Relationships between growth, quality, and stocking within managed old-growth northern hardwoods

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Abstract: An understanding of long-term growth dynamics is central to the development of sustainable uneven-aged silvicultural systems for northern hardwood forests in eastern North America. Of particular importance are quantitative assessments of the relationships between stocking control and long-term growth and quality development. This study examined these relationships in a long-term silviculture experiment established in northern hardwood stands in the Upper Peninsula of Michigan, USA. Stands were old growth at the onset of the experiment and were maintained at three residual stocking levels (11.5, 16.1, and 20.7 $m^2 \cdot ha^{-1}$) over a 57-year period. Several aspects of long-term stocking control were evaluated, including the effects of residual stocking on tree quality development and the relationships between stand stocking and individual tree growth and stand-level production. Results suggest that residual stocking had little impact on quality development, likely due to the initial old-growth condition of the stands examined. In contrast, our results indicate that a range of stand densities will maintain acceptable rates of stand-level production in selection systems and that growth can be shifted between diameter classes depending on desired future stand conditions.

Résumé : La compréhension de la dynamique de la croissance à long terme est essentielle pour mettre au point des systèmes sylvicoles durables appliqués aux forêts inéquiennes de feuillus nordiques dans l'est de l'Amérique du Nord. Il est particulièrement important de quantifier les relations à long terme entre la surface terrière résiduelle et la croissance et le développement de la qualité. Cette étude se penche sur ces relations dans le cadre d'une expérience sylvicole de longue durée établie dans des peuplements de feuillus nordiques sur la péninsule supérieure du Michigan, aux États-Unis. Au début de l'expérience, la surface terrière de ces vieux peuplements a été abaissée à trois niveaux différents (11,5, 16,1 et 20,7 $m^2 \cdot ha^{-1}$) qui ont été maintenus pendant une période de 57 ans. Plusieurs aspects du maintien de la surface terrière ont été évalués, dont l'effet de la surface terrière résiduelle sur le développement de la qualité des arbres et la relation entre la surface terrière et la croissance aux échelles de l'arbre individuel et du peuplement. Les résultats indiquent que la surface terrière résiduelle a eu peu d'impact sur le développement de la qualité, probablement parce que les peuplements étudiés étaient initialement des vieilles forêts. Par contre, nos résultats indiquent qu'une gamme de densités résiduelles est en mesure de maintenir des taux acceptables de production à l'échelle du peuplement dans les systèmes de jardinage et que la croissance peut être déplacée entre les classes de diamètre en fonction des conditions futures du peuplement que l'on désire.

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Introduction

Selection silvicultural systems are a widely implemented approach to the management of forests around the globe (e.g., Assmann 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 (e.g., cutting cycle and stocking level) on tree quality development and tree and stand growth (Nyland 1998).

One of the fundamental aims of selection silviculture in eastern North America has been the improvement of tree quality (Eyre and Zillgitt 1953; Arbogast 1957; Guldin and Fitzpatrick 1991) through removal of dying or defective trees, retention of a substantial volume of large vigorous crop trees, and removal of low-value or high-risk species (Arbogast 1957; Nyland 2007). The quality of trees produced in stands managed using selection systems strongly influences the value of timber products and is therefore an important aspect of the economic viability of this management approach in the region (Niese et al. 1995). 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).

Despite the emphasis on tree quality development in selection silviculture guidelines, few studies have rigorously evaluated the long-term influence of residual stand stocking level on tree quality in single-tree selection systems. Residual stocking level directly affects the distribution of tree grades by influencing the number of below-grade trees that can be removed in a given harvest entry (Strong et al. 1995). Corre-

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spondingly, studies of northern hardwood tree grade in the upper Great Lakes region of North America suggest that low to medium stocking levels result in the greatest improvement in tree grade when converting second-growth, even-aged stands to uneven-aged structure (Strong et al. 1995); however, there is little information on how different stocking levels affect long-term residual quality in managed uneven-aged stands in this region (Godman and Books 1971; Strong et al. 1995). Due to the extended time periods over which single-tree selection systems are applied, evaluations in long-term silvicultural experiments may provide useful insights into factors affecting quality development in stands managed using selection systems.

Rates of individual tree growth also have an important influence on tree quality development due to the importance of tree diameter in the assignment of tree grades, particularly higher quality classes (Strong et al. 1995). The relationships between stand stocking level and patterns of individual and stand-level tree growth have been widely examined; however, the vast majority of this work has been conducted in even-aged stands (e.g., Curtis and Marshall 1993; Pretzsch 2005; D'Amato et al. 2010). Nevertheless, the 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 multiaged ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) were similar to those found in even-aged forests, demonstrating that the biological maximum in growth and productivity is related to stand occupancy as well as stand structure.

