameter growth (cm year$^{-1}$) |
|---|---|
| **(a)Trees 11.4 cm to 24.3 cm** | |
| 6.9 | 0.30 (0.02) *a* |
| 11.5 | 0.29 (0.01) *a* |
| 16.1 | 0.26 (0.01) *b* |
| 20.7 | 0.22 (0.01) *c* |
| **(b)Trees 24.4 cm to 39.6 cm** | |
| 6.9 | 0.35 (0.01) *ab* |
| 11.5 | 0.35 (0.01) *a* |
| 16.1 | 0.30 (0.01) *b* |
| 20.7 | 0.26 (0.01) *c* |
| **(c)Trees > 39.6 cm** | |
| 6.9 | 0.35 (0.02) *a* |
| 11.5 | 0.36 (0.02) *ab* |
| 16.1 | 0.33 (0.01) *b* |
| 20.7 | 0.27 (0.01) *c* |

**Table 4.** Mean annual residual growth, ingrowth, gross growth, and mortality from 1952 – 2002 for each treatment by size class at the Dukes Experimental Forest, MI. Numbers in parentheses represent standard errors, n = 3 for the 6.9 m$^2$ ha$^{-1}$ treatment, all other treatments n = 9. Treatments with the same letter within each variable were not statistically different at p = 0.05.

| Stocking Level (m$^2$ ha$^{-1}$) | Residual growth | Ingrowth | Gross growth | Mortality |
|---|---|---|---|---|
| **(a) Trees 11.4 cm to 24.3 cm (m$^2$ ha$^{-1}$ year$^{-1}$)** | | | | |
| 6.9 | 0.07 | 0.09 | 0.17 | 0.02 |
| | (0.01) *a* | (0.02) *a* | (0.02) *a* | (0.01) *a* |
| 11.5 | 0.07 | 0.09 | 0.15 | 0.02 |
| | (0.01) *a* | (0.01) *a* | (0.01) *b* | (0.01) *a* |
| 16.1 | 0.06 | 0.06 | 0.12 | 0.01 |
| | (0.01) *b* | (0.01) *b* | (0.01) *b* | (0.01) *a* |
| 20.7 | 0.05 | 0.05 | 0.10 | 0.01 |
| | (0.01) *b* | (0.01) *c* | (0.01) *c* | (0.01) *a* |
| **(b) Trees 24.4 cm to 39.6 cm (m$^2$ ha$^{-1}$ year$^{-1}$)** | | | | |
| 6.9 | 0.07 | 0.15 | 0.22 | 0.02 |
| | (0.01) *a* | (0.01) *a* | (0.01) *a* | (0.01) *a* |
| 11.5 | 0.07 | 0.16 | 0.22 | 0.02 |
| | (0.01) *a* | (0.01) *a* | (0.01) *a* | (0.01) *a* |
| 16.1 | 0.06 | 0.12 | 0.18 | 0.01 |
| | (0.01) *ab* | (0.01) *b* | (0.01) *b* | (0.01) *a* |
| 20.7 | 0.06 | 0.09 | 0.15 | 0.02 |
| | (0.01) *b* | (0.01) *c* | (0.01) *c* | (0.01) *a* |
| **(c) Trees > 39.6 cm (m$^2$ ha$^{-1}$ year$^{-1}$)** | | | | |
| 6.9 | 0.08 | 0.18 | 0.26 | 0.02 |
| | (0.02) *a* | (0.01) *a* | (0.02) *a* | (0.01) *ab* |
| 11.5 | 0.12 | 0.17 | 0.29 | 0.02 |
| | (0.01) *b* | (0.01) *a* | (0.01) *a* | (0.01) *a* |
| 16.1 | 0.15 | 0.18 | 0.33 | 0.04 |
| | (0.01) *c* | (0.01) *a* | (0.01) *b* | (0.01) *b* |
| 20.7 | 0.16 | 0.14 | 0.30 | 0.07 |
| | (0.02) *c* | (0.01) *b* | (0.01) *a* | (0.01) *c* |

