



The 'other' hardwood: Growth, physiology, and dynamics of hickories in the Central Hardwood Region, USA

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ABSTRACT

Hickories (*Carya* spp.) are common species in eastern US forests. Despite being a noted component of the most prevalent forest type in the eastern US, remarkably little is known about the ecology and silvics of the genera, especially compared to oaks (*Quercus* spp.). To improve our understanding about the dynamics of hickories in stand development and forest succession, we used a variety of datasets from oak-hickory forests of the Central Hardwood Region to assess growth, physiology, and demography. Our findings suggest that hickories may have a conservative root-centered growth strategy that exceeds that of oaks, with highly plastic physiology. This allows for long-term persistence of hickories in the mid and understory while being responsive to favorable increases in available light. The reproduction dynamics of hickories suggest a gradual and consistent recruitment to the mid and overstory in contrast to the single, unimodal age distribution of oaks following historic disturbance. This is achieved by periods of higher growth rates and lower mortality rates, especially in subordinate canopy positions when compared to oaks. These findings suggest that contemporary removal of historic disturbance regimes may continue to support hickory recruitment to the overstory, but active forest management is necessary to maintain the oak-hickory forest type in the Central Hardwood Region.

1. Introduction

Oak-hickory (*Quercus-Carya*) forests are the most prevalent forest type in the eastern US, and the research conducted toward understanding oak demography, recruitment, and best management practices is vast (e.g., Goodrum et al. 1971; Brose et al., 1999b; Kabrick et al. 2008a; Greenberg et al., 2013; Swaim et al. 2016; Johnson et al. 2019). However, relatively little attention has been given to the other eponym of this forest type, the hickories. Of the 19 species of hickory worldwide, 12 occur in eastern US forests where they provide important ecological goods and services, including timber products, wildlife habitat and hard mast. Although hickories typically co-occur with oaks, they are rarely dominant (Braun 1950; Monk et al. 1990). Thus, their specific ecological role in the oak-hickory forest community is not well understood (Rose

and Rosson 2007). With increasing threats to the resilience of oak-hickory forests from invasive insects, plants, pathogens, and mesophication (Shifley et al. 2014; Moser et al. 2016; Alexander et al., 2021) and their interactions with a changing climate (Wood et al., 2018), understanding the regeneration and recruitment processes of hickories is important for abating wholesale forest type transitions and reducing interruptions of important ecological goods and services.

In the Central Hardwood Region, the oak-hickory forest type represents 79 percent (5.4 million hectares) of the total forest land in the region (Brandt et al., 2014). Dominant species in the upland forest and woodland communities include black oak (*Q. velutina* Lam.), white oak (*Q. alba* L.), post oak (*Q. stellata* Wangenh.), northern red oak (*Q. rubra* L.), blackjack oak (*Q. marilandica* Münchh.), scarlet oak (*Q. coccinea* Münchh) and black hickory (*C. texana* Buckley), shagbark hickory

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[*C. ovata* (Mill.) K. Koch], pignut hickory [*C. glabra* (Mill.) Sweet], bitternut hickory [*C. cordiformis* (Wangenh.) K. Koch], and mockernut hickory [*C. tomentosa* (Lam.) Nutt]. However, most of these oak-dominated forests are in the process of a significant community composition shift, especially on productive sites (Nowacki and Abrams 2008; Fei et al. 2011). While large, mature oak and hickory trees still dominate the overstory of many stands, the regeneration layer is typically dominated by shade tolerant species such as maples (*Acer* spp.) and American beech (*Fagus grandifolia* Ehrh.), although there is notable variation across the region (e.g., McCarthy et al. 2001; Aldrich et al. 2005; McNab 2011). Declining oak regeneration success is likely due to a variety of factors, including 20th century fire suppression, land use changes, shade tolerance and successional dynamics, increased deer browsing, and mesophication (reviewed in McEwan et al. 2011). Management efforts to increase oak and hickory regeneration have focused on overstory reductions, prescribed burning and/or herbicide to increase light and reduce competition (Loftis 1990; Brose et al. 1999b; Brose et al. 2013; Brose et al. 2014). While oak regeneration has certainly benefited from these approaches (Barnes and Van Lear 1998; Iverson et al. 2008), there is a general lack of information about how hickories respond (separately from oaks). The prevailing paradigm is that hickories will display the same dynamics, and respond to the same management prescriptions, as the oaks.

