Forest Science, 2023, **69**, 213–227
https://doi.org/10.1093/forsci/fxac053
Advance access publication 9 December 2022
Research Article

Silviculture

Stand-Density Effects on Aboveground Carbon Dynamics in Secondary *Pinus* and *Quercus* Forests of Central USA

Samantha Anderson,[1,3] Benjamin O. Knapp,[1,*] and John M. Kabrick[2]

[1]School of Natural Resources, University of Missouri, 203 Anheuser-Busch Natural Resources Building, Columbia MO 65211, USA.
[2]USDA Forest Service, Northern Research Station, 202 Anheuser-Busch Natural Resources Building, Columbia MO 65211, USA.
[3]Current Affiliation: Missouri Department of Conservation, Chillicothe, MO 64601, USA

[*]Corresponding author email: knappb@missouri.edu. Phone: (573) 882 0867

Abstract

Temperate forests play an important role in the sequestration and storage of carbon. We evaluated the long-term effects of manipulating stand density on aboveground live tree carbon dynamics and volume production for separate pine (*Pinus* spp.) and oak (*Quercus* spp.) forests of central USA. For both species groups, stand-level carbon storage in standing live trees was greatest without management, with unthinned pine plateauing around 100 Mg/ha of carbon at approximately 50 years old and the oak stands increasing to around 100 Mg/ha of carbon by about 80 years old. In the pine stands, stand-level carbon sequestration was greatest in stands that were thinned but maintained fully stocked conditions. Consequently, the gross carbon that accumulated during the study period, which included standing carbon in live trees and carbon from trees that were harvested or otherwise died, was maximized when stand stocking was maintained at an average of around 80% stocking during the study period. These results were compatible with the production of sawtimber volume, which was greatest for stands that were maintained in fully stocked but not overstocked conditions. Our results demonstrate that thinning can be a forest management strategy to achieve multiple objectives, including those for carbon management and sawtimber production.

Study Implications: Our results support stand-density management (i.e., thinning) as a forestry practice compatible with carbon objectives and more traditional objectives of timber production. Aboveground carbon stored in live trees was greatest without thinning, but gross production and sequestration rates were greatest when stand density was maintained in fully stocked but not overstocked conditions. Active forest management during stand development can provide managers with the flexibility to address multiple objectives and may be used with other carbon management practices such as extended rotations or continuous canopy cover, particularly in the central and northeastern United States where forests are generally aging uniformly throughout the region.

Keywords: carbon management, Central Hardwood Region, stand stocking, thinning

Temperate forests provide a variety of commodity and ecosystem services, including the uptake and storage of carbon (Fahey et al. 2010; Pan et al. 2011a). Aboveground, live biomass makes up an important carbon storage pool within temperate forests, with various studies estimating it to contribute the greatest proportion of total carbon storage or second behind the contribution of soil carbon (Tyrrell et al. 2012; Wilson et al. 2013). Aboveground, live biomass is also the most dynamic carbon pool, with potential to change rapidly with disturbance events and more gradually through stand development processes and forest aging (Houghton 2005; Tyrrell et al. 2012; Woods and Kern 2022). Across much of the northeastern United States, forestland is dominated by secondary forests established after land clearing before the 1900s, resulting in extensive areas of forests maturing at a similar rate (Birdsey et al. 2006; Pan et al. 2011b; Shifley et al. 2014).

In recent years, there has been increased interest in forest management strategies that affect carbon dynamics (Fahey et al. 2010; McNulty et al. 2018; Ameray et al. 2021). A wide variety of approaches have been proposed, such as protecting existing forestland to reduce carbon loss and increasing forestland through afforestation (McKinley et al. 2011; Ontl et al. 2019). On existing forestland, silvicultural practices may be prescribed for carbon management objectives (Ameray et al. 2021). Silvicultural practices can affect the amount of carbon stored on the site at a given point in time (i.e., carbon storage) or the rate of carbon accumulation through time (i.e., carbon sequestration) (D'Amato et al. 2011). Previous studies have suggested practices such as extending rotation ages to increase carbon storage, increasing age or structural complexity to reduce risk of loss, and managing stand density to improve tree vigor and growth rates (Galik and Jackson 2009; Ameray et al. 2021; Kaarakka et al. 2021).

Manipulating forest stand density through thinning is a common silvicultural practice used for a variety of reasons, including improving the health or vigor of the stand, recovering product loss due to mortality, and changing species composition (Smith et al. 1997). A primary function of thinning is the purposeful allocation of biomass production

Received: September 1, 2022. Accepted: November 2, 2022.

to specific individual trees. Although stand density reductions have consistently been found to increase the biomass of residual trees, density effects on stand-level production have been debated (Zeide 2001). Previous studies have shown that thinning practices can affect both carbon storage and sequestration (Hoover and Stout 2007; D'Amato et al. 2011). Carbon storage in aboveground live biomass has consistently been found to be greatest in unmanaged forest stands (Powers et al. 2011; Puhlick et al. 2016), but rates of carbon sequestration have been reported to be more variable across studies and through time (Dwyer et al. 2010; D'Amato et al. 2011; Tao and Williams 2013). The incorporation of carbon dynamics into forest management decisions requires consideration of trade-offs among various objectives (Bradford and D'Amato 2012; Burton et al. 2013). Stand-density management may be implemented in ways that are compatible with carbon objectives and other objectives such as timber production (Schaedel et al. 2017), although additional research is needed to understand these effects across species and regions.

Long-term forestry experiments provide valuable empirical information on stand development through time (Pretzsch et al. 2019). Although research interests shift with contemporary management problems, long-term studies often provide insights into emerging questions of interest (Lugo et al. 2006). Growth and yield studies established on USDA Forest Service (Forest Service) experimental forests in the mid-1900s provide an experimental framework for evaluating stand-density effects on carbon dynamics (e.g., D'Amato et al. 2011). This work is based on two long-term thinning studies initiated 1952 and 1961, respectively, on the Sinkin Experimental Forest of the Mark Twain National Forest in Missouri. The two studies included the Pine Stocking Study (PSS) and the Oak Stocking Study (OSS), which were both designed to assess the effects of stand density on growth and volume yield in Missouri Ozark upland forests. Our specific objectives are to (1) evaluate temporal patterns in carbon storage and carbon sequestration in relation to forest stand density for shortleaf pine (*Pinus echinata* Mill.) and upland oak (*Quercus* spp.) forests, (2) evaluate effects of stand-density management on gross aboveground carbon production over the period of a rotation, and (3) contrast stand-density effects on carbon dynamics with merchantable timber volume production.

Methods

Study Site

The Sinkin Experimental Forest (SEF) is in Dent County in southeastern Missouri. Located in the Current River Hills subsection of the Ozark Highlands ecological section (Nigh and Schroeder 2002), the SEF was designated as an experimental forest by the Forest Service in 1950 and was maintained by the Forest Service Northern Research Station as part of the Mark Twain National Forest. The SEF contains acidic soils with low nutrient supply capacity derived from highly weathered sandstone and dolomite parent materials (Adams et al. 2004). Common soil series include Clarksville very gravelly silt loam and Coulstone-Clarksville complexes (Soil Survey Staff, 2022). Topography on the SEF is characterized by narrow ridges with steep side slopes, and elevations range from 335 m to 412 m above mean sea level. Both the OSS and PSS were confined to xeric broad ridge top, shoulder, and upper backslope positions with slopes ranging from 4% to 32%. A few plots in both studies contained steep drainages that channeled water during and immediately following heavy rains. Average annual precipitation from 1918 to 2015 was 1,100 mm with 60% falling from April to September. Average daily temperature ranged from 1.7°C from December to February to 24.2°C from June to August.

Oak-pine forests typical of the Ozark Highlands dominate the SEF. Common tree species include black oak (*Quercus velutina* Lam.), white oak (*Q. alba* L.), northern red oak (*Q. rubra* L.), pignut hickory (*Carya glabra* [Mill.] Sweet), mockernut hickory (*Carya tomentosa* [Lam.] Nutt.), shortleaf pine, black walnut (*Juglans nigra* L.), black cherry (*Prunus serotina* Ehrh.), and flowering dogwood (*Cornus florida* L.). The forests on the SEF are mostly secondary forests established following heavy harvesting in the late 19th and early 20th centuries. Historically, shortleaf pine comprised about half of the basal area on the SEF but now makes up about 15%–20% (Adams et al. 2004). A site index (base age 50, shortleaf pine) of 18.3 m was measured in 1952 for the PSS, and a site index (base age 50, black, scarlet, and white oaks) of 20–24 m was measured in 1961 for the OSS.

Experimental Design

The PSS and the OSS have similar establishment histories, and both were set up to determine effects of stand-density management on growth and yield. The even-aged shortleaf pine stands of the PSS were initiated through natural seeding after an oak-pine stand was harvested from 1918 to 1920. In 1934, the Civilian Conservation Corps, charged with the task of locating and releasing shortleaf pine stands to encourage regeneration and growth, cut and girdled the hardwood overstory that remained in the stands. During that time, the pines were thinned from about 2,700 to 1,480 trees per hectare (TPH). The even-aged oak-hickory stands of the OSS were initiated through advanced regeneration and stump sprouts following a clearcut harvest in 1920. Before study initiation, the oak stands were fully stocked with characteristic Ozark species, including black oak, white oak, scarlet oak (*Quercus coccinea* Münchh.), post oak (*Quercus stellata* Wangenh.), northern red oak, and hickories. Average basal area of the OSS before treatment was 22.0 m^2/ha, with an average of 1,900 TPH and an arithmetic mean diameter of 12.2 cm.

PSS

The original PSS used a randomized complete block design that included three blocks, each with ten plots. Each plot was thinned to one of four levels of basal area (11.5, 16.1, 20.7, or 25.3 m^2/ha) or maintained as an unthinned control (30 m^2/ha; two controls per block). Each block included three 16.1 m^2/ha plots to test the effects of different methods of thinning on stand development and growth. In addition to selection thinning (applied to all other plots), one 16.1 m^2/ha plot was thinned from below and one was thinned from above in each block. Each measurement plot was 0.2 ha and included a 9 m treated buffer to decrease edge effects.