**Table 5.** Summary of type 3 fixed effects, including source of variation, degrees of

freedom for both numerator and denominator, F-values and probability values for the

repeated measures of stand growth and tree growth at all inter-treatment periods at the

Dukes Experimental Forest, MI.

| Source of variation | d.f. (numerator) | d.f. (denominator) | Stand growth $(m^2\ ha^{-1}\ yr^{-1})$ | | Tree growth $(m^2\ ha^{-1}\ yr^{-1})$ | |
|---|---|---|---|---|---|---|
| | | | $F$ | $P$ | $F$ | $P$ |
| Stocking | 3 | 8 | 8.58 | $\leq 0.007$ | 5.10 | $\leq 0.029$ |
| Year | 4 | 32 | 65.04 | $\leq 0.001$ | 91.76 | $\leq 0.001$ |
| Stocking x Year | 12 | 32 | 2.88 | $\leq 0.008$ | 1.50 | $\leq 0.177$ |

# CHAPTER 3


# FIGURES

**Figure 1.** (a) Gross annual stand basal area growth and (b) mean individual tree basal area growth for the four treatments at each measurement period at the Dukes Experimental Forest, MI . Error bars represent standard errors, n = 3 for the 6.9 m$^2$ ha$^{-1}$ treatment, all other treatments n = 9.
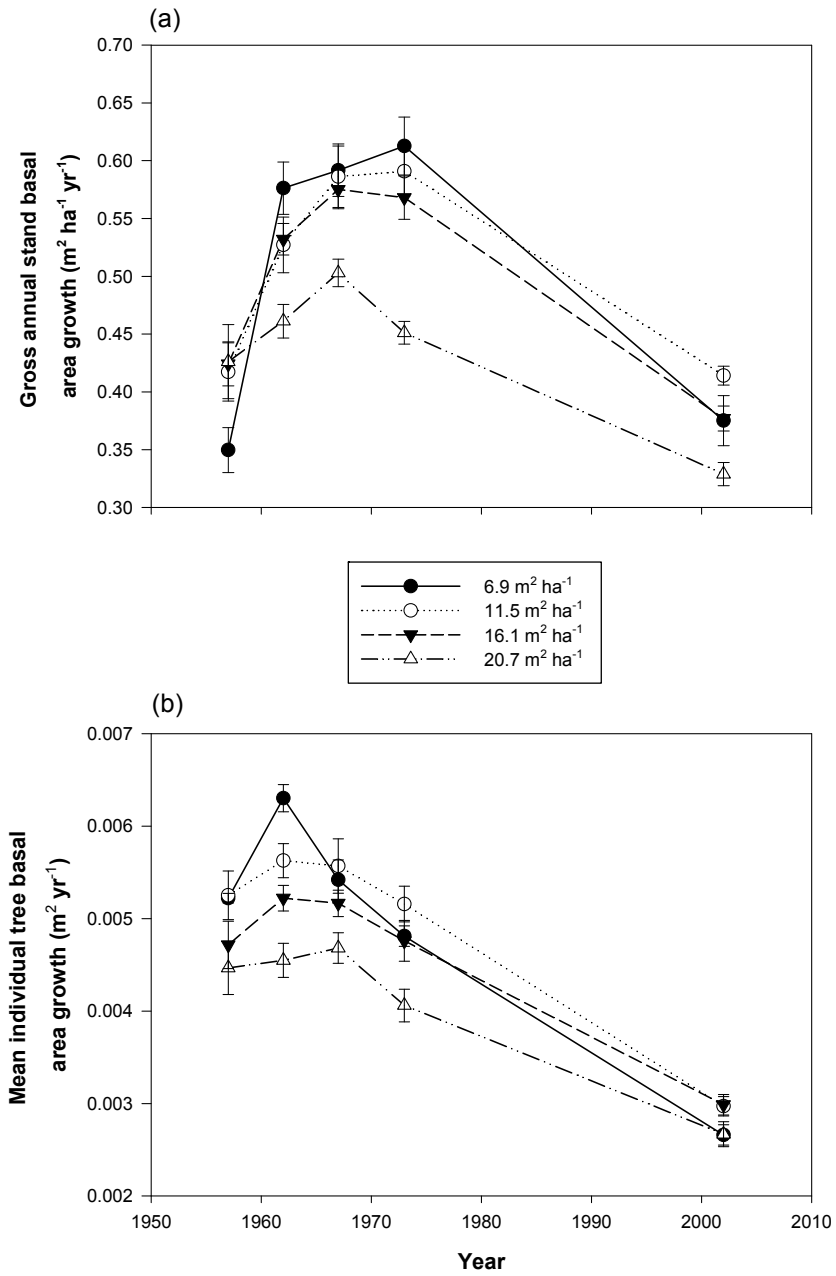