Hickories are variously classified as intolerant to tolerant of shade (Smalley 1990; Smith 1990) with an ability to accumulate advance reproduction under moderately dense canopies (Iverson et al. 2017). These differences in perceived shade tolerance are often attributed to changes in light requirements with age; seedlings and saplings having higher shade tolerance and an ability to recover more rapidly following suppression than larger trees (Baker 1949, Trimble 1975). A recent study by Lefland et al. (2018) found hickory saplings up to 40 years old, suggesting that hickory may have considerable shade tolerance and thus the ability to persist in a suppressed state in the midstory and understorey. Similar to oaks, hickories have been reported to decline in forest understories without overstory disturbance (Peet and Christensen 1980; Sork 1983) or prescribed fire (Brose et al. 2013) and moderate increases in light levels from thinning or harvesting are believed to promote hickory recruitment to the forest overstory, particularly on dry sites (Iverson et al. 2017). However, there is a limited understanding on the capacity to create pools of hickory advance reproduction by modifying the light environment (Smith 1990) and further, a lack of information on the canopy recruitment dynamics of hickories.

We addressed uncertainties of hickory dynamics in the Central Hardwoods Region at scales ranging from the individual to the ecosystem, across broad temporal and spatial scales. Our synthesis included information on individual seedlings and seedling population responses to altered overstory light conditions, long-term patterns in recruitment and mortality in mature, unmanaged forests, and regional analyses of contemporary demographics. We used data from (1) greenhouse studies focused on seedling growth and physiology, (2) a long-term shelterwood study across two levels of site productivity, (3) unmanipulated permanent plots in two mature, unmanaged oak-hickory forests, and (4) region-wide inventories from the national Forest Inventory and Analysis (FIA) database (Table 1). For our purposes, the Central Hardwood Region refers to oak-hickory forests within selected Ecological Provinces described in Table 1 (see Fig. 1). Specifically, we sought to address the following questions:

- (1) How do juvenile growth and physiology of hickories compare to those of red and white oaks in a controlled greenhouse setting?
- (2) How does the abundance and growth of hickory reproduction compare to that of red and white oaks following changes to forest overstory conditions in the field?
- (3) What is the longevity of hickories in the midstory?

- (4) How do size distributions, growth, recruitment, and mortality of hickories compare to red and white oaks in mature, unmanaged forests?
- (5) What are the contemporary demographics of hickories across the Central Hardwood Region and how do they compare to oaks?