Many studies of growth and production in selection systems are based on relatively short-term field experiments and have resulted in stand structural targets thought to produce optimum sustained yields (Eyre and Zillgitt 1953; Leak et al. 1969; Baker et al. 1996). In most cases, these guides have been based on a reverse-J target diameter distribution 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.

To better understand how single-tree selection affects tree growth and quality, we utilized the results of a long-term silviculture experiment 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 northern hardwoods across several residual stocking levels. The study was established in what was initially primary old-growth forest, which is unique in that it allows us to examine quality–growth relationships in previously unmanaged uneven-aged stands that contain a wide range of tree quality conditions at the onset. The objectives of this study were to (1) evaluate the effects of 57 years of single-tree selection on tree quality development within primary northern hardwoods and (2) examine the relationships between residual stocking levels and tree and stand growth, including trade-offs between stand-level and individual tree growth. Based on the findings of work done in second-growth northern hardwood stands (Strong et al. 1995), we predicted that stands managed with lower residual basal areas would have higher average tree grade than stands managed at higher residual basal areas. We further predicted 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.

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). The experimental forest is located 12–14 km south of the shore of Lake Superior, resulting in a relatively cool and humid climate. 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. Study treatments were established in a randomized complete block design within a sugar maple (*Acer saccharum* Marsh.) dominated forest with limited history of human disturbance prior to the establishment of the experiment. Three blocks were established each with 10 treatment combinations that included three cutting cycles (5, 10, and 15 years) combined with three residual stocking levels (11.5, 16.1, and 20.7 $m^2 \cdot ha^{-1}$) of residual basal area in trees greater than 24 cm in diameter. One additional treatment consisting of a 20-year cutting cycle at 6.9 $m^2 \cdot ha^{-1}$ residual basal area was also established in each block. Treatment blocks were 45–65 ha with each individual treatment encompassing 4–6 ha. Treatments were applied according to the prescribed cutting cycles from the time of establishment (1952–1954) until 1972–1974 when the cutting cycles portion of the study was abandoned. One block within the study was again cut to the appropriate stocking levels in 1986 but no further cutting in any of the treatments had occurred at the time of data collection in 2008. We found no statistical difference in current stand conditions between the block treated in 1986 and the remaining blocks (data not shown). Given the lack of recent treatment, residual basal areas averaged (±SE) 25.5 ± 2.2, 27.9 ± 1.1, 29.3 ± 1.3, and 31.3 ± 0.5 $m^2 \cdot ha^{-1}$ for the 6.9, 11.5, 16.1, and 20.7 $m^2 \cdot ha^{-1}$ treatments, respectively, at the time of the last measurement (2002–2004). Each treatment stand contained 6–17 permanent 0.08 ha circular plots.

Field measurements

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 5 years thereafter until 1972–1974. Data were not collected prior to the partial stocking level treatment in 1986. Renewed interests in the long-term effects of the treatments spurred remeasurement of the plots in 2002–2004. Additionally, a subset of five plots per treatment was randomly selected in 2008 for measurement of tree quality (see methods below). Also at that time, five additional plots of the same design as those in the treatments were established in the uncut hardwood section of the Dukes Research Natural Area (RNA), an area directly adjacent to the treated stands. The close proximity of this relatively undisturbed old-growth forest and its nearly identical composition and structure as the treatment forest prior to cutting make it an ideal benchmark for comparison with the treated stands in terms of tree quality. Due to the lack of replication of this unmanaged condition among the treatment blocks, any results from these comparisons should be interpreted with caution.

Tree quality was assessed using a grading method that evaluates the value of individual hardwood trees on the stump. In the summer of 2008, we measured tree grade per Miller et al. (1986) on all trees greater 11 cm on the five randomly selected subplots in each treatment and the RNA. With this method, evaluation of tree grade is a process that uses a dichotomous key to evaluate the quality of a tree. The tree grade is determined by evaluating the best 3.7 m section of the butt (base) 4.9 m of the tree (whichever portion results in a higher grade). 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. 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.

Data analysis

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. We analyzed the distributions of trees separately within three corresponding size classes: 24.4–31.8, 31.9–39.6, and greater than 39.6 cm. This analysis allowed for an examination of 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 nonparametric 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 of the other treatment distributions to detect differences. For these and all other analyses, all species were combined for analysis due to the low sample sizes for species other than sugar maple (see Gronewold et al. (2010) for detailed species composition of these areas).