**Figure 2.** Mean annual stand basal area growth for the stands in the four treatments as a function of %SDI$_{max}$ for all measurement periods and trees 11 cm and greater in diameter at the Dukes Experimental Forest, MI .
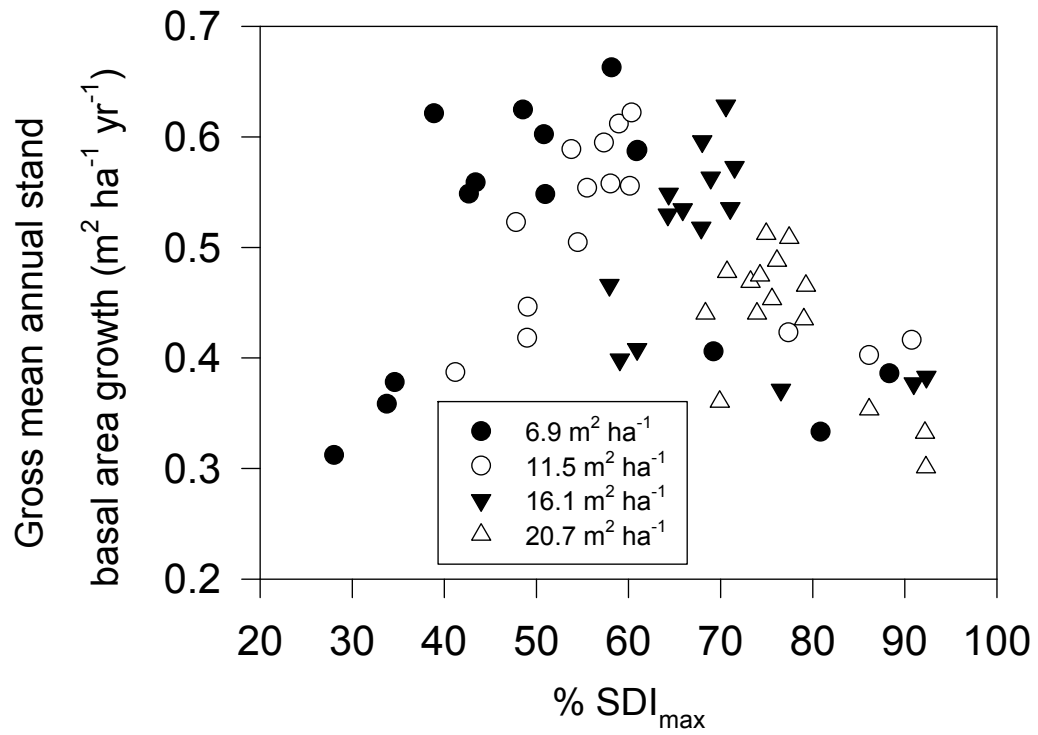
**Figure 3.** Percentage of mean annual stand basal area growth as a function of $\%SDI_{max}$ within the (a) 11.4-24.3 (b) 24.4-39.6, and (c)> 39.6 cm size classes for all treatment stands and measurement periods at the Dukes Experimental Forest, MI . Curves represent the best fit of the data



Panel (a) Trees 11.4 - 24.3 cm
$R^2 = 0.67, P < 0.001$
$y = -9.0528 + 2.3102x - 0.04074x^2 + 0.000203x^3$

Panel (b) Trees 24.4 - 39.6 cm
$R^2 = 0.18, P < 0.001$
$y = 36.4362 - 0.08140x$

Panel (c) Trees > 39.6 cm
$R^2 = 0.64, P < 0.001$
$y = 33.6378 - 0.03868x + 0.003040x^2$