2. Methods

2.1. Seeding growth and physiology

To examine juvenile growth and physiology of hickories, we compared data from greenhouse grown mockernut and bitternut hickories to published data for similarly grown red and white oaks, as well as other species. Mockernut hickory seeds were collected in the Vinton Furnace Experimental Forest in southeastern Ohio in October 2005 and planted in April 2006. Bitternut hickory seeds were collected from the Delaware County Fairgrounds in central Ohio in October 2006 and planted in April 2007. Seedlings were grown over one growing season in a greenhouse at the USDA Forest Service Laboratory, Delaware, Ohio and harvested in October (2006 and 2007, respectively for mockernut and bitternut). For both species, seeds were planted in 15 cm diameter by 41 cm tall (7.3 L) PVC pots containing 2-parts mixed Metro-Mix 510 (Sungro Horticulture, Agawam, MA) to 1-part mixed fine loam (Buchanan-Ernest Series) forest soil collected in Monongalia County, WV. Day and night temperatures were maintained at 25 and 20 °C, respectively, and natural light was supplemented to create 12 h day⁻¹. We recorded stem height (cm), shoot diameter (mm, average of two measurements), root collar diameter (mm, average of two measurements), taproot length (cm), and total number of leaves. Total leaf area (leaf blade plus petiole) was determined using a LI-COR LI-3100 area meter (LI-COR Biosciences, Lincoln, NE). Seedlings were dissected into roots, leaves, stem, and branches and oven-dried at 70 °C to constant mass and weighed to determine the component mass. We calculated the root:shoot ratio as the proportion of belowground mass to aboveground mass without leaves. Additionally, for mockernut hickory, light response curves were conducted on 10–11 October 2007 on the first leaflet of a fully expanded leaf for 15 randomly selected seedlings using a LI-COR (Lincoln, Nebraska) 6200 portable photosynthesis system. Light response curves were generated in a climate-controlled greenhouse maintained at approximately 28 °C from 1000 to 1500 EST. Light levels included 0, 50, 100, 400, 800, and 1200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ with 3 min of equilibration time between light levels. From these light response curves, mean estimates of light compensation point, maximum carbon exchange rate, and quantum efficiency were derived from individual seedling curves fit to the Hanson model by a modified Gauss-Newton nonlinear iterative method until model convergence was achieved (SAS Institute Inc., 2012) using methods similar to Rebbeck et al. (2012).

2.2. Reproduction response to changes in the light environment

To examine the response of hickories, red oaks, and white oaks to changes in overstory light levels, we used data from a long-term shelterwood study that tracked the reproduction abundance by species group and height class across two levels of site productivity. The shelterwood experiments were located in mature (70 years old), even-aged stands on the Sinkin Experimental Forest (SEF, lat. 37.5°N, long. 91.3°W; Fig. 1), on the Mark Twain National Forest in the Ozark Highlands of southeastern Missouri. The studies were established in 1979 and 1980, on sites representing 'Average' and 'Good' productivity respectively, for the area (Table 1). Overstory treatments included harvesting to a residual stocking of 40, 50, or 60% (Ginrich 1967), leaving primarily the larger, more vigorous oaks (Schlesinger et al. 1993), in three complete blocks for each site type. Treatment units were 0.4 ha with 0.12 ha vegetation monitoring plots located in the center. The overstory was removed on all treatments in the winter of 1998–99,

Table 1
Study information including location, history, and treatments for each dataset.