All plots were thinned twice in the first ten years of the study: in 1952 to establish the treatment levels and in 1960, following that year's stand inventory, to thin back to the originally assigned basal areas. In 1972, the study was altered to address new management questions regarding large pole and sawtimber production. Four of the 16.1 m^2/ha plots were harvested completely to determine what species would become dominant after pine removal. Those plots were subsequently dropped from the study. Remaining plots were reassigned basal areas that were within 4.6 m^2/ha of their original assignment or kept the same. Additionally, four of the six control plots were thinned from approximately 46 m^2/ha basal area to 11.5 m^2/ha and subsequently dropped from the study. Following the changes made in 1972, eight plots were thinned in 1985, 16 plots were thinned in 1995, and five plots were thinned in 2007. The treatment history and resulting stand stocking levels for each plot are provided as Table S1 and Figure S1.

The changes made to the treatments in 1972 resulted in stocking levels fluctuating through time for some plots, making it inappropriate to retain those plots in their original density treatment assignments. We created three treatment groups that included plots in which stand density was relatively consistent through time and distinct from other treatments when averaged across the full study period (1952–2007). These treatment groups are defined as low (n = 2, including one plot from the original 11.5 m^2/ha and one plot from the original 16.1 m^2/ha treatment), medium (n = 4, with all plots from the original 16.1 m^2/ha treatment), high (n = 4, with two plots from the original 20.7 m^2/ha and two plots from the original 25.3 m^2/ha treatments), and an untreated control (n = 1) (Table 1, Figure S1).

OSS

The OSS was established as a completely randomized design with 36 plots located within even-aged oak-hickory stands at several locations within the Mark Twain National Forest. The original study design included two stand ages (20 and 40 years old) at the time of the first thinning in 1961, three site index groups (20, 23, and 26 m at base age 50), and stand-density treatments defined by basal area (6.9, 11.5, 16.1, and 20.7 m^2/ha). From the original design, 20 plots in the 40-year-old age group were located on the SEF and were used in the current study.

Similar to the PSS, plot design for the OSS consisted of 0.2 ha plots with a 9 m surrounding buffer. The study was thinned in 1961 and 1974 using free thinning, with the goal of maintaining evenly spaced crop trees. The 1961 thinning established the assigned plot densities, with leave trees chosen based on their crop tree potential. Species chosen as leave trees were favored in the following order: black oak, northern red oak, white oak, scarlet oak, and post oak. Herbicide (2, 4, 5-T) was applied to cut stumps to control hardwoods following thinning in 1962 and 1974. Between thinnings, foliar sprays were applied in 1963, 1965, and 1975. During the time of the OSS, tree-area relationships were developed to define stand stocking for upland hardwoods (Gingrich 1967), and the thinning in 1974 redefined treatments based on stocking rather than basal area. All plots that were originally thinned to 20.7 m^2/ha were deemed "check" plots and did not receive a thinning in 1974. After the 1974 cut, for undocumented reasons, no further thinnings were applied to any of the remaining plots. Many plots were abandoned, with only 11 of the original 36 plots retained through 2015, all of which were located on the SEF.

Similar to the PSS, we created treatment groups based on stocking levels throughout the study period (1961–2001). Throughout the study period, the treatments applied did not vary as much as in PSS, but the thinning application in 1974 was to slightly higher density targets than in 1961 for all plots (Figure S2). Consistent with the PSS, we defined treatments as low (n = 3; original 6.9 m^2/ha treatment), medium (n = 4; original 11.5 m^2/ha treatment), high (n = 3; original 16.1 m^2/ha treatment), and an untreated control (n = 1; original 20.7 m^2/ha) (Table 1, Figure S2).

Data Collection

Trees that were ≥ 1.5 cm diameter at breast height (DBH) and located inside PSS and OSS plots at study initiation were tagged with numbered aluminum tags. Only shortleaf pines were tagged in the PSS. Inventories of the tagged trees of the PSS were completed every two years from 1952 to 1960. Following 1960, inventories were spaced at approximately five-year intervals and were made in 1965, 1971, 1976, 1980, 1985, 1990, 1995, 2000, and 2007. Inventories of tagged trees in the OSS were made approximately every five years: 1961, 1967, 1971, 1974, 1976, 1981, 1986, 1991, 1996, and 2001. Plot inventories preceded a thinning (if one occurred) in the same year, and no ingrowth was tagged or measured in either study.

Data Analysis

Due to treatment and design differences between the PSS and OSS, the two studies were analyzed separately but with the same analytical approaches. For each study, data were summarized by plot and year, expanded to a per hectare basis, and averaged by treatment group. Descriptive stand statistics included TPH, quadratic mean diameter (QMD; cm), basal

Table 1. Summary of stand structure for treatment groups used in PSS and OSS. Values represent means across the study periods, 1952–2007 for PSS and 1961–2001 for OSS.

Study	Treatment group	Number of plots	QMD (cm)	TPH	Basal area (m^2/ha)	Stocking (%)
PSS	Low	2	27.7	289	17.4	47.7
	Medium	4	27.8	335	20.4	56.0
	High	4	25.5	513	26.2	73.6
	Control	1	21.5	1099	40.0	119.2
OSS	Low	3	34.9	141	13.5	46.8
	Medium	4	29.6	271	18.6	67.4
	High	3	27.9	363	22.2	82.0
	Control	1	23.5	560	24.3	94.1

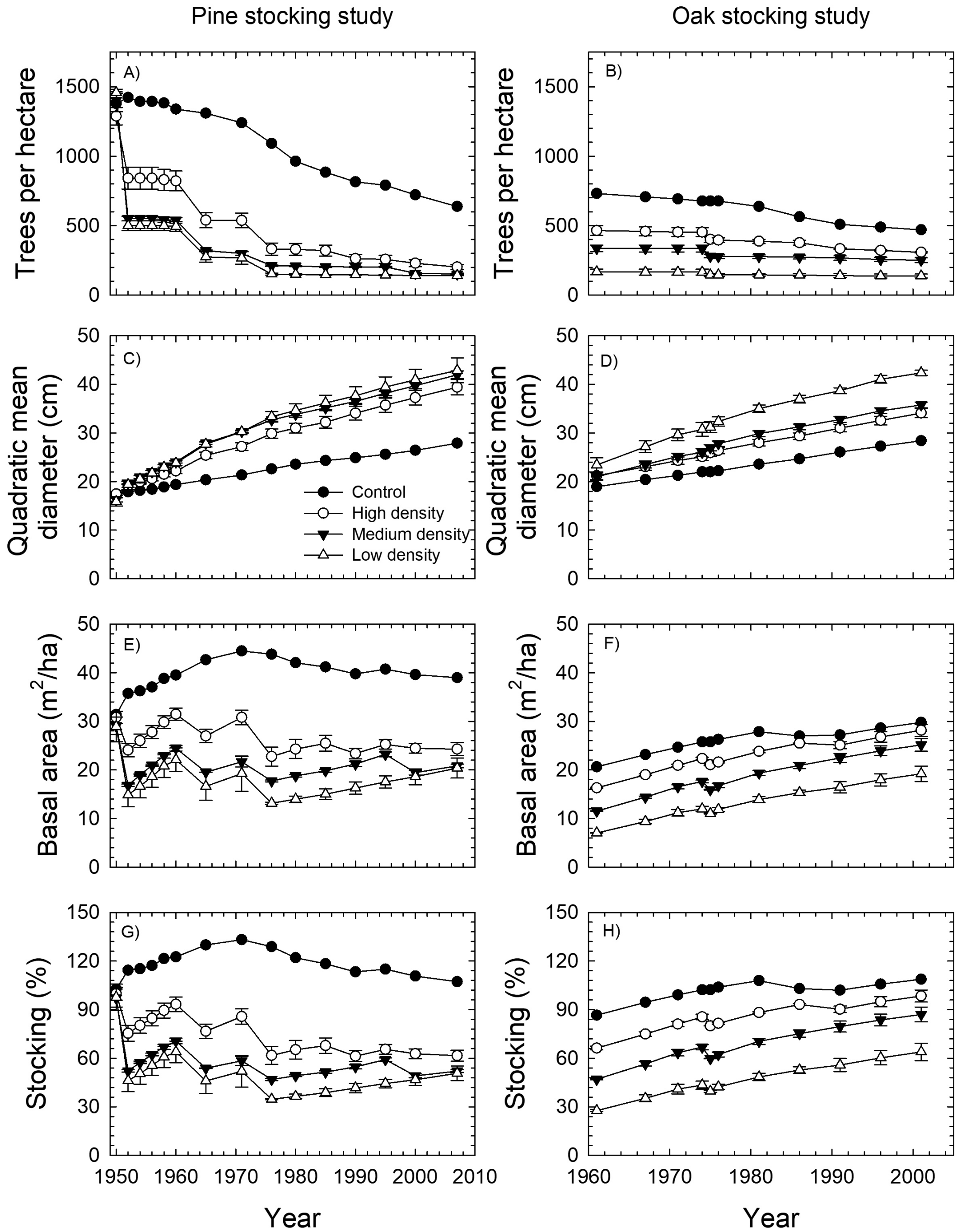

Figure 1. Stand structure through time by stand density treatment (mean ± one standard error) for the PSS and OSS, including: trees per hectare (A, B); quadratic mean diameter (C, D); basal area (E, F); and stocking (G, H).

area (BA; m²/ha), and percent stocking (Figure 1). Stocking is a measure of relative stand density that describes growing space occupancy given stand structure. In overstocked stands (stocking > 100%), individual trees have the minimum growing space needed to survive, reducing growth rates. Through time, overstocked stands experience tree mortality and stocking levels trend back toward 100%. In understocked stands, generally represented as below the point of crown closure, there is available growing space unused by trees in the stand. For the OSS, percent stocking was calculated using the minimum tree area relationship equation from Gingrich (1967). For the PSS, percent stocking was calculated using a minimum tree area equation developed for shortleaf pine in Missouri from Rogers (1983).

Total aboveground biomass (megagrams per hectare) was determined using species-specific allometric equations based on individual-tree diameter (Chojnacky et al. 2013) and was then converted to aboveground carbon (megagrams per hectare) by multiplying biomass by 0.5, assuming that carbon accounts for 50% of a tree's dry weight (Jenkins et al. 2003; D'Amato et al. 2011). Individual-tree aboveground carbon (megagrams per tree) was calculated by dividing total aboveground carbon by TPH for each inventory year. Stand-level carbon sequestration rates (megagrams per hectare per year) were calculated by finding the periodic annual increment (PAI) of carbon for trees that survived from one measurement year to the next for each of the measurement periods in both studies. PAI was calculated by determining the change in stand-level carbon storage in surviving trees in each measurement period and dividing that amount of carbon by the number of years in the measurement period. Individual-tree carbon sequestration rates (megagrams per tree per year) were found by dividing carbon sequestration rate by TPH.