Individual-tree-level diameter measurements were used for calculating average annual basal area growth 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 (trees that grew to the minimum diameter for that diameter class), gross growth (residual plus ingrowth), and mortality were calculated for all measured trees by diameter class using the same size classes as in 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.

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 we chose to focus solely on stocking level. By eliminating cutting cycle and examining only stocking levels, the number of sample units increased from $n = 3$ to $n = 9$ in the 11.5, 16.1, and 20.7 $m^2 \cdot ha^{-1}$ stocking levels with $n = 3$ in the 6.9 $m^2 \cdot ha^{-1}$ stocking level treatment. 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 ith replication, T_j is the effect of the jth treatment, RT_{ij} is the interaction between the ith replication and the jth treatment, and E_{ij} is the residual error. Within treatment, stocking level was a fixed effect and replication was a random effect. The difference in the number of sample units among treatments ($n = 3$ for the 6.9 $m^2 \cdot ha^{-1}$ 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 treatment (Shaw and Mitchell-Olds 1993). Tukey–Kramer multiple comparison tests were run to determine where specific significant differences existed between stocking levels (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, μ is the overall mean, P_i is the effect of the ith measurement period, T_j is the effect of the jth treatment, PT_{ij} is the interaction between the ith measurement period and the jth treatment, R_k is the random effect of the kth replication, and E_{ijk} is the residual error. For all ANOVAs, residuals were checked for normality and data transformations were applied where necessary.

Although mean annual growth rates were analyzed in an ANOVA framework, we 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 examine the relationships between tree and stand growth and stocking levels more thoroughly, we calculated stand density index for all 12 individual sample units at each measurement period in the study. Stand density index 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). We calculated the stand density index of all 12 sample units at all measurement periods using the additive method for uneven-aged stands found in Woodall and Fiedler (2005). We then used the maximum biologically attainable stand density index for sugar maple dominated forest as calculated in Woodall et al. (2005) and calculated relative density based on this value to allow for comparisons of periodic growth of trees and stands at different relative densities. Mean annual basal area growth was calculated for each measurement interval and relative densities were based on the stand density index at the beginning of a given interval. Because of the wider range of tree sizes and ages found within uneven-aged versus even-aged stands, we 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 stocking levels (Table 1). Mean tree grade ranged from 2.75 to 2.92 in the treated stands and was only slightly lower in the unmanaged RNA (2.97) (Table 1). There were limited differences among stocking levels 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 stocking levels in the 24.4–31.8 cm size class (Table 2), while the distribution of tree grades in the 31.9–39.6 cm size class differed significantly between the unmanaged RNA and the managed stands (Table 2). 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 with the managed stands (Table 2). 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 2); however, only the comparison between the RNA and the 6.9 $m^2 \cdot ha^{-1}$ stocking level was significant (Table 2).

Tree and stand growth

Annual tree diameter growth ranged from 0.22 to 0.36 $cm \cdot year^{-1}$ (Table 3). Mean annual diameter growth differed significantly among stocking levels (Table 3). For all diameter classes, annual diameter growth was greatest in the 6.9 and 11.5 $m^2 \cdot ha^{-1}$ residual stocking levels and decreased as residual stocking level increased (Table 3). There was no significant difference between the 6.9 and 11.5 $m^2 \cdot ha^{-1}$ residual stocking levels in any of the diameter classes. The 20.7 $m^2 \cdot ha^{-1}$ stocking level had significantly less diameter growth than the other stocking levels in all diameter classes. The 16.1 $m^2 \cdot ha^{-1}$ stocking level was significantly lower than the 6.9 and 11.5 $m^2 \cdot ha^{-1}$ stocking levels in the 11.4–24.3 cm diameter class, lower than the 11.5 $m^2 \cdot ha^{-1}$ stocking level but not the 6.9 $m^2 \cdot ha^{-1}$ stocking level in the 24.4–39.6 cm diameter class, and significantly lower than the 6.9 $m^2 \cdot ha^{-1}$ stocking level but not the 11.5 $m^2 \cdot ha^{-1}$ stocking level for trees greater than 39.6 cm.

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

Table 1. Mean tree grade in various stocking levels and the Research and Natural Area in 2008 at the Dukes Experimental Forest, Michigan.

Stocking level ($m^2 \cdot ha^{-1}$)	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
Research and Natural Area	2.97

Note: Stocking level treatments were only maintained from 1952 to 1986, and therefore, current conditions do not fully reflect these residual stocking levels (see Materials and methods for average stocking levels at the time of most recent measurement). Numbers in parentheses represent standard errors; $n = 3$ for the 6.9 $m^2 \cdot ha^{-1}$ treatment and $n = 9$ for all other treatments. Stocking level treatments with the same letter are not statistically different at $P = 0.05$.