Objective	Outcome	Study	Location ¹	Species	Site Index ²	Management History	Overstory Treatments ³		
Relate early growth and physiology of hickories to other species	biomass allocation; root-to-shoot ratio; light compensation point; maximum carbon exchange; dark respiration; quantum efficiency	Greenhouse	Delaware, OH	Hickories: <i>C. tomentosa</i> , <i>C. cordiformis</i>	X	X	X	X	X
Compare abundance and size of reproduction following reductions in overstory across two levels of site productivity	Reproduction abundance by height class over 18 years	Shelterwood 'Average Sites' ⁴	Sinkin Experimental Forest, Mark Twain National Forest, MO	Hickories: <i>C. texana</i> , <i>C. glabra</i> , <i>C. tomentosa</i> ; Red Oaks: <i>Q. coccinea</i> , <i>Q. velutina</i> ; White Oaks: <i>Q. alba</i> , <i>Q. muehlenbergii</i> ;	18 m	Shelterwood canopy reductions in spring 1981	40% stocking	50% stocking	60% stocking
		Shelterwood 'Good Sites' ⁴			23 m	Shelterwood canopy reductions in winter 1979–80	40% stocking	50% stocking	60% stocking
Determine the persistence of hickories in the midstory	Age by diameter	Demo burn ⁵ , Wolf oak ⁶ , and other adjacent areas Study 27 ⁷	Vinton Furnace Experimental Forest, OH	Hickories: <i>C. glabra</i> , <i>C. tomentosa</i>	17–20 m	Second-growth originating from the mid- to late 1800s	X	X	X
Compare size distribution, growth, recruitment, and mortality in undisturbed forests	DBH class distribution; diameter growth rate; recruitment rate; mortality rate		Vinton Furnace Experimental Forest, OH	Hickories: <i>C. glabra</i> , <i>C. ovata</i> , <i>C. cordiformis</i> , <i>C. tomentosa</i> ; Red Oaks: <i>Q. rubra</i> , <i>Q. velutina</i> , <i>Q. coccinea</i> ; White oaks: <i>Q. alba</i> , <i>Q. montana</i> ;	20–22 m	Second-growth originating from clearcutting in 1868	X	X	X
		Kaskaskia Woods ⁸	Kaskaskia Experimental Forest, Shawnee National Forest, IL	Hickories: <i>C. ovata</i> , <i>C. ovalis</i> , <i>C. tomentosa</i> ; Red Oaks: <i>Q. rubra</i> , <i>Q. velutina</i> , <i>Q. coccinea</i> ; White oaks: <i>Q. alba</i> ;		Never cleared. Selective harvesting occurring in 1880s and 1910s	X	X	X
Assess contemporary demographics across the entire Central Hardwoods Region	stem abundance; relative abundance of advanced reproduction; overstory crown class; recruitment rate; mortality rate	Region-wide Status and Assessment	Forest Inventory and Analysis: 10,170 plots across six Ecological Provinces within the Central Hardwood Region	Hickories: <i>C. glabra</i> , <i>C. ovata</i> , <i>C. cordiformis</i> , <i>C. tomentosa</i> , <i>C. texana</i> ; Red Oaks: <i>Q. rubra</i> , <i>Q. velutina</i> , <i>Q. coccinea</i> , <i>Q. falcata</i> , <i>Q. marilandica</i> , <i>Q. ellipsoidalis</i> , <i>Q. imbricaria</i> , <i>Q. shumardii</i> , <i>Q. palustris</i> ; White oaks: <i>Q. alba</i> , <i>Q. montana</i> , <i>Q. stellata</i> , <i>Q. macrocarpa</i> , <i>Q. muehlenbergii</i> , <i>Q. bicolor</i> ;		Mature (>75 years) oak-hickory stands with no history of disturbance or treatment within the past 5–7 years	X	X	X

¹ Ecological Provinces (see Cleland et al. 2007; McNab et al. 2007) within the Central Hardwood Region Midwest Broadleaf Forest (222), Central Interior Broadleaf Forest (223), Ozark Broadleaf Forest (M223), Central Appalachian Mixed Forest (M221), Prairie Parkland Temperate, and western portions of Eastern Broadleaf Forest Province (221).

² Site index based on a based age of 50 for black oak (*Q. velutina*).

³ Overstory shelterwood treatments retained residual stocking levels based on Ginrich 1967. Establishment cuts retained the larger, more vigorous oaks with removals down to 4.1 cm DBH.

⁴ Soils included Clarksville gravelly silt loam and Coulstone very gravelly silt loam (Loamy-skeletal, siliceous, semiactive, mesic Typic Paleudults) and Scholten gravelly silt loam (Loamy-skeletal, siliceous, active, mesic Typic Fragiudults).

⁵ Soils included Germano fine sandy loam (Coarse-loamy, mixed, mesic Typic Hapludults), Gilpin channery silt loam (Fine-loamy, mixed, active, mesic Typic Hapludults), and Rarden silt loam (Fine, mixed, active, mesic Aquultic Hapludalts).

⁶ Soils included Gilpin channery silt loam (Fine-loamy, mixed, active, mesic Typic Hapludults) and Steinsburg gravelly loam (Coarse-loamy, mixed, mesic Typic Dystrochrepts).

⁷ Soils included Germano fine sandy loam (Coarse-loamy, mixed, mesic Typic Hapludults), Gilpin channery silt loam (Fine-loamy, mixed, active, mesic Typic Hapludults), and Steinsburg gravelly loam (Coarse-loamy, mixed, mesic Typic Dystrochrepts).

⁸ Soils included Alford silt loam (Fine-silty, mixed, superactive, mesic Ultic Hapludalts).