To address objective 1, we used generalized linear mixed models to test the fixed effects of density group (low, medium, high, control), year, and interactions between density and year on four response variables: stand-level carbon storage (megagrams per hectare); tree-level carbon storage (megagrams per tree); stand-level carbon sequestration (megagrams per hectare per year); and tree-level carbon sequestration (megagrams per tree per year). Models included a repeated measures on year, with the plot as the subject and a first-order autoregressive covariance structure. In the event of significant interaction between density and year, we tested for significance of each effect within all levels of the other effect. Without a significant interaction between density and year, we tested the probability of significant marginal effects. Pair-wise comparisons with a Tukey's honestly significant adjustment were used to determine probability of differences among each pair of treatment levels within any significant fixed effects. Models were run separately for the PSS and the OSS.

To address objective 2, we calculated the gross carbon across each study period by including the last recorded measure of aboveground carbon from trees that died (through harvest or otherwise) during the study period. Gross carbon (megagrams per hectare) was calculated in two ways: (1) gross carbon stored during the study period, which included all the carbon stored in the stands following the first year of thinning; and (2) gross carbon accumulated during the study period, which included only carbon that was stored after the first year of thinning, calculated by subtracting the existing carbon at the first year of thinning from each subsequent year's measurement. Pretreatment data did not exist for OSS and was collected in a different way in the PSS, making it impossible to include all existing carbon before the first thinning in the gross carbon calculations.

We used two approaches to analyze gross carbon stored and gross carbon accumulated across the study period of PSS (1952–2007) and OSS (1961–2001). First, we used generalized linear models to test for the fixed effect of density group (low, medium, high, control) on gross carbon. Pair-wise comparisons with a Tukey's honestly significant adjustment were used to determine probability of differences among each pair of treatment levels within any significant fixed effects. Second, we used plot-level measures to model gross carbon based on the average stand stocking across the full study period of PSS and OSS. To do this, we first calculated the average stand stocking across time for each plot. We then used generalized linear mixed models to model gross carbon (stored and accumulated, separately) in relation to average stand stocking at the plot level using a polynomial model form. This approach provided two benefits: (1) it allowed us to consider the relationships with stand density treated as a continuous variable, providing greater information on the form of the relationship; and (2) it allowed us to use all the plots from the PSS.

To address objective 3, we assigned each tree record from each measurement year into a product class based on tree diameter: pulpwood DBH < 20.3 cm; chip-n-saw 20.3 ≤ DBH < 25.4 cm; and sawtimber DBH ≥ 25.4 cm. For each tree, we calculated volume (cubic meters per hectare) based on species-specific equations developed for the central states (Hahn and Hansen 1991), assuming site index of 18.3 m for PSS and 21.3 m for OSS. We determined the proportional contribution of each product class by density group through time to compare the rate of development of sawtimber. In addition, we calculated the total volume of the sawtimber product class during each year, both for standing volume and for gross volume stored, which included the volume of trees that had died (harvested or otherwise) during the study period. We used generalized linear mixed models, following the same approach as taken for objective 1, to test the fixed effects of density group (low, medium, high, control), year, and interactions between density and year on standing volume and on gross carbon stored. We considered statistical significance when $P < 0.05$, and all analyses were completed in SAS (version 9.4; SAS Institute, Inc., Cary, NC).

Results

Carbon Storage

For the PSS, there was a significant interaction between the stand-density treatment and time on stand-level carbon storage (Table 2; Figure 2A). In 1950, before the first thinning treatment, stand-level carbon storage did not differ among the treatments ($P = 0.458$) but differed among treatments in each subsequent measurement year ($P < 0.001$ in all years). The uncut control treatment resulted in the greatest stand-level carbon storage across the study period. By 2007, the last year of the study, there were no differences in stand-level carbon storage among the low, medium, and high-density treatments ($P \geq 0.997$). Stand-level carbon storage varied through time across all treatments, showing patterns of reduction due to thinning followed by gradual recovery. In the untreated control plot, stand-level carbon storage gradually increased through 1970 and then remained constant. For the OSS, the interaction between stand-density treatment and time was not significant for stand-level carbon storage (Table 2; Figure 2B). The effect of stand-density treatment was significant, with the low-density treatment resulting in less stand-level carbon storage than the each of the other treatments ($P < 0.040$). There were no differences among the other stand-density treatments. There was also a significant effect of time, with increases in the marginal means at each interval other than from 1974 to 1976 ($P = 0.986$), during which a thinning treatment was applied. For both the PSS and OSS studies, the maximum amount of stand-level carbon stored was approximately 100 Mg/ha.

Tree-level carbon storage was also affected by a significant interaction between stand-density treatment and time in the PSS (Table 2; Figure 2C). There were no significant differences among stand-density treatments in years before 1971 ($P \geq 0.142$), after which significant stand-density effects were present in each subsequent measurement year ($p \leq 0.027$). The control treatment had the lowest tree-level carbon storage, and there were no significant differences in tree-level carbon storage among the low, medium, and high-density treatments in any year ($P \geq 0.642$). Across all treatments, tree-level carbon storage increased through time. The pattern of

Table 2. Results of generalized linear mixed models testing fixed effects of stand density treatment, time, and their interaction on carbon variables.

Variable	Study	Effect	Numerator degrees of freedom	Denominator degrees of freedom	*F* value	*P* value
Stand-level carbon storage	PSS	Density	3	7.3	24.07	<0.001
		Year	14	30.6	21.55	<0.001
		Density*Year	42	30.6	3.84	<0.001
	OSS	Density	3	6.4	16.15	0.002
		Year	9	59.8	98.16	<0.001
		Density*Year	27	59.8	1.51	0.093
Tree-level carbon storage	PSS	Density	3	7.0	7.40	0.014
		Year	14	98.0	151.47	<0.001
		Density*Year	42	98.0	5.31	<0.001
	OSS	Density	3	7.2	19.59	0.001
		Year	9	40.8	251.76	<0.001
		Density*Year	27	40.8	13.44	<0.001
Stand-level carbon sequestration	PSS	Density	3	7.6	10.58	<0.001
		Year	12	48.5	65.42	<0.001
		Density*Year	36	48.5	3.52	<0.001
	OSS	Density	3	8.8	1.02	0.428
		Year	8	32.6	1.50	0.194
		Density*Year	24	32.6	0.61	0.891
Tree-level carbon sequestration	PSS	Density	3	7.1	6.99	0.016
		Year	12	58.5	6.76	<0.001
		Density*Year	36	58.5	1.02	0.463
	OSS	Density	3	7.0	84.55	<0.001
		Year	8	56.0	1.38	0.226
		Density*Year	24	56.0	0.50	0.968

results was similar in the OSS, with a significant interaction between stand-density treatment and time (Table 2; Figure 2D). Beginning in 1967 and for each year following, there were significant differences among stand-density treatments within years ($P \leq 0.046$). In general, the low-density treatment resulted in the greatest tree-level carbon storage and the control treatment resulted in the least.

Carbon Sequestration

For the PSS, there was a significant interaction between treatment and time for stand-level carbon sequestration (Table 2, Figure 3A). The stand-level carbon sequestration differed among treatments for all years other than 1976 ($P = 0.077$), 1985 ($P = 0.167$), and 2007 ($P = 0.281$). For most of the study years, sequestration in the control treatment was the lowest. Sequestration in the high-density treatment was the greatest, followed by the medium-density and then low-density treatments, although statistical significance among treatments varied among the years. For all the treatments, stand-level carbon sequestration generally decreased through 1980 and then remained relatively stable (Figure 3A). For the OSS, the interaction between treatment and time was not significant (Table 2, Figure 3B). Stand-level carbon sequestration did not differ among the four treatments and did not vary through time.

The results for tree-level stand sequestration were similar for the PSS and OSS. The interaction between treatment and time was not significant in either study (Table 2, Figure 3CD). For both studies, tree-level carbon sequestration was greater in the low-density and medium-density treatments than in the control, with no difference between the high-density treatment and any other study treatment. In the PSS, tree-level sequestration was lower in 1954, 1956, 1958, and 1960 than 1995 and 2007 ($P \leq 0.021$). In the OSS, tree-level carbon sequestration did not vary through time.

Gross Carbon

The gross carbon stored by the end of the study period varied by stand-density treatments in the PSS ($P = 0.019$) and in the OSS ($P = 0.001$). In the PSS, more gross carbon was stored in the high-density treatment than in the low-density treatment, with medium-density and control treatments not different from other treatments (Figure 4A). In the OSS, the low-density treatment resulted in less gross carbon stored when compared to all the other treatments (Figure 4B). The stand-density treatments also affected the gross carbon accumulated during the study period in the PSS ($P = 0.023$) but not in the OSS ($P = 0.355$). In the PSS, there was more gross carbon accumulated in the high-density treatment than in the control, with the low- and medium-density treatments not different from other treatments (Figure 4C).