Results of the mixed-model 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 $m^2 \cdot ha^{-1}$ stocking level compared with the other stocking levels (Fig. 1). During the active treatment period from 1957–1972, both individual tree and stand growth generally showed significant stocking level effects independent of time period, with growth inversely related to stocking level (Fig. 1).

Effects of residual density on individual and stand-level growth

Average annual stand basal area growth varied as a function of relative stand density across all stocking levels and was generally greatest at relative densities between 25% and 50% (Fig. 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 (Fig. 3). In trees 11.4–24.3 cm, there was a decrease in the percentage 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 (Fig. 3*a*). The 24.4–39.6 cm tree size class constituted a rela-

Table 2. Proportion of trees in each grade by diameter class and stocking level and Research and Natural Area at the Dukes Experimental Forest, Michigan.

		Stocking level ($m^2 \cdot ha^{-1}$)				
Diameter class (cm)	Tree grade	6.9	11.5	16.1	20.7	Research and Natural Area
24.4–31.8		a	a	a	a	a
	Grade 1	—	—	—	—	—
	Grade 2	—	—	—	—	—
	Grade 3	65.6	67.9	68.5	61.1	66.6
	Below grade	34.4	32.1	31.5	38.9	33.3
No. of trees graded		57	209	178	162	9
31.9–39.6		a	a	a	a	b
	Grade 1	—	—	—	—	—
	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
No. of trees graded		41	135	127	109	11
>36.9		a	ab	ab	ab	a
	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
No. of trees graded		84	254	309	319	37

Note: Stocking level treatments were only maintained from 1952 to 1986, and therefore, current conditions do not fully reflect these residual stocking levels (see Materials and methods for average stocking levels at the time of most recent measurement). Stocking level treatments with the same letter did not have significantly different distributions of tree grades at $P = 0.05$. —, not available.

Table 3. Mean annual diameter growth during 1952–2002 by size class at the Dukes Experimental Forest, Michigan.

Stocking level ($m^2 \cdot ha^{-1}$)	Mean annual diameter growth ($cm \cdot year^{-1}$)
Trees 11.4–24.3 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
Trees 24.4–39.6 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
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

Note: Stocking level treatments were only maintained from 1952 to 1986, and therefore, current conditions do not fully reflect these residual stocking levels (see Materials and methods for average stocking levels at the time of most recent measurement). Numbers in parentheses represent standard errors; $n = 3$ for the 6.9 $m^2 \cdot ha^{-1}$ treatment and $n = 9$ for all other treatments. Stocking level treatments with the same letter within a diameter class were not statistically different at $P = 0.05$.

tively constant and moderate proportion of total stand growth across stocking levels (Fig. 3*b*), 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 (Fig. 3*c*).

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

Discussion

Our findings indicate that several applications of single-tree selection over a 50-year period have had limited effect on average tree quality development within previously unmanaged old-growth northern hardwood systems. Overall mean grade was relatively unaffected by residual stocking level. However, there was a significant difference in grade distribution within the managed stands relative to the control, with a greater proportion of grade 1 trees in the larger diameter classes in the lowest stocking treatment compared with the control. Nonetheless, these results should be interpreted with caution given the lack of replication of the unmanaged control conditions among treatment blocks. In contrast, individual tree size increased with decreasing density and stand growth increased with increasing density, consistent with Long (1985). Due to the importance of individual tree growth in developing tree quality within stands managed using single-tree selection, these trade-offs need to be consid-

Table 4. Mean annual residual growth, ingrowth, gross growth, and mortality from 1952 to 2002 for each treatment by size class at the Dukes Experimental Forest, Michigan.

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

Note: Mean annual gross growth = residual growth + ingrowth. Stocking level treatments were only maintained from 1952 to 1986, and therefore, current conditions do not fully reflect these residual stocking levels (see Materials and methods for average stocking levels at the time of most recent measurement). Numbers in parentheses represent standard errors; $n = 3$ for the 6.9 $m^2 \cdot ha^{-1}$ treatment and $n = 9$ for all other stocking levels. Stocking level treatments with the same letter within each variable were not statistically different at $P = 0.05$.

Table 5. Summary of mixed-effects repeated-measures ANOVAs including source of variation, degrees of freedom, *F* values, and probability values for the repeated measures of stand growth and tree growth at all intertreatment periods at the Dukes Experimental Forest, Michigan.