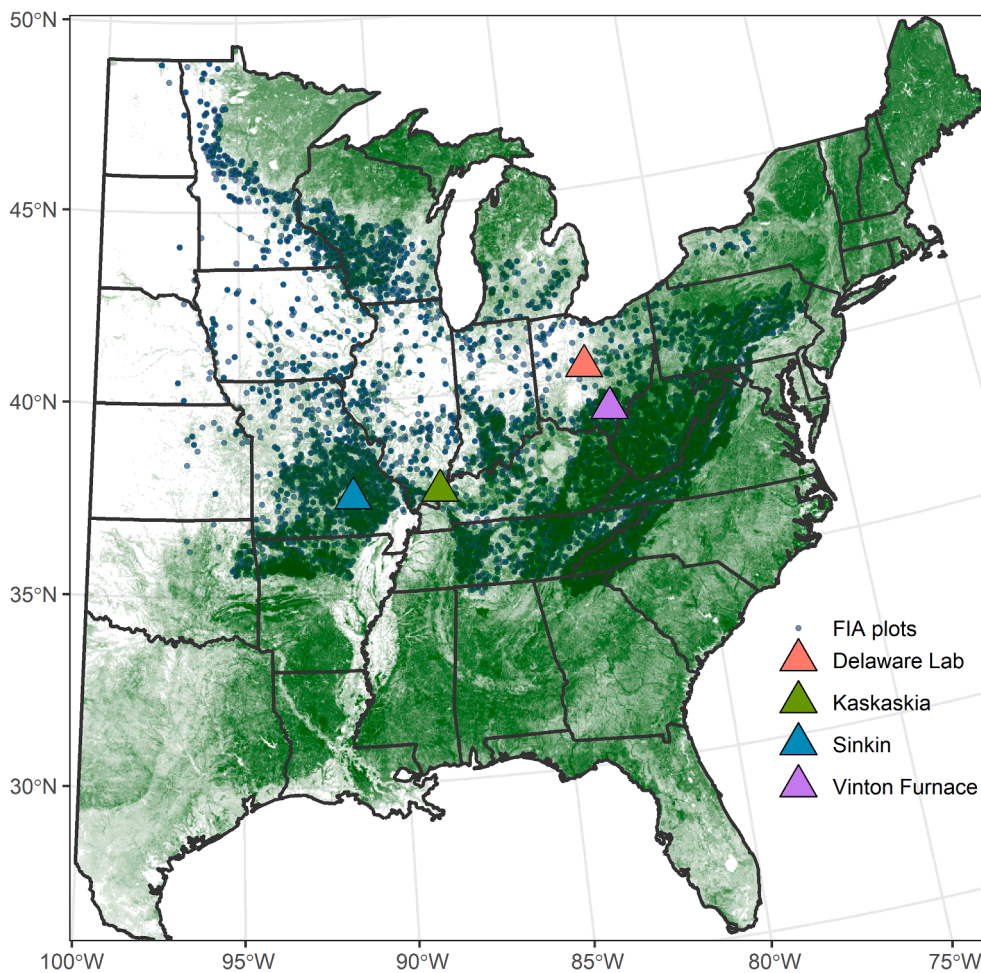


Fig. 1. Map of hardwood forests in the eastern US displayed as NLCD estimated canopy cover obtained from <https://www.mrlc.gov/data>. Blue circles indicate Forest Inventory and Analysis (FIA) plots within the Central Hardwood Region. Study locations: 1) Delaware Lab (greenhouse), 2) Kaskaskia Experimental Forest (mature, unmanaged forest), 3) Sinkin Experimental Forest (shelterwood management), and 4) Vinton Furnace State Experimental Forest (mature, unmanaged forest and midstory persistence). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

one year prior to the final measurement (year 18). Reproduction was measured on twenty 1.13 m radius subplots nested within each vegetation plot. Subplots were measured during the winter for pre-treatment (1979 and 1980), 1 or 2 years post-overstory treatment (for Average and Good sites, respectively) and again after years: 4 (1981–1982), 10 (1989–90), 15 (1997–1998), and 18 (1999–2000) post-treatment. During each measurement, the number of stems were tallied by species and by 10 cm height classes up to 250 cm tall.