We fit polynomial relationships between the average stand stocking during the duration of the study period and the gross carbon stored and accumulated, allowing us to use all of the study plots in PSS and to examine the shape of the relationships across the gradient of stand stocking values. In the PSS, the relationship for gross carbon stored was significant ($P < 0.001$; $R^2 = 0.809$), with gross carbon stored

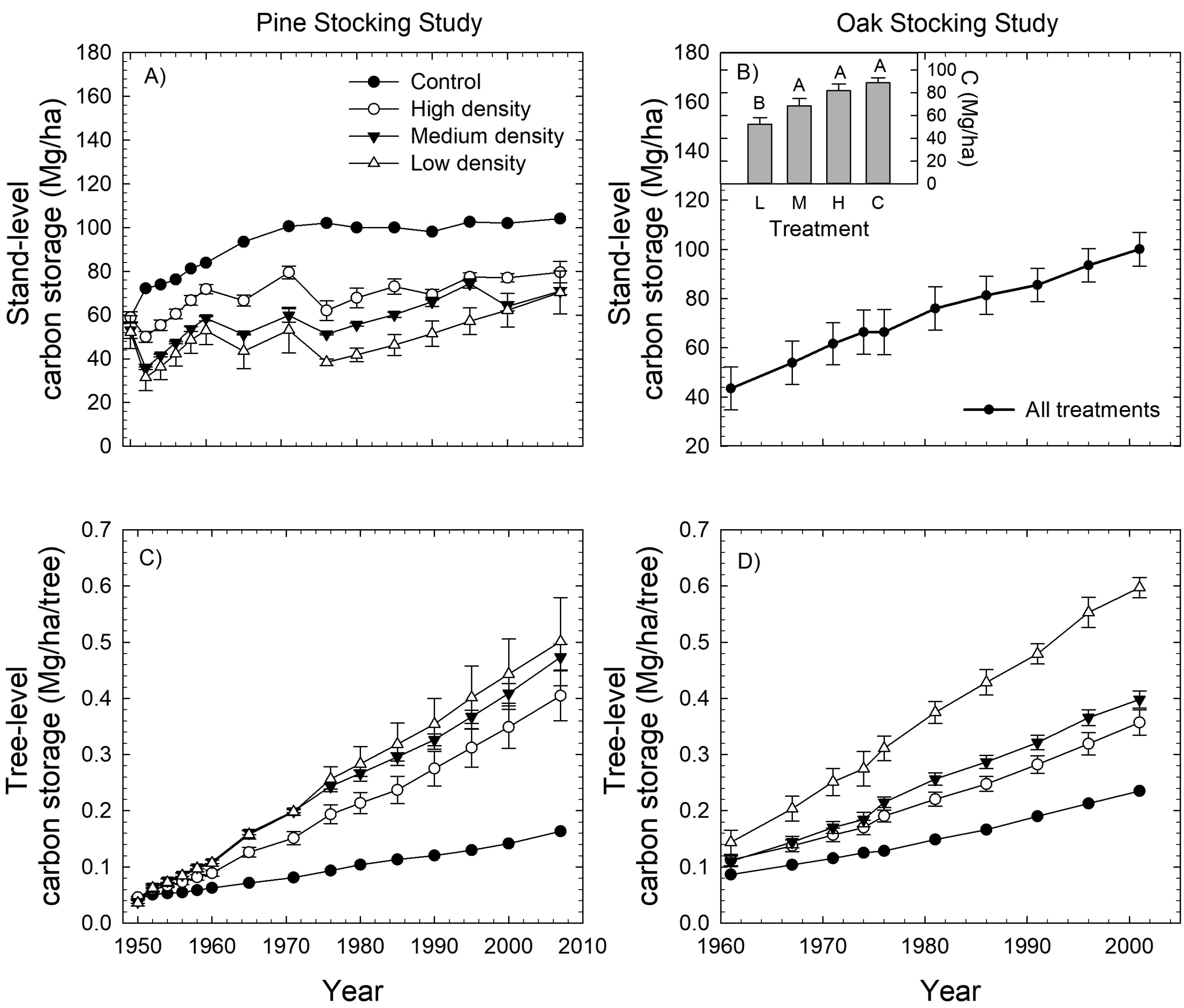

Figure 2. Carbon storage (mean ± one standard error) for the PSS and OSS, including: stand-level carbon storage through time by stand density treatment for PSS (A); marginal means of stand-level carbon storage by year (B) and stand-density treatment (B inset) for OSS; and tree-level carbon storage through time by stand-density treatment for PSS (C) and OSS (D).

increasing across average stocking values to peak around 90% stocking and slightly decrease for stocking values greater than 100% (Figure 5A). The model for gross carbon accumulated was similar ($P < 0.001$; $R^2 = 0.661$), although the unimodal shape was more pronounced with a peak around 80% stocking and greater decrease in gross accumulated carbon at greater stocking levels (Figure 5C). In the OSS, the gross carbon stored increased as average stand stocking increased ($P < 0.001$; $R^2 = 0.968$) but did not peak and decrease (Figure 5B). Gross carbon accumulation, however, peaked around 80% average stand stocking (Figure 5D) although model fit was not as strong ($P = 0.027$; $R^2 = 0.596$).

Sawtimber Volume

In the PSS, there were significant interactions between density treatment and time for both standing sawtimber volume and gross sawtimber volume (Table 3, Figure 6AC). For standing sawtimber volume, there were no differences among treatments prior to 1960, after which there were treatment differences in each year. The high-density treatment consistently had the greatest standing sawtimber volume, and the control treatment had the least standing sawtimber volume in 1965 and 1971. Through time, standing sawtimber volume in the control treatment increased, and by the last year of the study, it was numerically and statistically similar to the high-density treatment. Gross sawtimber volume numerically ranked as high-density > medium-density > low-density > control treatment after 1975, with the treatment effect becoming more pronounced through time. For the OSS, the patterns for standing sawtimber volume and gross sawtimber volume were similar to each other (Figures 6BD). For both variables, there were no differences among treatments until 1986, after which volume was lowest on the low-density plots and the other treatments similar.

In the PSS and OSS, the stand-density treatments had similar effects on the proportional distribution of trees across product classes (Figure 7). In the control treatments, less than half the trees were sawtimber size by the end of the study period, with a greater proportion of trees remaining in pulpwood size class in OSS than in PSS. In contrast, all remaining trees were in the sawtimber size class by the end of the study

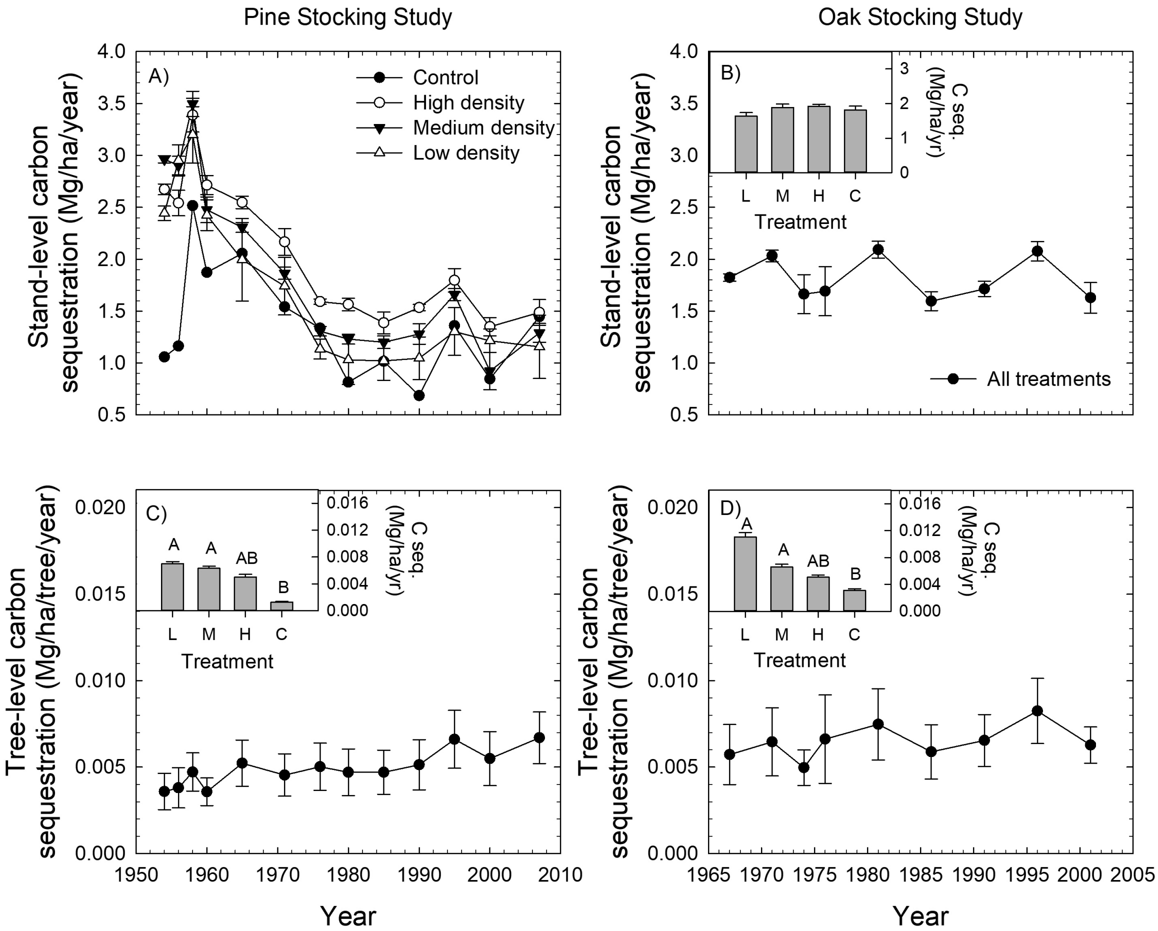

Figure 3. Carbon sequestration (mean ± one standard error) for the PSS and OSS, including: stand-level carbon sequestration through time by stand-density treatment for PSS (A); marginal means of stand-level carbon sequestration by year (B) and stand-density treatment (B inset) for OSS; and marginal means of tree-level carbon sequestration by year (C, D) and stand-density treatment (C inset, D inset) for PSS and OSS, respectively.

period in both PSS and OSS. Across the temporal scales of each study, increasing stand density resulted in longer retention of trees in pulpwood and chip-n-saw size classes. By the end of the period, however, all trees were in the sawtimber size class in PSS for all treatments other than the control.

Discussion

The silvicultural manipulation of stand density is a common forest management practice that affects the distribution of growing space and biomass production within the forest stand. Our results show the expected trade-off between stand-level and tree-level production across stand-density levels (Pretzsch et al. 2019). For both species, we found the greatest stand-level carbon storage in the control treatment and the least stand-level carbon storage in the low-density treatment; in contrast, the greatest tree-level carbon storage was in the low-density treatment and the least tree-level carbon storage was in the control. These findings are supported by stand-density measures of basal area, stocking, and quadratic mean diameter.

Carbon storage in aboveground, live biomass reached approximately 100 Mg/ha at maximum for both the shortleaf pine and upland oak stands in our study, despite greater maximum stand basal area for shortleaf pine stands (~40 m^2/ha) than for the oak stands (~30 m^2/ha). Differences in tree architecture and growing space requirements between shortleaf pine and oaks allow shortleaf pine stands to support greater basal areas at given stocking levels (Gingrich 1967; Rogers 1983). However, shortleaf pine has lower wood density than upland oaks, resulting in similar levels of carbon storage despite the differences in basal area (Kabrick et al. 2017). These results suggest that variation in species composition from pure shortleaf pine to pure upland oak would have little effect on maximum carbon storage in this region. In contrast, other studies have demonstrated that total production may disproportionately increase in mixed-species stands relative to pure stands (Waskiewicz et al. 2013; Pretzsch et al. 2019) or increase proportional to the abundance of one of the species that occur in mixtures (Kabrick et al. 2017).