			Stand growth ($m^2 \cdot ha^{-1} \cdot year^{-1}$)		Tree growth ($m^2 \cdot ha^{-1} \cdot year^{-1}$)	
Source of variation	df (numerator)	df (denominator)	*F*	*P*	*F*	*P*
Stocking	3	8	8.58	≤0.007	5.10	≤0.029
Year	4	32	65.04	≤0.001	91.76	≤0.001
Stocking × year	12	32	2.88	≤0.008	1.50	≤0.177

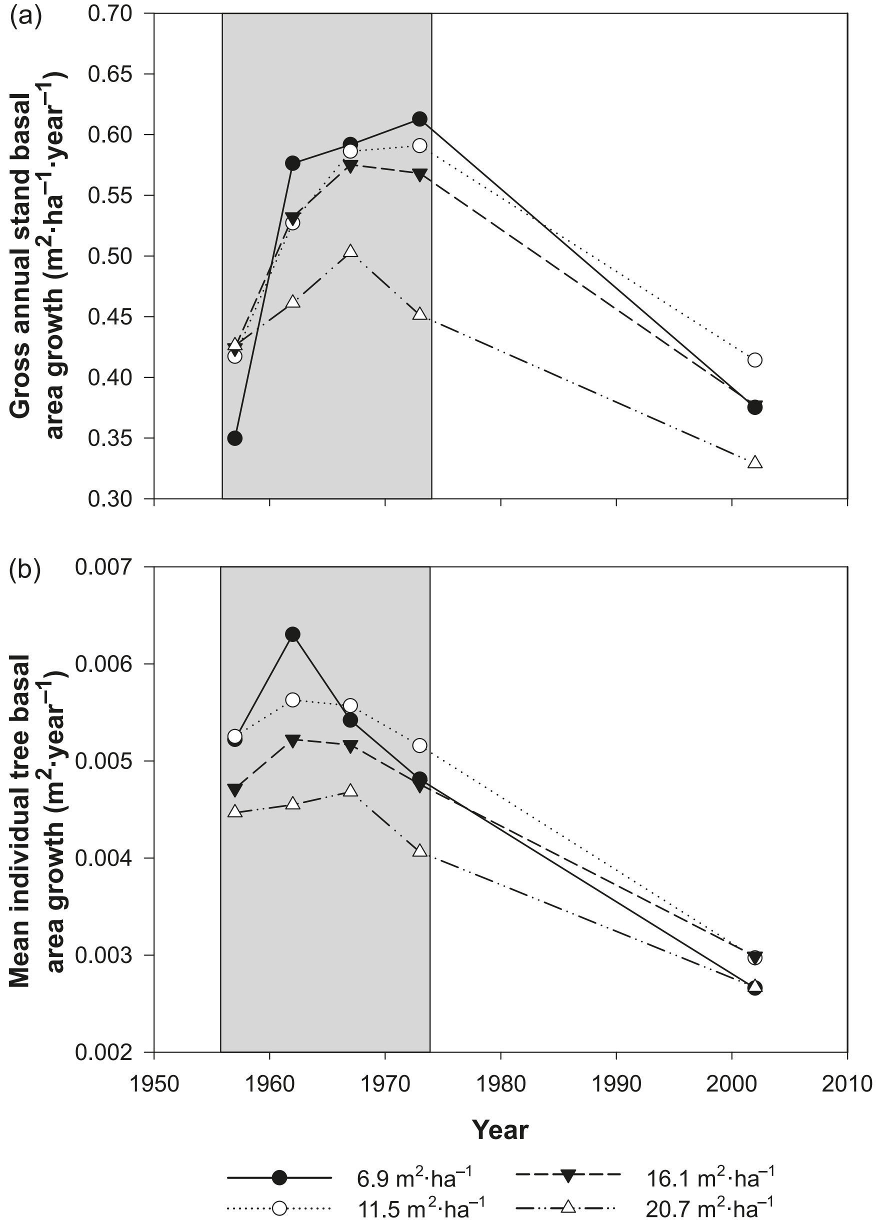
ered when assessing the long-term impacts of this management approach on residual stand quality and growth.

Quality development

Our hypothesis that stands managed at lower stocking levels would show strong quality improvement was unsupported by the data when examined as whole-stand averages. In particular, we expected that the removal of defective trees at each harvest would allow smaller crop trees to develop into larger high-quality trees as the stocking level 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 our 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 separate periods during treatment application, whereas we 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. 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.