Y-axis: % Mean annual stand basal area growth
X-axis: $\% SDI_{max}$
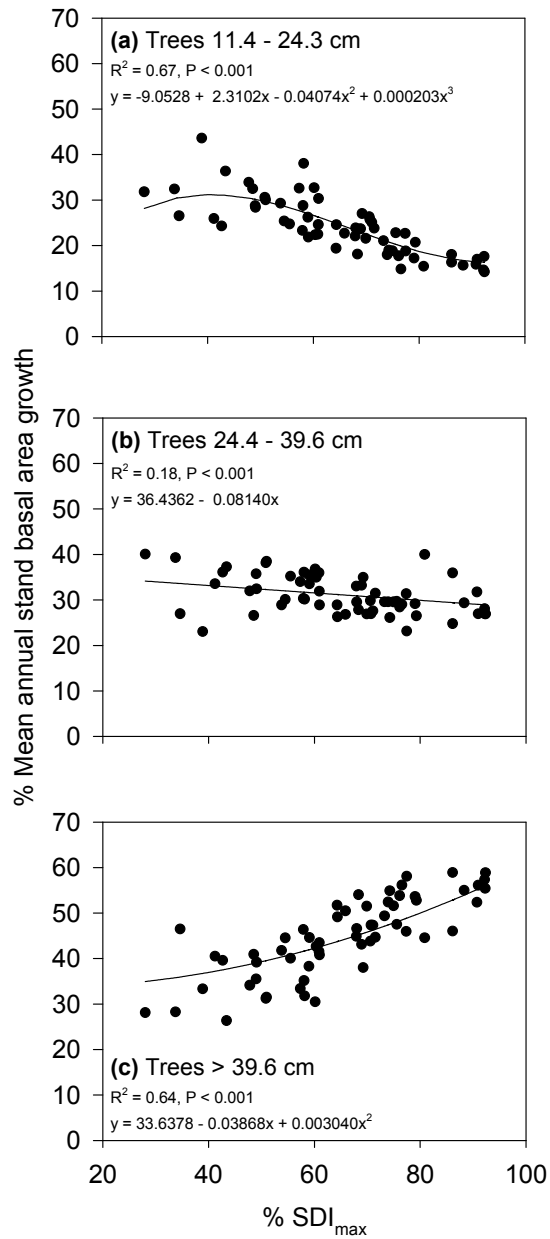
**Figure 4.** Mean annual tree basal area growth as a function of %$SDI_{max}$ within the (a) 11.4-24.3 (b) 24.4-39.6, and (c)> 39.6 cm size classes for all treatment stands and measurement periods at the Dukes Experimental Forest, MI . Curves represent the best fit of the data.



(a) Trees 11.4 - 24.3 cm
$R^2 = 0.86$, $P < 0.001$
$y = -0.00002 + 0.00031x - 5.8E\text{-}6x^2 + 2.676E\text{-}8x^3$

(b) Trees 24.4 - 39.6 cm
$R^2 = 0.80$, $P < 0.001$
$y = -0.01777 + 0.00149x - 0.00002x^2 + 1.106E\text{-}8x^3$

(c) Trees > 39.6 cm
$R^2 = 0.60$, $P < 0.001$
$y = 0.03260 - 0.00028x$

Mean annual tree basal area growth (m$^2$ yr$^{-1}$)