In the absence of disturbance, carbon stored in live aboveground biomass is expected to increase asymptotically through time (Taylor et al. 2007; Harmon et al. 2009; McKinley et al. 2011). Our results suggest that maximum carbon storage was reached around 1975 (at a stand age of approximately 55 years) in the unthinned shortleaf pine stands. Carbon dynamics of old-growth forests are commonly used as benchmarks for potential carbon storage, with reports of aboveground live carbon storage in temperate forests of eastern North America ranging from ~ 100 Mg/ha to >200 Mg/ha (Brown et al. 1997; Burrascano et al. 2013). There have been few studies on carbon storage for old-growth

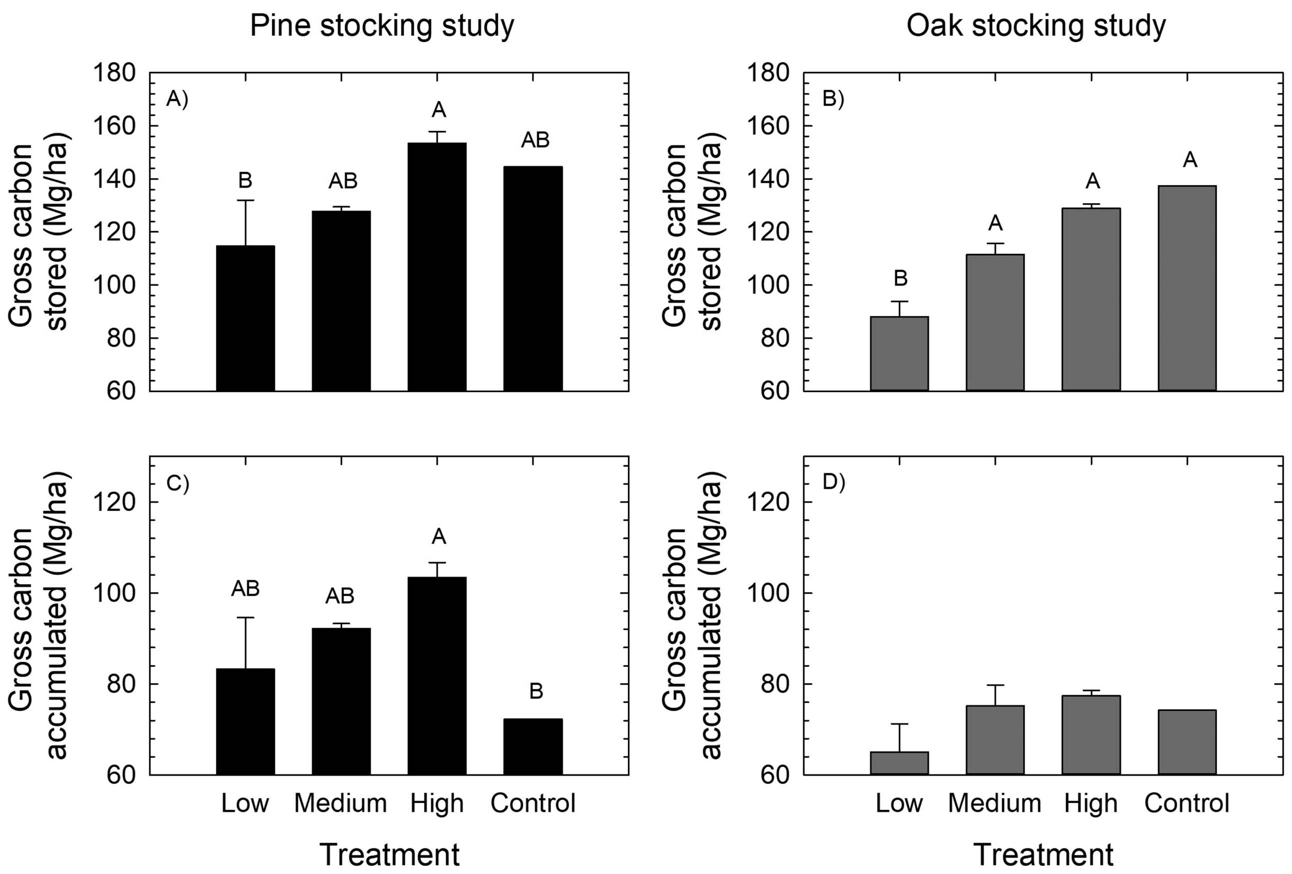

Figure 4. Gross carbon (mean ± one standard error) stored (A, B) and accumulated (C, D) by stand-density treatment during the study period for the PSS and OSS.

forests of the study region, but Spetich and Parker (1998) reported a maximum of ~110 Mg/ha C in trees >10 cm dbh monitored over a 70-year period (1926–1992) from an old-growth forest in Indiana. Generally, site productivity is lower in our Missouri study sites than that in Indiana (Spetich et al. 1999), and it is likely the maximum carbon storage observed in our study approximates site capacity.

There has long been interest as to whether stand-density management can increase total stand productivity (Zeide 2001). Models supporting this idea conceptualize a range of stand stocking levels that maximize production, with a reduction in total production in understocked or excessively stocked stands (Smith et al. 1997; Zeide 2001; Pretzsch et al. 2019). Our results provide some support for this concept. The gross carbon accumulated during the study period, which included growth on trees that were removed or otherwise died during the study period, peaked at approximately 80% stand stocking (averaged across all study years) for both the pine and oak studies. When the carbon stored before the initiation of the thinning treatments was included, the strength of this effect diminished for the shortleaf pine study and was removed from the oak study. Following the principles of stand stocking, growing space occupancy is not fully used below ~60% stocking for upland oaks and shortleaf pine (Gingrich 1967; Rogers 1983); thus, the low and medium density treatments used in our study maintained understocked conditions through most of the study period for both the pine and oak stands. For stands maintained at stocking levels that exceeded 100%, total production during the study period was also reduced in the pine study. In the oak study, where this pattern was not so clear, average stand stocking reached 100% on only one plot, perhaps limiting our ability to detect these effects due to poor representation of overstocked conditions.

The pine and oak stands differed in the patterns of stand-level carbon sequestration. Stand-level periodic annual increment is generally expected to peak at relatively young ages and then decline through time (Gower et al. 1996; Ryan et al. 1997), although this pattern has been shown to vary among forest types (He et al. 2012). Our results were similar to those from USDA Forest Service Forest Inventory and Analysis data reported by He et al. (2012), showing that live tree productivity of southern pine species peaks early and then declines quickly to a relatively stable level by age 40, whereas that for eastern oaks remains more stable, with gradual decline through stand ages of 100. We found no evidence that stand density affected stand-level carbon sequestration in the oak stands during the study period, indicating that greater tree-level sequestration in low-density stands offset the differences in tree density among the treatments with regard to stand-level productivity. In the pine stands, however, greater stand-level sequestration rates in the high-density treatment than the unthinned control contributed to the greater gross carbon accumulation throughout the study period for the high-density treatments.

Tree-level carbon sequestration showed similar treatment effects for the pine and oak stands, with greater tree-level productivity associated with lower density stands. For the pine

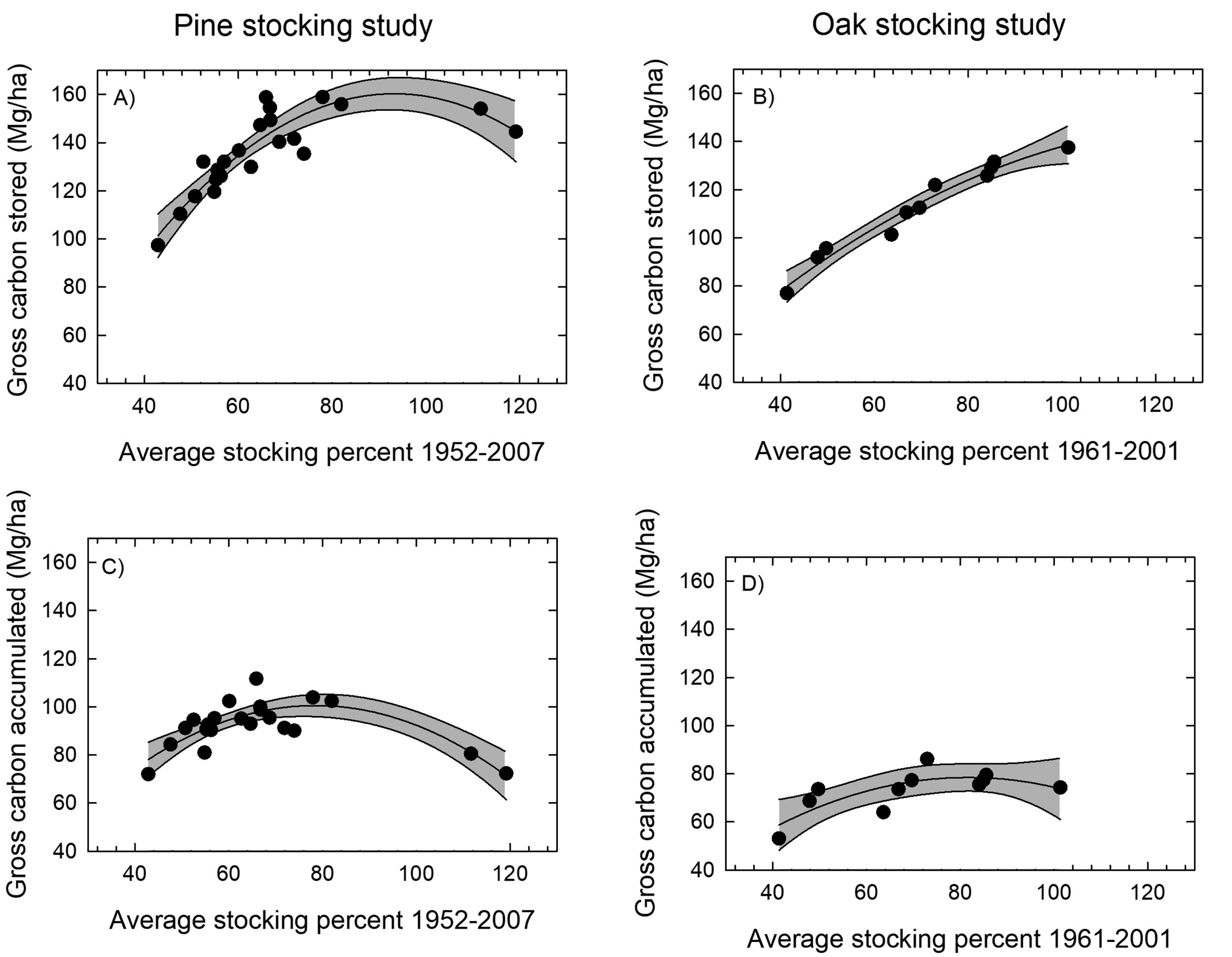

Figure 5. Relationship between gross carbon stored (A, B) or accumulated (C, D) and average stand stocking during each respective study period (modeled mean with 95% confidence intervals shaded).

