



The influence of cutting cycle and stocking level on the structure and composition of managed old-growth northern hardwoods

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ABSTRACT

Forest management approaches are increasingly being focused on restoring or retaining structurally complex old forest conditions. Evaluations of the long-term impacts of different management regimes on the maintenance and restoration of these conditions are critical for informing and refining current management approaches. To this end, we examined the long-term effects of differing intensities of single-tree selection harvest on stand structural attributes within northern hardwood forests in the Upper Peninsula of Michigan, USA. Stands in this study were classified as old growth at the onset of the experiment and were repeatedly treated and maintained at three residual stocking levels (11.5, 16.1, and 20.7 m² ha⁻¹ in trees greater than 24 cm DBH) with three different cutting cycle lengths (5, 10, and 15 years) over a 57-year period. Conditions within an adjacent, unmanaged old-growth system were used as a benchmark for comparing stand structural attributes, including abundance of downed woody debris (DWD), regeneration, and large diameter trees.

Stand stocking level was the primary factor affecting the long-term trends in stand structure and composition observed among stands. In particular, stands maintained at a 11.5 m² ha⁻¹ stocking level had significantly lower amounts of DWD, snags, and large overstory trees compared to the 20.7 m² ha⁻¹ stocking level. Similarly, the highest stocking level treatment had the greatest abundance of *Betula alleghaniensis* relative to the other two stocking level treatments. In addition, long-term trends in diameter distribution forms indicated that the two highest stocking level treatments largely displayed increasing *q* and negative exponential curve forms over time, whereas the 11.5 m² ha⁻¹ stocking level was primarily characterized by concave distribution forms.

Ordination analyses of stand structural attributes indicated that stands managed with the highest residual stocking levels contained stand structural characteristics approximating those found within the unmanaged, old-growth benchmark stand, whereas the lowest stocking level was much less complex. These results suggest that single-tree selection systems that maintain high stand residual basal areas, a portion of which is made up of large diameter, below-grade, defective trees, could serve as a potential means to integrate or retain old-growth forest elements in managed stands.

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1. 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 20th 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 have also resulted in the deliberate removal

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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 the 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 > 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, the 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 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, we 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.

2. Methods

2.1. 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. Microtopography is dominated by pit-mounds which originate from past windthrow events (Beatty, 1981, 1984; Putz, 1983). 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% *A. saccharum*, 10% *Betula alleghaniensis* (yellow birch), <10% *Fagus grandifolia* (American beech) and <10% other species, including *Acer rubrum* (red maple), *Ostrya virginiana* (ironwood), *Abies balsamea* (balsam fir), *Tilia americana* (basswood), *Tsuga canadensis* (hemlock), and *Ulmus americana* (American elm).

2.2. 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 m²/ha of residual basal area in trees greater than 24 cm in diameter. One additional treatment of a 20-year cutting cycle at 6.9 m² ha of residual basal area (in trees >24 cm) was also established in each replication, but is not used in this study. Each treatment unit is 4–6 ha in size and contains 6–17, 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 1972–1974, 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 was 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, five 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.

2.3. 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° from vertical and DWD if more than 45°. 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 our 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 our estimates of downed DWD. We used four randomly oriented 100 m 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 (1–4) were assigned to all DWD based on the methods described in Fraver et al. (2002). Species was determined in the field for decay classes 1 and 2. The degree of decay for decay classes 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:

$$V = ((1/3)\pi L) \times (D_1^2 + D_2^2 + D_1D_2)$$

where V is volume (m³), 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 was 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:

$$V = \frac{(\pi^2 \sum d^2)}{8L}$$

where V is volume (m³), 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

Table 1

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

Treatment		Establishment cut ^a	2nd cut	3rd cut	4th cut	5th cut ^b
Stocking level (m ² ha ⁻¹)	Cutting cycle (years)					
11.5	5	1952–1954		1962–1964	1967–1969	1973–1974
11.5	10	1952–1954		1962–1964	1967–1969	1973–1974
11.5	15	1952–1954			1967–1969	
16.1	5	1952–1954	1957–1959	1962–1964	1967–1969	1973–1974
16.1	10	1952–1954		1962–1964	1967–1969	1973–1974
16.1	15	1952–1954			1967–1969	
20.7	5	1952–1954	1957–1959	1962–1964	1967–1969	1973–1974
20.7	10	1952–1954		1962–1964	1967–1969	1973–1974
20.7	15	1952–1954			1967–1969	

^a 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.

^b 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 online archive for type 3 fixed effects and associated p -values for ANOVAs).

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, *A. saccharum* and *B. 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, we 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.