% $SDI_{max}$
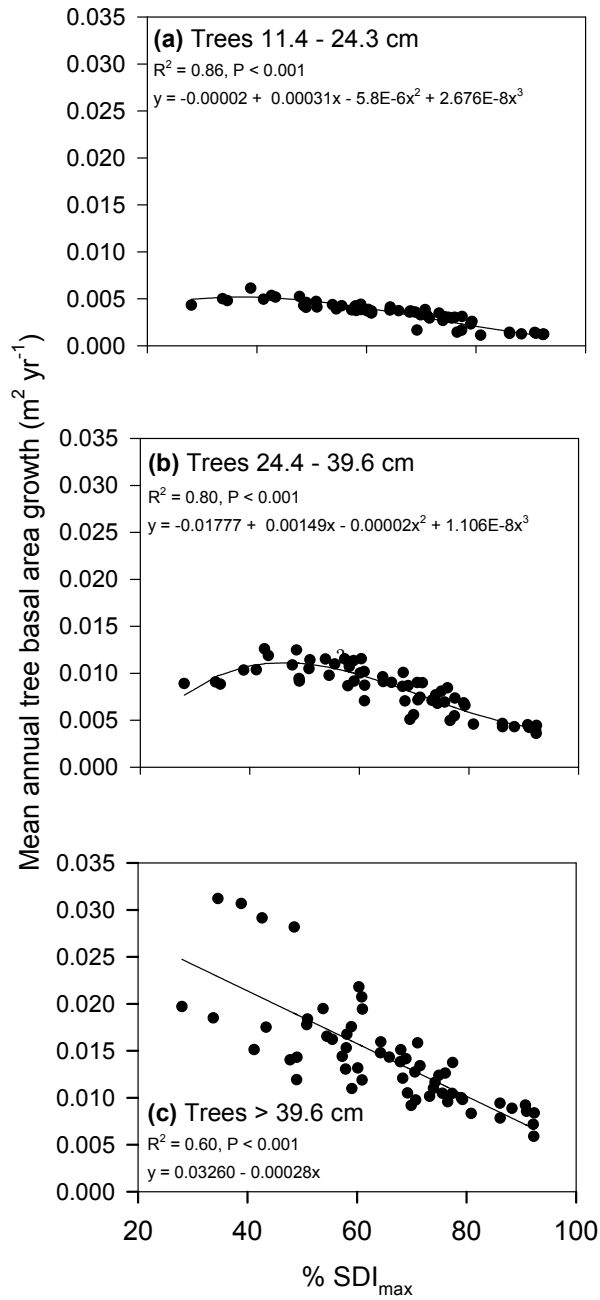
# CHAPTER 4

# THESIS CONCLUSION

Robust-long-term silvicultural experiments like the one examined in this thesis can be an invaluable source of scientific knowledge. The longevity of trees, particularly medium to long-lived trees, often makes it challenging to infer the long-term effects of management treatments on the development of forest ecosystems using short-term experiments. As demonstrated in the preceding chapters, detailed data collected on basic variables in forest systems such as tree species, diameter, and stand density can be adapted and utilized many years after the original intent of a study has already been accomplished. I was able to take a study designed to examine selection silviculture for maximizing growth and volume production over a twenty-year period, and re-examine the system after fifty years under an entirely different forest management paradigm. At the inception of the original study, the interest was primarily in maximizing production, but now forest managers are interested in both the value of extractable products, and the value of the ecological, social, and cultural functions of the forest (Seymour and Hunter 1999). Forest managers who must perform this balancing act are more likely to succeed if they have the kinds of detailed scientific knowledge that long-term studies like this one, which examined production ecology and quality as well as ecosystem complexity, provide.

In Chapter 2, I reported significant differences in the structural complexity of stands managed at higher residual stocking levels versus stands managed at lower residual stocking levels. Stands managed at the 20.7 $m^2$ $ha^{-1}$ residual stocking level, appeared significantly closer in structural complexity to the unmanaged RNA than stands managed at lower residual stocking levels. Additionally, the 20.7 $m^2$ $ha^{-1}$ treatment had

much less variability in diameter distribution forms than stands managed at lower residual stocking levels. I also observed a significant decline in the proportion of *Betula alleghaniensis* in all of the treatment stands suggesting that single-tree selection does not favor the reproduction of this species. The results presented in this chapter more or less indicate a gradient in ecological distance that corresponds with the stands in this study that were managed at higher residual stocking levels being the closest to the unmanaged state and proceeding further from this condition with decreased residual stocking.