Table 3. Results of generalized linear mixed models testing fixed effects of stand density treatment, time, and their interaction on volume variables.

Variable	Study	Effect	Numerator degrees of freedom	Denominator degrees of freedom	*F* value	*P* value
Standing sawtimber volume	PSS	Density	3	8.7	4.2	0.044
		Year	13	44.9	73.7	<0.001
		Density* Year	39	44.9	2.9	<0.001
	OSS	Density	3	6.9	3.0	0.107
		Year	9	59.7	93.2	<0.001
		Density* Year	27	59.7	1.9	0.025
Gross sawtimber volume	PSS	Density	3	7.2	2.4	0.148
		Year	13	90.2	258.2	<0.001
		Density* Year	39	90.2	4.5	<0.001
	OSS	Density	3	7.7	5.2	0.029
		Year	9	60.2	179.2	<0.001
		Density* Year	27	60.2	3.1	<0.001

stands, we also observed an increase in tree-level carbon sequestration through time, regardless of treatment, that was not observed for the oak stands. In contrast to expected patterns of stand productivity, individual trees have been shown to increase carbon accumulation with tree size and age (Stephenson et al. 2014). In addition to their contributions to carbon sequestration and storage, large old trees increase structural complexity and provide unique habitat values (Franklin et al. 2002), and their purposeful retention has been incorporated into recent silvicultural approaches (Keeton 2006; Palik et al. 2020).

Our results highlight several key effects of density management on the production of merchantable volume. Thinning increased the proportion of sawtimber trees throughout the study period and produced a greater proportion of sawtimber trees at younger ages for both the pine and oak stands. This is due to greater growth rates of residual trees following thinning as well as the removal of smaller trees during the thinning operation. In the pine stands, the stand-density treatments affected the rate at which standing sawtimber accumulated through time. The slower growth of individual trees in the overstocked control treatment reduced standing sawtimber throughout most of the study period, but standing sawtimber volume for the control treatment caught up with the other treatments by the last measurement period. Gross sawtimber volume production, which included trees removed in the

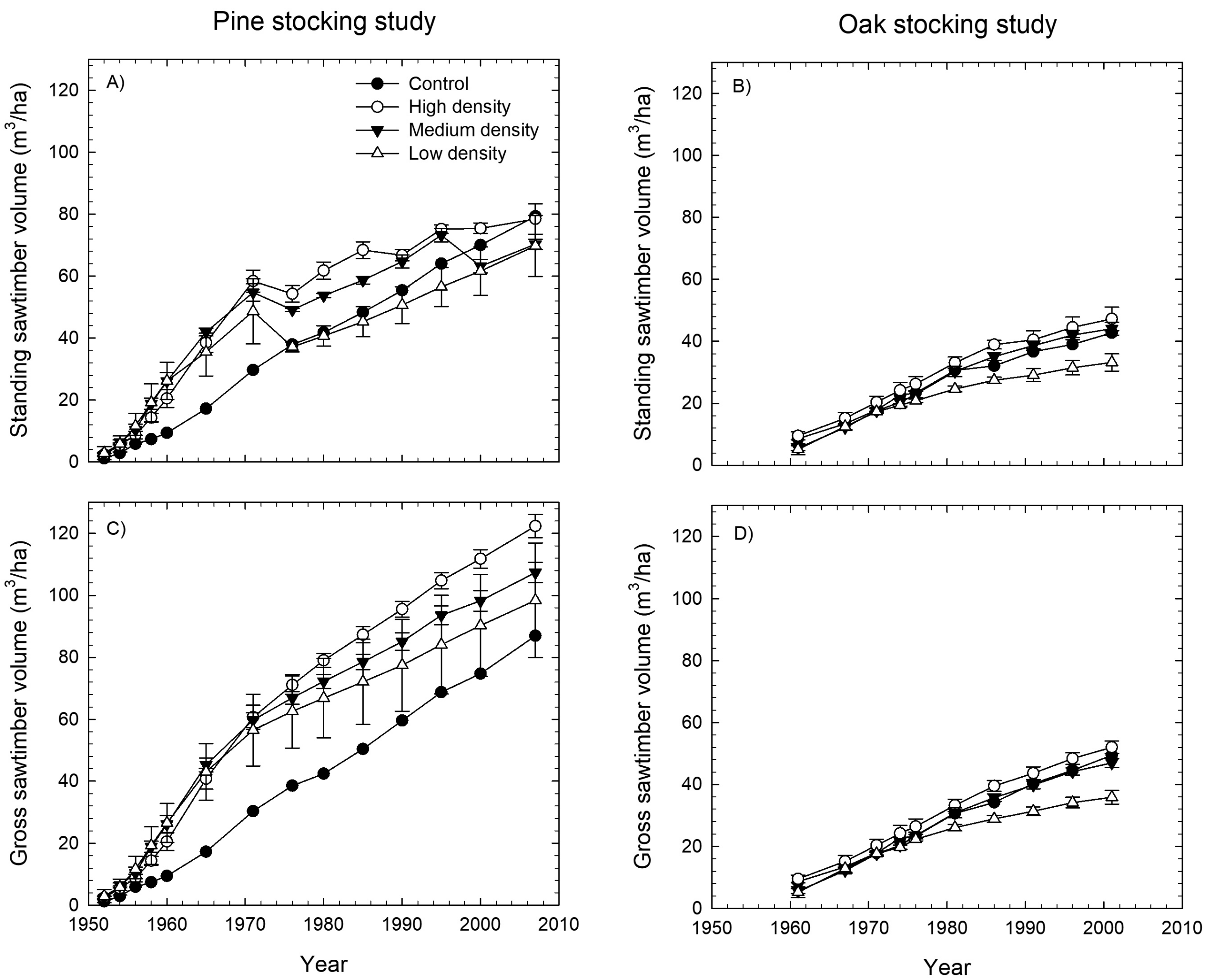

Figure 6. Sawtimber volume (mean ± one standard error) for the PSS and OSS, including: standing sawtimber volume through time by stand density treatment for PSS (A) and OSS (B); and gross sawtimber volume (including harvest or dead trees) through time by stand-density treatment for PSS (C) and OSS (D).

thinning operations, remained greater for each thinning treatment than the control throughout the study period, indicating the potential to increase financial opportunities and long-term carbon storage in forest products (McKinley et al. 2011). For both the pine and oak stands, gross sawtimber volume production was greatest in the high-density treatment and lowest in the low-density treatment. These results support an optimal level of stand density for balancing tree-level and stand-level production. Maintaining an overstocked condition reduces individual tree growth and limits the rate of sawtimber volume production, and maintaining an understocked condition does not use all available growing space.

As common with long-term empirical field experiments, there are important limitations to consider. Direct comparisons of the carbon dynamics for the pine and oak stands are complicated by differences in the experimental designs for each study. The pine study generally maintained consistent stand-density levels throughout the study period, but the oak stands were thinned only twice, the original thinning in 1961 and the second, lighter thinning in 1974. Consequently, there were few differences between the standing sawtimber volume and gross sawtimber volume in the oak study. For both studies, tree measurements were limited to individuals present when the studies were installed, without the addition of new trees growing into the stands through time. The removal of overstory trees can increase growth of midstory or understory vegetation, resulting in reallocation of some aboveground carbon (Chiang et al. 2008; Carroll et al. 2012). This is most likely when stand densities are below fully stocked levels; therefore, we expect the stand-level carbon storage was most strongly underestimated for the low-density and medium-density treatments in our study. Finally, our study is limited to estimates of live aboveground carbon of trees and does not consider carbon dynamics in deadwood, the understory, the forest floor, or belowground carbon pools.

Management Implications

Our results offer new insights into the role of forest management for carbon objectives. Protecting existing old-growth/primary forests is commonly recommended to prevent the loss of large amounts of stored carbon (Harmon et al. 1990; Luyssaert et al. 2008; Ameray et al. 2021), because the storage typically exceeds that of secondary forests and is understood to represent the capacity for a site or forest type (McKinley et al. 2011; McGarvey