Although mean stand grade did not differ among stocking levels, the stocking level treatments did affect the distribution of tree grades within stands, particularly when compared with 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% of the growing stock within a stand (Eyre and Zillgitt 1953). The percentage of below-grade trees above 31.9 cm diameter at breast height 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) in the lowest stocking treatment where a significant reduction in below-grade trees and a corresponding increase in grade 1 trees were observed relative to the unmanaged RNA. A similar shift towards a greater proportion of higher quality trees was observed in a 48-year study of tree quality in managed old-growth northern hardwoods in New Hampshire (Leak and Sendak 2002). This shift 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.

Fig. 1. (*a*) Gross annual stand basal area growth and (*b*) mean individual tree basal area growth for the four stocking levels at each measurement period at the Dukes Experimental Forest, Michigan. The shaded region corresponds to the portion of the experiment in which active basal area control was applied to all treatment blocks. Note that one treatment block was also treated in 1986. Error bars represent standard errors; $n = 3$ for the 6.9 m^2·ha^{-1} stocking level and $n = 9$ for all other stocking levels.

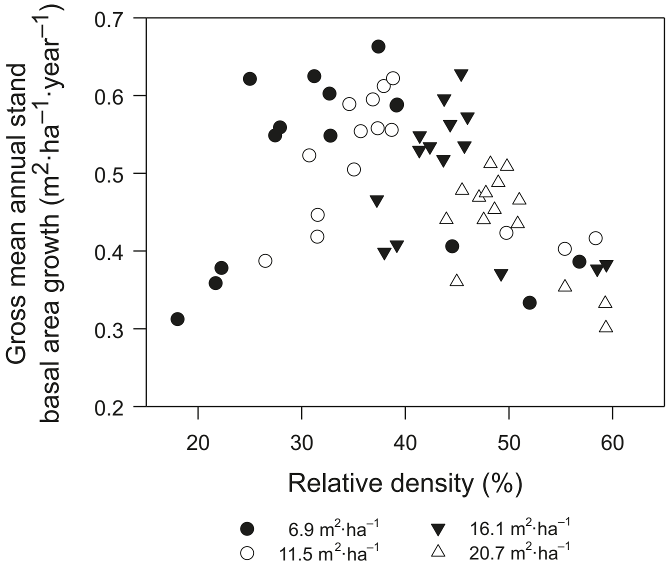


Tree and stand-level growth responses to stocking level treatments

As expected, the greatest mean annual diameter growth rates occurred within the lowest stocking levels (Assmann 1970; Zhang and Oliver 2006), reflecting the higher levels of resources available to residual trees in these stands. Similarly, we observed a general decline in individual tree basal area growth and increased mortality with increasing stand stocking, consistent with the idea that increased intertree competition at higher stand densities causes a decline in individual tree vigor (Drew and Flewelling 1979; Powers et al. 2010). In particular, we 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 24.4–39.6 cm diameter class where reduced basal area growth also occurred at very low densities. By comparison, the trends in stand-level growth demonstrated little variation in stand basal area production across a wide range of stand densities. Only at very low or high stand densities was stand growth at its lowest.

The relationships between stand-level growth and stocking that we 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 levels, suggesting that stands of this type maintained at stocking levels optimum for stand-level production may not exhibit an appreciable difference in stem

Fig. 2. Mean annual stand basal area growth for the stands in the four stocking levels as a function of relative density (percentage of maximum stand density index) for all measurement periods at the Dukes Experimental Forest, Michigan. Mean annual basal area growth was calculated for each measurement interval and relative densities correspond to the stand density index at the beginning of a given interval. Data are for trees greater than 11 cm diameter.



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. Some loss of individual tree growth and quality improvement is likely under the typical, higher densities commonly recommended for use in selection systems, e.g., Arbogast (1957) recommended 15–17 m^2·ha^{-1} in trees at least 25 cm diameter. Nonetheless, it is important to note the degree to which tree growth declines between relative densities of 40% and 60%. In particular, individual tree growth declined in all size classes at these stocking levels.

Despite the overall decline in individual tree growth documented at higher stocking levels, we observed varying degrees of stand growth in different size classes, with 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. We observed a greater proportion of growth in the largest trees in the highest stocking level stands (Fig. 3*c*) and the most even allocation of growth among size classes in the lowest stocking level stands. These differences might be due to the significant crown overlap in shade-tolerant trees within uneven-aged stand structures that allows for significant layering of both foliage and rooting depth (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 multilayered 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).

Fig. 3. Percentage of mean annual stand basal area growth as a function of the percentage of maximum stand density index within the (*a*) 11.4–24.3, (*b*) 24.4–39.6, and (*c*) >39.6 cm size classes for all stocking levels and measurement periods at the Dukes Experimental Forest, Michigan. Mean annual basal area growth was calculated for each measurement interval and relative densities correspond to the stand density index at the beginning of a given interval. Curves represent the best fit of the data.