In Chapter 3, I reported that mean tree grade was relatively unaffected by 50 years of treatment at different residual stocking levels using single-tree selection. I saw little evidence that variation in stocking level was having any effect on tree quality despite the fact that stands with lower relative stand densities showed more individual tree basal area growth than stands with greater relative stand densities. The expectation was that with greater individual tree growth I would observe a greater abundance of higher quality trees. Although I was unable to quantitatively determine the reason for not seeing this hypothesized result, I can speculate that in a younger stand, as opposed to the stands of old-growth origin examined in this study, the change in tree quality might still occur. In particular, my study stands had an abundance of large old trees that carried significant defects. Despite the lack of difference in mean tree quality, I did see a difference in the distribution of tree grades in the managed stands when compared to the unmanaged RNA, suggesting that the removal of defective trees throughout the study was increasing the proportion of higher quality trees in the stands. If the study treatments had continued, it is possible that a change in quality might still occur.

It is important to note that I observed a significant reduction in individual tree growth at the stand densities most commonly used in single-tree selection systems (60% SSDI and greater). Stand densities less than 60% SSDI only occurred in stands managed at 6.9 and 11.5 $m^2$ $ha^{-1}$. Although individual tree growth, and thus the greatest chance for quality development, is increased in stands managed with these stocking levels, they are generally not recommended in existing selection system guides for northern hardwoods. It is also important to note that changes were observed in the overall stand basal area growth of different size classes at different residual densities, with an optimum level of overall stand growth occurring between 50% and 80% SSDI for these stands. I observed stand growth that declined with increasing density in the smallest size class. Correspondingly, stand growth increased with increasing stand density in the largest size class. Together, these ideas suggest that managers can shift growth from cohort to cohort by manipulating stand density while maintaining an optimum and acceptable level of stand production.

Forest managers interested in increasing stand structural complexity in single-tree selection systems through the recruitment of snags, DWD, and large trees, should consider utilizing a high residual stand stocking level in their selection prescriptions. Replication of old growth forest conditions in managed forests may never be completely obtainable, or at the very least quite cost prohibitive to do so. Despite this, managers may be able to more closely replicate the stand structural characteristics found in unmanaged old growth through relatively simple modifications of traditional selection silviculture (Keeton 2006). For example, my study indicated that the increasing-q diameter distribution structure may be a useful target for managers seeking to enhance

structural complexity in their stands. Similarly, retention of snags and DWD are a common part of many contemporary management prescriptions, but where *recruitment* of additional large sized DWD and snags is desired, this may be achieved over time by utilizing higher stocking levels. This study indicated that selection systems in old-growth northern hardwoods using 20.7 $m^2$ $ha^{-1}$ will continue to maintain recruitment of DWD and snag levels approaching, although not completely equal to those found in an unmanaged state. As residual stocking decreases beyond this level, retention of these elements will decline. It is important to keep in mind however, that the stands in this study were old-growth at the onset of treatment and underwent a long period of no treatment prior to my measurements of structure complexity attributes. High stocking levels alone may not quickly achieve structural complexity goals, particularly in relatively young second-growth stands. As noted in Chapter 3, increased diameter growth in mid-sized trees will likely occur more quickly at lower residual stocking levels, and thus might provide sources of larger trees and other structural attributes related to large trees. Another important point is to note that the reduction of structural attributes is likely related to guidelines that suggest removing dead, dying, and diseased trees as part of a harvest. These recommendations likely do not apply if the goal is the enhancement or retention of stand structural complexity.

While stand structural complexity is certainly a leading priority for forest managers under the ecological forestry paradigm, very few managers will be exempt from producing an acceptable degree of value from extractable timber. This study further confirms that single-tree selection systems can provide a continuous supply of extractable timber at a variety of residual stand stocking levels. Of particular importance is that the