For analysis, plots were averaged to the treatment unit level by species group (hickories, red oaks, and white oaks) and one of three height classes: small (0–50 cm), medium (51–150 cm), and large (151–250 cm) reproduction. Due to differences in the sequencing of plot censuses, we analyzed the two site class types separately. Reproduction abundance was compared across species groups and overstory residual stocking treatments for each height class within a site type by using a repeated measures analysis of variance. The repeated measures linear mixed effects model included fixed effects of treatment, species group, and their interaction with block specified as a random factor. As our data violated the assumption of sphericity, the Huynh-Feldt epsilon correction based on [Lecoutre \(1991\)](#) was employed.

2.3. Midstory persistence

To explore the potential longevity of hickory currently occupying the midstory of mature mixed-oak stands, we collected basal cross-sections from 49 live hickory stems, ranging from 4 to 22 cm DBH. The cross-sections were obtained in 2007–2008 from mature, mixed-oak stands at Vinton Furnace Experimental Forest (VFEF, 39.11N, 82.22W; [Fig. 1](#)) in southeast, OH. The VFEF is located within the Southern Unglaciated

Allegheny Plateau Section. Approximately one-half of the cross-sections were collected from two SW-facing stands, the Demo Burn ($n = 12$), and Wolf Oak ($n = 11$) and the remainder were collected from a variety of upland stands at VFEF. In the laboratory, cross-sections were sanded with progressively finer sandpaper to reveal the detail of annual rings. Rings were magnified and counted under a dissecting microscope. Given the exploratory nature of this information, we limited our analysis to simple summary statistics for stem age.

2.4. Long-term dynamics under minimal disturbance

We examined the successional dynamics of hickories, red oaks, and white oaks in forests without recent disturbance using data from two long-term permanent plot series. The first (Study 27) is located at VFEF. Study 27 originated from secondary regrowth stands after clearcutting for the charcoal iron industry around 1868. Three 0.4 ha plots were established in 1977, with every tree >9 cm DBH marked and identified to species. Each subsequent year, DBH was re-measured, dead trees noted and removed from the database, and new recruits added (i.e., those that have reached the minimum DBH size of 9.0 cm). These stands are on sites of average to good productivity for the area and have an overstory dominated by oaks and hickories ([Table 1](#)). We used 40 years of data (from 1979 to 2019) in our analyses (described below).

The second set of long-term forest plots are from Kaskaskia Experimental Forest (KEF, 37°30'N, 88°30'W) which is located in the Interior Low Plateau-Shawnee Hills in southeastern Illinois. Kaskaskia Woods, a special management area within the KEF, was never cleared, however selective harvesting of large oaks, hickories, and yellow-poplar (*Liriodendron tulipifera* L.) likely occurred in the 1880s for railroad ties

(Zaczek et al. 2002) (Table 1). A second selective harvest for white oak and some hickory also occurred in the 1910s but no additional disturbances have occurred in the last 100 years. Kaskaskia Woods has many of the characteristics of an old-growth deciduous forest and many of the overstory trees are over 150 years old and up to 160 cm DBH (Zaczek et al. 2002). In 1935, eight 0.1 ha plots were established with every tree >4.0 cm DBH marked and identified to species. The plots were re-measured in 1940, 1958, 1963, 1973, 1978, 1983, 1992, 1997 and 2012. We used 77 years of data (from 1935 to 2012) in our analyses (described below).