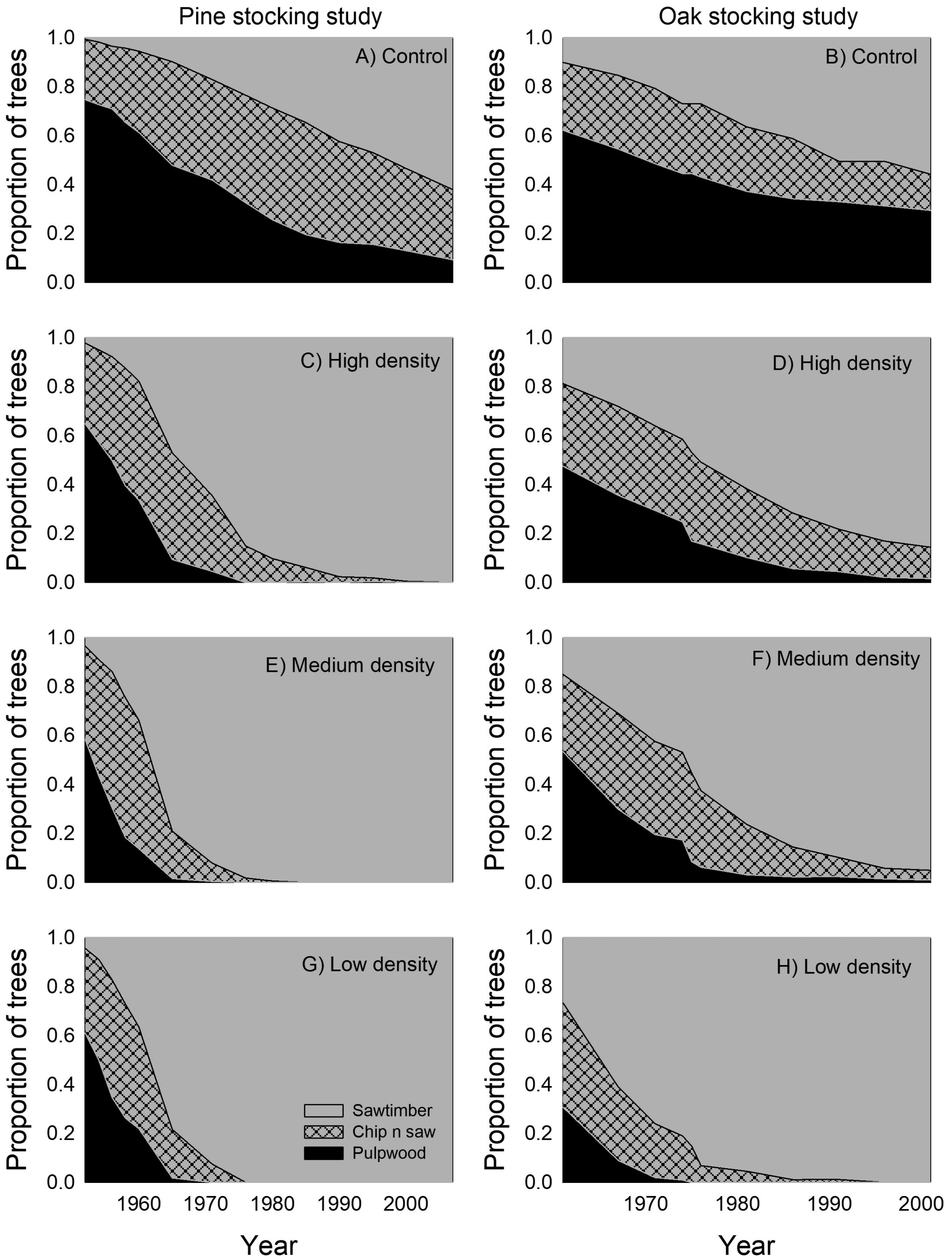

Figure 7. Proportion of trees in each product class through time for each stand-density treatment for PSS (A, C, E, G) and OSS (B, D, F, H).

et al. 2015). However, old-growth forests make up less than 5% of the forested area of the eastern United States (Davis et al. 1996), and, consequently, secondary forests constitute the majority of the landscape affecting carbon dynamics. Although some recommend using no management in secondary forests to maximize carbon benefit (Moomaw et al. 2019), our results show that thinning to maintain fully stocked but not overstocked conditions can increase stand-level sequestration and gross carbon accumulation in aboveground, live tree biomass. Carbon in harvested forest products may further contribute to long-term storage, although a full carbon life-cycle analysis is complex (Birdsey et al. 2006; McKinley et al. 2011) and unknown for this study.

Extending rotations is a commonly recommended forest management strategy to maintain high levels of carbon storage (D'Amato et al. 2011; Ontl et al. 2019; Ameray et al. 2021). Forest management systems designed to maximize timber production have traditionally determined rotation length based on economic efficiency, using silvicultural practices that shorten the rotation (Fox et al. 2007; Carroll et al. 2012). Although young stands have high rates of stand-level productivity (He et al. 2012; Tao and Williams 2013), carbon storage is compromised by short rotations, potentially reaching only 20% of carbon stored in old-growth or late successional forests (Cooper 1983; Carroll et al. 2012). In the central and northeastern regions of the United States, short-rotation production forestry is not common, with rotation ages for upland oak forests closer to 100 years (Knapp et al. 2014). The age structure of forestland across the region is characterized by an approximately normal distribution that peaks for stands established around the 1930s, similar to our study sites (Pan et al. 2011b; Shifley et al. 2014). Thus, many stands are currently nearing the typical rotation age. With the exception of stands dominated by more short-lived species, such as scarlet oak in the Ozark region, rotations may be further extended to increase carbon stores while using thinning to manage stand density and generate timber products. Alternatively, silvicultural practices may be used to transition to multi-aged structure through irregular shelterwood or selection systems (Loewenstein 2005; Raymond et al. 2009) to maintain carbon storage on-site in perpetuity.

Our results show that managing for carbon objectives can be compatible with production of sawtimber. Although we observed a trade-off between maximizing the standing carbon stored in aboveground biomass and sawtimber production in the pine stands, as has been shown with previous studies (Bradford and D'Amato 2012), the high-density thinning treatment had the greatest sawtimber volume production and the greatest gross carbon accumulation. Moreover, the thinning treatments increased sawtimber volume earlier in stand development, providing landowners more opportunity for financial return throughout the rotation. The optimal balance for both carbon and sawtimber volume production was the high-density thinning treatment, which was the only treatment that maintained fully stocked conditions throughout the study period. These results support an optimal stand-density level for production, above and below which production suffers.

Overall, our results support the use of thinning as a density management tool with benefits towards multiple use management for forestland that is not set aside as ecological forest reserves or used for intensive production forestry (Seymour and Hunter 1992). In addition to direct effects on biomass production and sawtimber yields, as reported in our study, density management is also important for addressing issues with forest health (Voelker et al. 2008; Clark and Schweitzer 2016) and maintaining characteristic forest structures (Dey et al. 2017; Bragg et al. 2020). The shortleaf pine and upland oak ecosystems of our study region are historically fire-maintained and can occur across a gradient of open canopy structure, and the removal of disturbance results in detrimental changes to ecosystem function (Hanberry et al. 2018). In open ecosystems, maximizing carbon storage in standing biomass may not align with other ecological considerations (Puhlick et al. 2022), highlighting the need to integrate the specific goals for carbon into the broader management context.

Acknowledgements

This research demonstrates the value of long-term forest experiments, and we appreciate the foresight and efforts of the USDA Forest Service scientists and technicians who designed, implemented, and maintained these studies during the past 50 to 70 years. We thank David Dick, Matthew Easton, David Mann, Kristy McAndrew, and Mike Rotondi for their assistance with recent data, as well as Texas Nall and Joseph DeRuiter III for their efforts to maintain the study over the years.

Funding

Funding for this research was provided by the USDA Forest Service, Northern Research Station and the National Institute of Food and Agriculture, U.S. Department of Agriculture, McIntire Stennis projects 233870 and 7001230.

Conflict of Interest

None declared.

Supplementary Materials

Supplementary data are available at *Forest Science* online.

Literature Cited

Adams, M.B., L. Loughry, and L. Plaugher. 2004. *Experimental forests and ranges of the USDA Forest Service*. USDA Forest Service, Gen. Tech. Rep. GTR-NE-321, Northeastern Research Station, Newtown Square, PA. 183 p.

Ameray, A., Y. Bergeron, O. Valeria, M. Montoro Girona, and X. Cavard. 2021. Forest carbon management: A review of silvicultural practices and management strategies across boreal, temperate and tropical forests. *Curr. For. Rep* 7(4):245–266.

Birdsey, R., K. Pregitzer, and A. Lucier. 2006. Forest carbon management in the United States. *Journal of Environmental Quality* 35(4):1461–1469.

Bradford, J.B., and A.W. D'Amato. 2012. Recognizing trade-offs in multi-objective land management. *Frontiers in Ecology and the Environment* 10(4):210–216.

Bragg, D.C., B.B. Hanberry, T.F. Hutchinson, S.B. Jack, and J.M. Kabrick. 2020. Silvicultural options for open forest management in eastern North America. *Forest Ecology and Management* 474(15):118383.

Brown, S., P. Schroeder, and R. Birdsey. 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. *Forest Ecology and Management* 96(1):37–47.

Burrascano, S., W.S. Keeton, F.M. Sabatini, and C. Blasi. 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *Forest Ecology and Management* 291:458–479.

Burton, J.I., A. Ares, D.H. Olson, and K.J. Puettmann. 2013. Management trade-off between aboveground carbon storage and understory plant species richness in temperate forests. *Ecological Applications* 23(6):1297–1310.

Carroll, M., B. Milakovsky, A. Finkral, A. Evans, and M.S. Ashton. 2012. Managing carbon sequestration and storage in temperate and boreal forests. P. 205–226 in *Managing Forest Carbon in a Changing Climate*. Mark S. Ashton, M.L. Tyrrell, D. Spalding, and B. Gentry (eds.) Springer, New York, NY.

Chiang, J.M., R.W. McEwan, D.A. Yaussy, and K.J. Brown. 2008. The effects of prescribed fire and silvicultural thinning on the aboveground carbon stocks and net primary production of overstory trees in an oak-hickory ecosystem in southern Ohio. *Forest Ecology and Management* 255(5):1584–1594.

Chojnacky, D.C., L.S. Heath, and J.C. Jenkins. 2013. Updated generalized biomass equations for North American tree species. *Forestry* 87(1):129–151.

Clark, S.L., and C.J. Schweitzer. 2016. Stand dynamics of an oak woodland forest and effects of a restoration treatment on forest health. *Forest Ecology and Management* 381(1):258–267.

Cooper, C.F. 1983. Carbon storage in managed forests. *Canadian Journal of Forest Research* 13(1):155–166.

D'Amato, A.W., J.B. Bradford, S. Fraver, and B.J. Palik. 2011. Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. *Forest Ecology and Management* 262(5):803–816.

Davis, M.B., S. Comers, C. Schaadt, A. Cook, J.M. Lynch, K. Seaton, R. White, A. Meier, J. Farrari, and B. Means. 1996. *Eastern Old-Growth Forests: Prospects for Rediscovery and Recovery*. Island Press, Washington, DC. 383 p.

Dey, D.C., J.M. Kabrick, and C.J. Schweitzer. 2017. Silviculture to restore oak savannas and woodlands. *Journal of Forestry* 115(3):202–211.

Dwyer, J.M., R. Fensham, and Y.M. Buckley. 2010. Restoration thinning accelerates structural development and carbon sequestration in an endangered Australian ecosystem. *Journal of Applied Ecology* 47(3):681–691.

Fahey, T.J., P.B. Woodbury, J.J. Battles, C.L. Goodale, S.P. Hamburg, S.V. Ollinger, and C.W. Woodall. 2010. Forest carbon storage: ecology, management, and policy. *Frontiers in Ecology and the Environment* 8(5):245–252.