study has shown that known principles relating to even-aged stand density and growth can be translated to uneven-aged management using selection systems. For example, the tradeoff between individual tree growth and stand level growth is an important factor when a manger is making decisions regarding the goals for a particular stand, and was demonstrated in this study similar to Long's (1985) approach in even-aged stands. Also, stand density measures such as Reineke's (1933) stand density index are demonstrated successfully here as a tool to manage for optimum growth in uneven-aged stands. As shown in Chapter 2, managers using selection systems in uneven-aged northern hardwoods will be able to maintain constant and optimum production when utilizing residual stocking levels between 11.5 $m^2$ $ha^{-1}$ and 20.7 $m^2$ $ha^{-1}$ so long as active treatment is maintained and densities are not allowed to reach the biological maximum. Managers can use this range along with the knowledge that individual tree growth declines in all size classes as stand density increases. If a manager wants to increase individual tree growth, maintaining a stand at or less than 16.1 $m^2$ $ha^{-1}$ will be preferable to higher densities while still maintaining optimum stand production. This stand density will also shift some of the growth from the larger cohorts in the stand to the smaller size classes as suggested by O'Hara (1996). As density is increased beyond this level, more of the growth will be shifted back to the larger trees in the stand (Chapter 2 - Figure 3). This may be a valuable tool if the priority is not individual tree growth, but is rather the maintenance of stand structural attributes. In this case, managing near 20.7 $m^2$ $ha^{-1}$ residual stocking my be preferred, where the manager can lessen the ecological distance from an old-growth conditions, yet still maintain optimum growth in the stand.

From a practical standpoint, stocking control whether through the use of leaf area index, stand density index, plenter systems, or a Q-factor approach is an essential part of the implementation of single-tree selection systems.  Moreover, a sustainable stand structure is an important goal for any stocking control system (O'Hara and Gersonde 2004).  The experiment examined in this thesis shows considerable evidence that more than one type of structure can be sustainable in uneven-aged forests.  The multiple goals demanded under contemporary ecological forestry may require a variety of stand structures to be utilized depending on the needs of a manager.  Although widely known and commonly applied, the BDq system utilizing a strict Q-factor is not always the most appropriate stocking control system.  As demonstrated in this study, retention of large trees in selection systems for biological, economic, and aesthetic needs is a sustainable and appropriate practice where these goals are desired.  This study has shown that multiple stand structures and stand densities can be utilized to meet the diverse outcomes desired by contemporary forest managers.

There were several limitations to this study.  The origin of the stand being old growth resulted in considerable effects introduced by the presence of an abundance of very large old trees in the stand.  While this may be a desirable condition in many instances, it is not a very common condition in most managed stands, many of which are second-growth stands to which managers are seeking to re-introduce elements of stand complexity.  Similarly, I was limited by the inability to measure change in many structural attributes and tree quality due to the single point in time at which these variables were measured.  Being able to quantify change over time would have been advantageous in these analyses.  Also, the lack of a true control prohibited a thorough

comparison to an untreated state.  The RNA was a useful benchmark, but replication

throughout the life of the experiment would have added a level of robustness to the study.

Although the replication of treatments, size of the study, detailed measurements, and

similarity of site conditions created by the proximity of the replications to one another

were an outstanding research opportunity, this study was limited to some degree by the

nature of single-tree selection as a silvicultural system.  The disadvantages of single-tree

selection, including the favoring of shade tolerant species and loss of mid-tolerant

species, may outweigh the usefulness of the practice, particularly to managers seeking to

increase biological diversity to stands.  In this case, other partial harvesting techniques,

such as group selection or patch selection may be more promising.

Additional research opportunities relating to this study are abundant.  Most

simply, continuing to collect data at the Cutting Cycles and Stocking Levels experiment

at the Dukes Experimental Forest can continue to provide us with valuable long-term

scientific data on the effects of single-tree selection using different residual densities.  As

outlined in Chapter 3, our knowledge of the science of density management in uneven

aged forests still needs further exploration.  Continued measurement of even the most

basic variables such as species and diameter on the existing permanent plots will provide

additional useful information.  In light of the results of this study and the changes in the

forest management paradigm over the last fifty years, it will be advantageous to continue

collecting data on stand structural attributes and additional measures of stand complexity.

Further study might also include an analysis of the understory plant community or other

indicators of biological diversity.  Although the study stands were treated again using the

single-tree selection in 2008-2010, future treatments might be altered to attempt to re-

establish species diversity through the use of group selection or other tools that would

replicate the natural disturbance regime.  Undoubtedly, further exploration of stocking

level studies even beyond this experiment can provide useful insight into how forest

management effects both production and ecosystem function in managed forests.

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