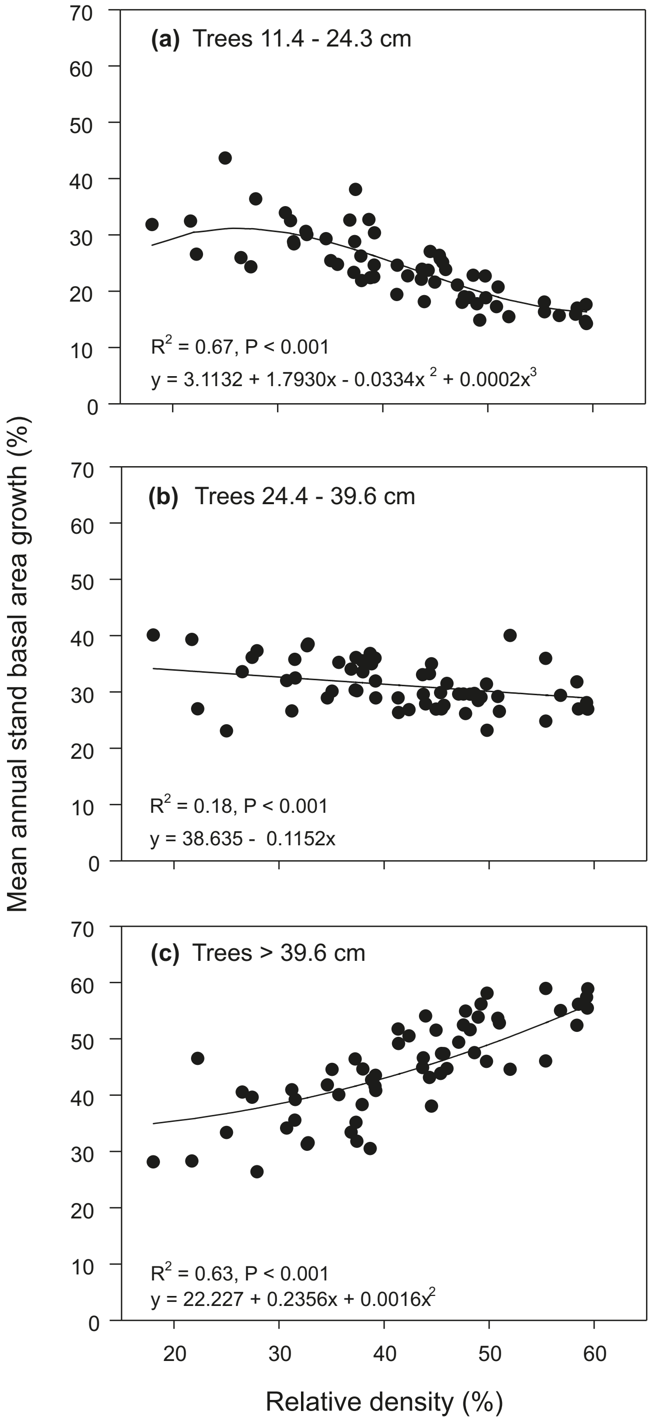
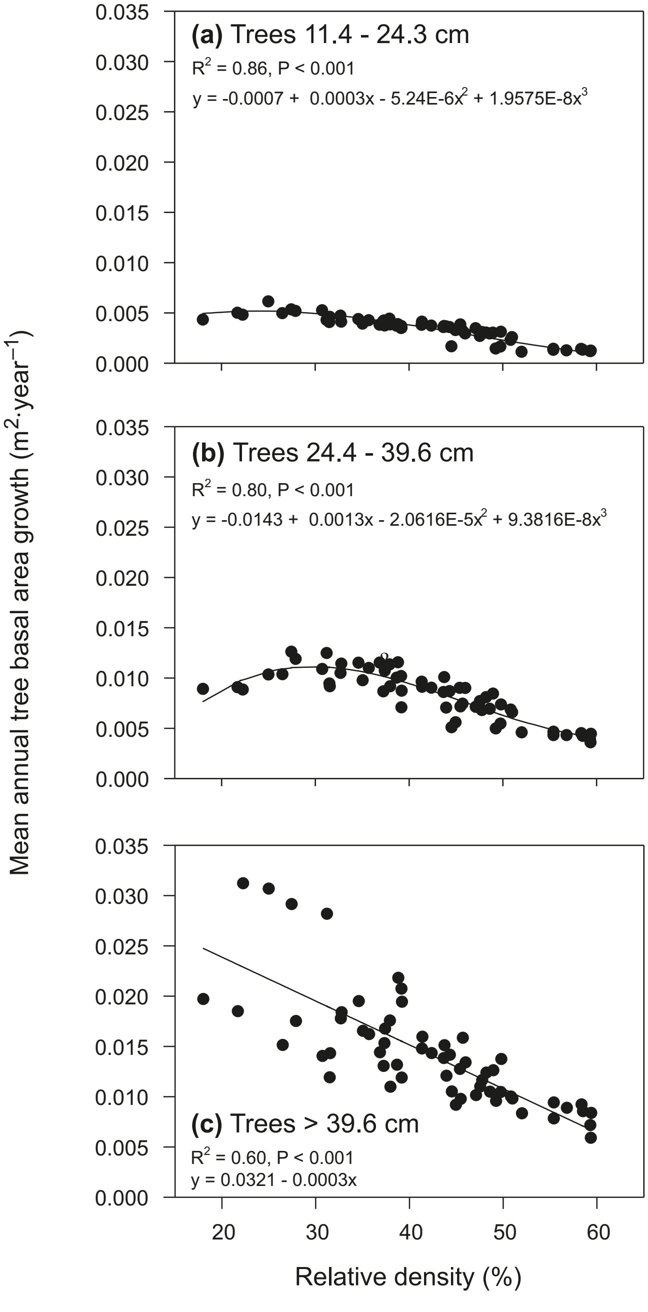