2.4. 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 we 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, μ 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 was then re-run in 3-dimensional space, reducing model stress until the final instability in the NMS was effectively zero. The NMS was then examined visually in two 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 τ statistic (SAS version 9.1, SAS Institute Inc., 2004).

Following NMS analysis, we 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 non-parametric procedure that complements NMS well by testing the hypothesis that there are no differences between the treatment groups. We 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, we 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, DBH², and DBH³ 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 Janowiak 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.

3. Results

3.1. Long-term stand development

Changes in species composition in the managed stands were observed across all treatments over the entire study period. In particular, we 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 m² 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 our 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 m² 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 m² 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 m² 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).

Table 2Mean proportion of the density of the two most important tree species (*A. saccharum* and *B. alleghaniensis*) in each stocking level.

Stocking level (m ² ha ⁻¹)	1952		2002		% Change	
	% <i>Acer. sacch.</i>	% <i>Betula alleg.</i>	% <i>Acer sacch.</i>	% <i>Betula alleg.</i>	<i>Acer sacch.</i>	<i>Betula alleg.</i>
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) [†]

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 $p=0.05$, $n=9$.

3.2. 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 and 70 cm) compared to the lowest stocking level treatment and similar densities as the 16.1 m² ha⁻¹ treatment (Table 3). Stem density in the RNA was considerably 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 m² ha⁻¹ ($p=0.05$) and the 16.1 m² ha⁻¹ ($p=0.10$) treatments both had significantly lower volumes of DWD than the 20.7 m² ha⁻¹ treatment. The volume of DWD in the RNA (97.0 m³ 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 m² ha⁻¹ stocking treatment (Table 3). The average DWD large end diameters in the 11.5 m² 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 we 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 among the treatments

were quite heterogeneous spatially and temporally (assuming decay rate is constant).

The number of snags across treatments ranged from 8 ± 1.5 to 10 ± 1.6 snags ha⁻¹ (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 ha⁻¹, which was slightly higher although similar to the levels observed in the treated stands. We divided snags into two size classes (>30 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 and 20.7 m² 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 m² 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 (Fig. 4a and b).

There were no statistical differences in regeneration densities among treatments (Table 3). It is worth noting that although we 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

Table 3Average 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.

Variable	Stocking level (m ² ha ⁻¹)			
	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	N/A
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
Stem density (trees ha ⁻¹)				
Trees ≥ 11 cm	347 (11)a	315 (14)ab	307 (8)b	260
Trees ≥ 50 cm	38 (3)a	46 (3)ab	56 (1)b	64
Trees ≥ 70 cm	5 (1)a	8 (2)ab	11(1)b	10
Density (stems ha ⁻¹) of seedlings and saplings by size class				
2.5–11 cm DBH, >1 m tall	341 (55)a	468 (65)a	512 (40)a	628
<2.5 cm DBH, >1 m tall	566 (217)a	3430 (1850)a	1630 (774)a	4780
0.5–1 m tall	2330 (1240)a	2890 (1060)a	3890 (1260)a	4000
0–0.5 m tall	375,000 (58,600)a	329,000 (77,200)a	466,000 (52,000)a	133,000

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 (a and b) within each variable were not statistically different at $p=0.05$.