Fox, T.R., E.J. Jokela, and H.L. Allen. 2007. The development of pine plantation silviculture in the southern United States. *Journal of Forestry* 105(7):337–347.

Franklin, J.F., T.A. Spies, R.V. Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmayer, *et al*. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155(1):399–423.

Galik, C.S., and R.B. Jackson. 2009. Risks to forest carbon offset projects in a changing climate. *Forest Ecology and Management* 257(11):2209–2216.

Gingrich, S.F. 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. *Forest Science* 13(1):38–53.

Gower, S.T., R.E. McMurtrie, and D. Murty. 1996. Aboveground net primary production decline with stand age: potential causes. *Trends in Ecology and Evolution* 11(9):378–382.

Hahn, J.T., and M.H. Hansen. 1991. Cubic and board foot volume models for the Central States. *Northern Journal of Applied Forestry* 8(2):47–57.

Hanberry, B.B., D.C. Bragg, and T.F. Hutchinson. 2018. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. *Ecosphere* 9(10):e02431.

Harmon, M.E., W.K. Ferrell, and J.F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. *Science* 247(4943):699–702.

Harmon, M.E., A. Moreno, and J.B. Domingo. 2009. Effects of partial harvest on the carbon stores in Douglas-fir/western hemlock forests: a simulation study. *Ecosystems* 12(5):777–791.

He, L., J.M. Chen, Y. Pan, R. Birdsey, and J. Kattge. 2012. Relationships between net primary productivity and forest stand age in U.S. forests. *Global Biogeochemical. Cycles* 26(3):GB3009.

Hoover, C., and S. Stout. 2007. The carbon consequences of thinning techniques: stand structure makes a difference. *Journal of Forestry* 105(5):266–270.

Houghton, R.A. 2005. Aboveground forest biomass and the global carbon balance. *Global Change Biology* 11(6):945–958.

Jenkins, J.C., D.C. Chojnacky, L.S. Heath, and R.A. Birdsey. 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49(1):12–35.

Kaarakka, L., M. Cornett, G. Domke, T. Ontl, and L.E. Dee. 2021. Improved forest management as a natural climate solution: A review. *Ecological Solutions and Evidence* 2(3):e12090.

Kabrick, J.M., K.L. Clark, A.W. D'Amato, D.C. Dey, L.S. Kenefic, C.C. Kern, B.O. Knapp, *et al*. 2017. Managing hardwood-softwood mixtures for future forests in eastern North America: Assessing suitability to projected climate change. *Journal of Forestry* 115(3):190–201.

Keeton, W.S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. *Forest Ecology and Management* 235(1):129–142.

Knapp, B.O., M.G. Olson, D.R. Larsen, J.M. Kabrick, and R.G. Jensen. 2014. Missouri Ozark Forest Ecosystem Project: A long-term, landscape-scale, collaborative forest management research project. *Journal of Forestry* 112(5):513–524.

Loewenstein, E.F. 2005. Conversion of uniform broadleaved stands to an uneven-aged structure. *Forest Ecology and Management* 215(1):103–112.

Lugo, A.E., F.J. Swanson, O.R. GonzáLez, M.B. Adams, B. Palik, R.E. Thill, D.G. Brockway, *et al*. 2006. Long-term research at the USDA Forest Service's experimental forests and ranges. *BioScience* 56(1):39–48.

Luyssaert, S., E. Schulze, A. Börner, A. Knohl, D. Hessenmöller, B.E. Law, P. Ciais, *et al*. 2008. Old-growth forests as global carbon sinks. *Nature* 455(7210):213–215.

McGarvey, J.C., J.R. Thompson, H.E. Epstein, and H.H. Shugart Jr. 2015. Carbon storage in old-growth forests of the Mid-Atlantic: toward better understanding the eastern forest carbon sink. *Ecology* 96(2):311–317.

McKinley, D.C., M.G. Ryan, R.A. Birdsey, C.P. Giardina, M.E. Harmon, L.S. Heath, R.A. Houghton, *et al*. 2011. A synthesis of current knowledge on forests and carbon storage in the United States. *Ecological Applications* 21(6):1902–1924.

McNulty, S., E. Treasure, L. Jennings, D. Meriwether, D. Harris, and P. Arndt. 2018. Translating national level forest service goals to local level land management: carbon sequestration. *Climate Change* 146(1):133–144.

Moomaw, W.R., S.A. Masino, and E.K. Faison. 2019. Intact forests in the United States: proforestation mitigates climate change and serves the greatest good. *Frontiers in Forests and Global Change* 2(27):1–10.

Nigh, T.A., and W.A. Schroeder. 2002. *Atlas of Missouri Ecoregions*. Missouri Department of Conservation, Jefferson City, MO. 212 p.

Ontl, T.A., M.K. Janowiak, C.W. Swanston, J. Daley, S. Handler, M. Cornett, S. Hagenbuch, *et al*. 2019. Forest management for carbon sequestration and climate adaptation. *Journal of Forestry* 118(1):86–101.

Palik, B.J., A.W. D'Amato, J.F. Franklin, and K.N. Johnson. 2020. *Ecological Silviculture: Foundations and Applications*. Waveland Press, Long Grove.

Pan, Y., R.A. Birdsey, J. Fang, R. Houghton, P.E. Kauppi, W.A. Kurz, O.L. Phillips, *et al*. 2011a. A large and persistent carbon sink in the world's forests. *Science*. 333(6045):988–993.

Pan, Y., J.M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011b. Age structure and disturbance legacy of North American forests. *Biogeosciences*. 8(3):715–732.

Powers, M., R. Kolka, B. Palik, R. McDonald, and M. Jurgensen. 2011. Long-term management impacts on carbon storage in Lake States forests. *Forest Ecology and Management* 262(3):424–431.

Pretzsch, H., M. Río, P. Biber, C. Arcangeli, K. Bielak, P. Brang, M. Dudzinska, *et al*. 2019. Maintenance of long-term experiments for unique insights into forest growth dynamics and trends: review and perspectives. *European Journal of Forest Research* 138(1):165–185.

Puhlick, J.J., S.T. Brantley, T.L. O'Halloran, L. Clay, and K.D. Klepzig. 2022. Perspectives: Carbon markets might incentivize poorer ecological outcomes in longleaf pine ecosystems. *Forest Ecology and Management* 520(15):120421.

Puhlick, J.J., A.R. Weiskittel, I.J. Fernandez, S. Fraver, L.S. Kenefic, R.S. Seymour, R.K. Kolka, *et al*. 2016. Long-term influence of alternative forest management treatments on total ecosystem and wood product carbon storage. *Canadian Journal of Forest Research* 46(11):1404–1412.

Raymond, P., S. Bédard, V. Roy, C. Larouche, and S. Tremblay. 2009. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. *Journal of Forestry* 107(8):405–413.

Rogers, R. 1983. Guides for thinning shortleaf pine. P. 217–225 in Proceedings of the second Biennial Southern Silvicultural Research Conference, Jones, E.J. (ed.). USDA Forest Service, Gen. Tech. Rep. GTR-SE-24, Southeastern Research Station, Asheville, NC.

Ryan, M.G., D. Binkley, and J.H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. P. 213–262 in *Advances in Ecological Research*, Begon, M., and A.H. Fitter (eds.). Academic Press, London.

Schaedel, M.S., A.J. Larson, D.L.R. Affleck, R.T. Belote, J.M. Goodburn, and D.S. Page-Dumroese. 2017. Early forest thinning changes aboveground carbon distribution among pools, but not total amount. *Forest Ecology and Management* 389(1):187–198.

Seymour, R.S., and M.L. Hunter. 1992. *New forestry in eastern spruce-fir forests: principles and applications to Maine*. College of Forest Resources, University of Maine Orono, ME, USA.

Shifley, S.R., W.K. Moser, D.J. Nowak, P.D. Miles, B.J. Butler, F.X. Aguilar, R.D. DeSantis, *et al*. 2014. Five anthropogenic factors that will radically alter forest conditions and management needs in the northern United States. *Forest Science* 60(5):914–925.

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton. 1997. *The Practice of Silviculture: Applied Forest Ecology*. John Wiley and Sons, Inc, 560 p.

Soil Survey Staff. 2022. Web Soil Survey. http://websoilsurvey.sc.egov.usda.gov/. Accessed March 23, 2022.

Spetich, M.A., and G.R. Parker. 1998. Distribution of biomass in an Indiana old-growth forest from 1926 to 1992. *American Midland Naturalist* 139(1):90–107.

Spetich, M.A., S.R. Shifley, and G.R. Parker. 1999. Regional distribution and dynamics of coarse woody debris in Midwestern Old-Growth Forests. *Forest Science* 45(2):302–313.

Stephenson, N.L., A.J. Das, R. Condit, S.E. Russo, P.J. Baker, N.G. Beckman, D.A. Coomes, *et al*. 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature*. 507(7490):90–93.

Tao, Y., and R.A. Williams. 2013. Carbon stocks and sequestration rates in oak-hickory forests of Ohio, USA. *Journal of Resources and Ecology* 4(2):115–124, 110.

Taylor, A.R., J.R. Wang, and H.Y.H. Chen. 2007. Carbon storage in a chronosequence of red spruce (*Picea rubens*) forests in central Nova Scotia, Canada. *Canadian Journal of Forest Research* 37(11):2260–2269.

Tyrrell, M.L., J. Ross, and M. Kelty. 2012. Carbon dynamics in the temperate forest. P. 77–107 in *Managing Forest Carbon in a Changing Climate*, Mark S. Ashton, M.L. Tyrrell, D. Spalding, and B. Gentry (eds.) Springer, New York, NY.

Voelker, S.L., R.M. Muzika, and R.P. Guyette. 2008. Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. *Forest Science* 54(1):8–20.

Waskiewicz, J., L. Kenefic, A. Weiskittel, and R. Seymour. 2013. Species mixture effects in northern red oak–eastern white pine stands in Maine, USA. *Forest Ecology and Management* 298(15):71–81.

Wilson, B.T., C.W. Woodall, and D.M. Griffith. 2013. Imputing forest carbon stock estimates from inventory plots to a nationally continuous coverage. *Carbon Balance Management* 8(1):1.

Woods, K.D., and C.C. Kern. 2022. Intermediate disturbances drive long-term fluctuation in old-growth forest biomass: an 84-yr temperate forest record. *Ecosphere* 13(1):e03871.

Zeide, B. 2001. Thinning and growth: A full turnaround. *Journal of Forestry* 99(1):20–25.