Fig. 4. Mean annual tree basal area growth as a function of the percentage of maximum stand density index within the (*a*) 11.4–24.3, (*b*) 24.4–39.6, and (*c*) >39.6 cm size classes for all stocking levels and measurement periods at the Dukes Experimental Forest, Michigan. Mean annual basal area growth was calculated for each measurement interval and relative densities correspond to the stand density index at the beginning of a given interval. Curves represent the best fit of the data.



Whether thinning increases total production in forest stands is a continuing debate in the literature that has been explored in considerable depth (Zeide 2001; Pretzsch 2005). One hypothesis is that optimum production can occur over a wide range of residual stand densities, and therefore, moderate thinning simply redistributes resources to the remaining trees (MarMoller 1947). In contrast, work examining growth – growing stock relationships in even-aged coast Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) highlighted that as stand density increased, total stand volume production similarly increased (Curtis et al. 1997). Within the context of our study, stand production, as measured by basal area increment, appeared to be optimized between relative densities of 25% and 50% (Figs. 2 and 3); however, the lack of volume measurements precluded us from testing if a similar stocking threshold existed for maximum volume production. 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 $m^2 \cdot ha^{-1}$, although with appropriate cutting cycle lengths residual stocking levels of 11.5 and 20.7 $m^2 \cdot ha^{-1}$ may also be warranted, particularly if other silvicultural goals such as increased stand structural complexity are management objectives (Gronewold et al. 2010).

In addition to overall stand stocking, an important consideration for uneven-aged management regimes is the optimal allocation of growing space to cohorts and size classes (O'Hara and Gersonde 2004). The findings of our study suggest that high levels of growth and productivity can be maintained over a range of stocking levels and size distributions. Across the stocking levels that we examined, the relative contribution of a given size class to stand-level productivity varied based on the allocation of growing space to a respective size class. 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. This principle is supported by the trends documented in Fig. 3, which suggest that different size classes make up similar proportions of growth at low and moderate stand densities. A relatively constant level of growth can be maintained at a variety of stand densities as this shift occurs. Notably, analyses of diameter distribution forms in these stands document that multiple stand structures exist in these systems over time ranging from reverse-J to increasing *q* (Gronewold et al. 2010). Nonetheless, analyses of growth trends from these stands (Fig. 2; Table 4) suggest that optimum growth was achieved at a variety of residual stocking levels despite this lack of a constant stand structure. These findings lend support to the notion 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 commonly utilized method of management for forests in North America (O'Hara 2002), the need for a comprehensive understanding of the expected outcomes, from both 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. Our findings suggest that although trade-offs can exist between individual tree quality, tree growth, and stand growth, the relatively small range in overall growth differences at different residual stand densities and the largely invariant tree quality development among stocking levels provide 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, management 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., retained 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 trade-off being less individual tree growth and less growth in the younger cohorts. Furthermore, the findings of this study lend further support to the utility of extending the largely even-aged concepts of density management and leaf area allocation to the management of uneven-aged stands using selection systems (Long 1985; O'Hara 1996).

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