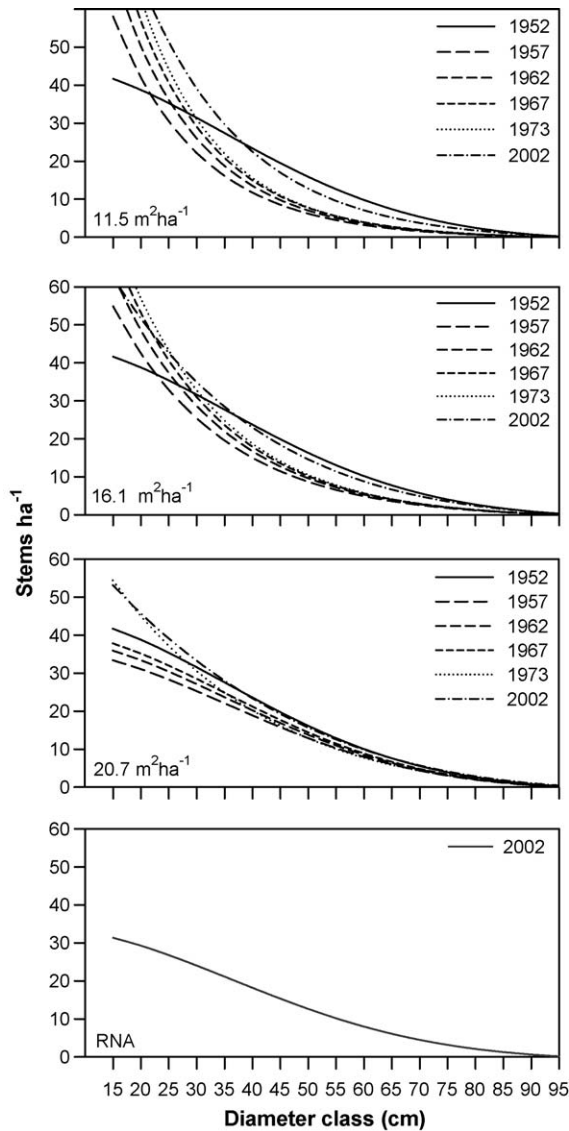


Fig. 1. Diameter distributions for all treatments and measurement periods at the Dukes Experimental Forest, MI. Curves represent the best fitted regressions using adjusted r^2 and RMSE following Janowiak et al. (2008).

variability observed on the plots in terms of seedling and sapling densities.

NMS ordination of the structural attributes was best explained by a 3-dimensional solution that explained 94.7% 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

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 ($m^2 ha^{-1}$)	Distribution shape					
	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 ^a

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

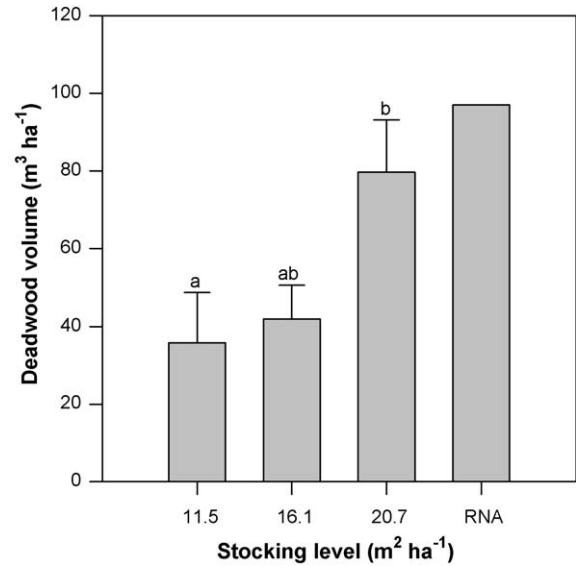


Fig. 2. Volume of downed woody debris by treatment at the Dukes Experimental Forest, MI. Error bars represent standard errors, $n = 9$. Columns with the same letters were not significantly different, $p = 0.05$.

a clear gradient in stands managed at the different stocking levels in the NMS, where stands managed at lower stocking (11.5 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 5). All structural attributes were found to be significantly correlated ($p = 0.05$) with at least one axis

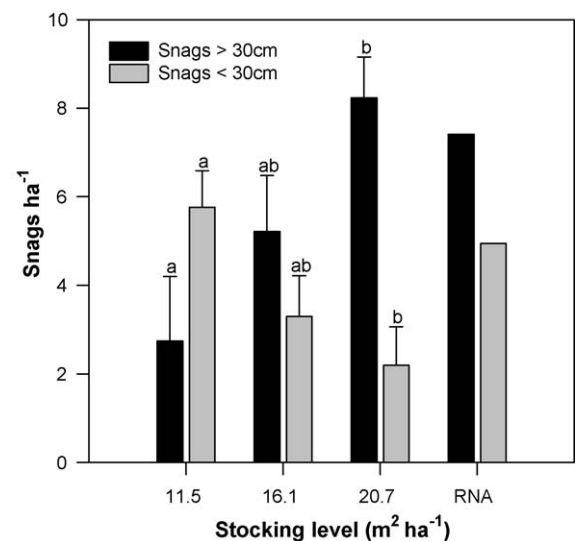


Fig. 3. Number of large (≥ 30 cm DBH) and small (< 30 cm DBH) snags across treatments within the Dukes Experimental Forest, MI in 2008. Error bars represent standard errors, $n = 9$. Columns for each size class with the same letters were not significantly different, $p = 0.05$. The total number of snags between treatments were not significantly different, $p = 0.05$.

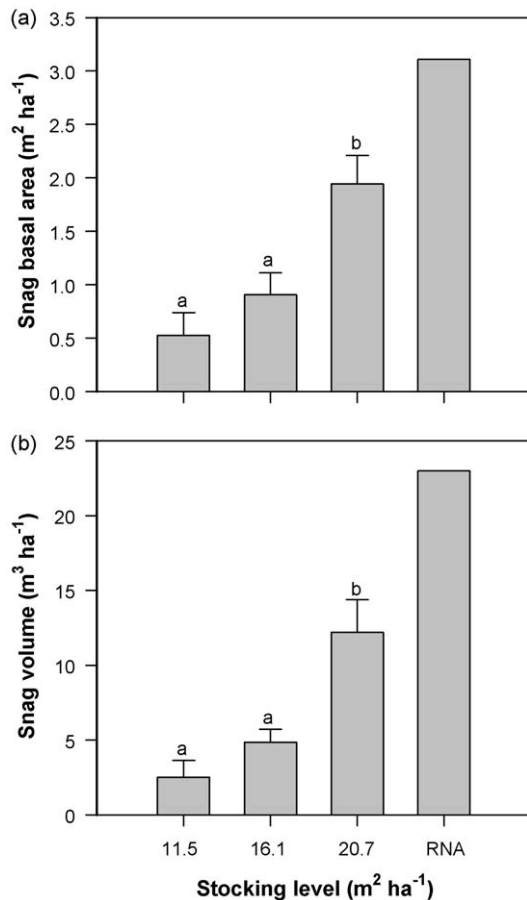


Fig. 4. (a) Basal area and (b) volume of snags across treatments at the Dukes Experimental Forest, MI in 2008. Error bars represent standard errors, $n = 9$. Columns with the same letters were not significantly different, $p = 0.05$.

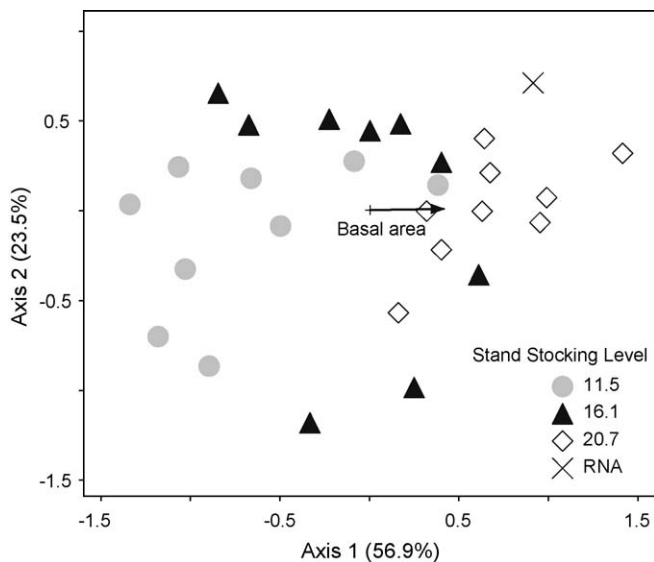


Fig. 5. Non-metric multi-dimensional scaling (NMS) ordination of treatment stands and an old-growth forest (RNA) benchmark in 2008. The percentage of the ordination explained by each axis is given in parentheses. Stands (treatments and RNA) are indicated by the legend symbols. Vector length represents the explanatory power of stand stocking level in explaining the variation in stand structure among treatments stands and the RNA.

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 5).

4. Discussion

4.1. Effects of treatments on species composition

Our 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).

4.2. 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 $m^2 ha^{-1}$ 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 our stands. In addition, our 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). 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

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

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 stand ($97.0 \text{ m}^3 \text{ ha}^{-1}$) was similar to those found in other eastern old-growth northern hardwoods (Goodburn and Lorimer, 1998; McGee et al., 1999). DWD volume in our 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). We 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 our study was fairly constant ($8\text{--}13 \text{ ha}^{-1}$) 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 ha^{-1} ; however, other studies have found similar densities to those in the stands we examined (Keeton, 2006; Kenefic and Nyland, 2007). Despite the relatively low density of snags across treatments and the RNA, we 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).

4.3. Effects of treatments on diameter distributions

Our 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 ($20.7 \text{ m}^2 \text{ ha}^{-1}$ residual stocking), we 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 $20.7 \text{ m}^2 \text{ ha}^{-1}$ 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 $11.6 \text{ m}^2 \text{ ha}^{-1}$ quickly resulted in a change to a concave or negative exponential distribution. Both negative exponential and concave distributions in our 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).

4.4. 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).

Our 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 our 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 > 70 cm) are left in the stand.

Maintaining high residual stocking will also help achieve structural objectives. For example, we observed higher density of trees greater than 24 cm diameter in stands managed at $20.7 \text{ m}^2 \text{ ha}^{-1}$, 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, our 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 m² 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.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.01.001.

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