Our analyses of the two long-term, permanent plot series included four metrics of comparison between hickories, red oaks, and white oaks: (1) the change in size class distributions over time, (2) relative growth rates, (3) recruitment rates and (4) mortality rates. For each location, the size class distributions from the first and last measurement years were compared with a Kolmogorov-Smirnov (KS) test. This statistic is used to test for similarity between distributions without any parametric assumptions. Due to the multiple KS tests that we ran, we used an alpha value of 0.01 to test for significance to minimize Type I error rates. Relative basal area (BA) growth rates for each tree (hereafter BA growth) were calculated with the formula (Hunt 1982; Pommerening and Muszta 2016) for mean annual growth rate (also called periodic relative increment):

$$\frac{\log(BA2) - \log(BA1)}{\text{years}}$$

where BA2 is the basal area in the final year it was measured (i.e., either the year before it died or the final census year), and BA1 is the basal area from the first year. Years represent the total number of years between the two measurements. Mean annual growth rates are intended to be a standardized measure of growth, to directly compare growth between large and small individuals. However, BA growth may be influenced by initial size as BA growth appears to decline in larger individuals (Pommerening and Muszta, 2016). Thus, we compared BA growth for smaller (i.e., DBH ≤ 25 cm) and larger individuals (DBH > 25 cm) based on their first measurement.

Annual mortality rates were calculated with the formula (Sheil et al., 1995):

$$m = 1 - [1 - N_t/N_0]^{1/t}$$

where N_0 is the number of trees alive in the previous census, N_t is the number of trees that died between the previous and current census, and t is the time between censuses in years. Annual recruitment rates were calculated with a similar formula, where N_r is the number of recruited trees since the previous census (Dionisio et al. 2018):

$$r = 1 - [1 - N_r/N_0]^{1/t}$$

To compare recruitment and mortality rates between VFEF and KEF, we binned census data from VFEF into decadal time slices (i.e., since VFEF had annual re-measurements). Relative growth rates (% year⁻¹), mortality (% year⁻¹) and recruitment (% year⁻¹) rates were all compared between the three groups (hickories, red oaks, and white oaks) with an ANOVA and Tukey-Kramer post-hoc comparisons.

2.5. Region-wide status and assessment

For a region-wide assessment of contemporary hickory and oak demographics we used publicly available Forest Inventory and Analysis (FIA) data (Bechtold and Patterson 2005; USDA Forest Service 2020) for the Central Hardwood Region. We defined the Central Hardwood region as FIA plots that fell within the oak-hickory forest type (see Arner et al. (2004) of select Ecological Provinces (see Cleland et al. (2007); McNab et al. (2007) for greater detail) (Table 1, Fig. 1). We selected only 'mature' plots (i.e., 'regeneration eligible' sensu Vickers et al. (2019); age ≥75 years with medium-large diameter stems predominant) with no

history of disturbance or treatment in the past 5–7 years.

We used the rFIA package (Stanke et al. 2020) for R statistical Software (R Core Team 2020) to calculate five comparative metrics for hickories, oaks, and other species from the FIA data. Our assessment included region-wide (i.e., population level sensu Pugh et al. (2018)) estimates of (1) absolute and (2) relative stem abundance by crown class (see Burrill et al. (2017)), (3) recruitment rates, (4) mortality rates, and (5) mortality rates by crown class. Estimates of absolute and relative density included both advance reproduction (DBH < 2.5 cm, total height ≥ 30.5 cm) and larger stems (DBH ≥ 2.5 cm). Estimates of recruitment and mortality rates included stems ≥ 12.7 cm DBH. We used the variance and sample sizes (number of measured plots in domain of interest) provided by rFIA to produce 95% confidence intervals around each estimate. All estimates reflect forestland conditions circa 2017.

3. Results

3.1. Seedling growth and physiology

After one growing season, both bitternut and mockernut hickories allocated much more growth below ground than to aboveground structures (Table 2). Leaf area averaged 173.2 ± 112.8 and 277.7 ± 155.3 cm² for bitternut hickory and mockernut hickory, respectively. The root:shoot ratios of bitternut (4.08 ± 0.15) and mockernut hickory (3.93 ± 0.09) were comparable to each other, but larger than what has been documented for several oaks and other associated species (Fig. 2). While all species of hickories and oaks examined allocated more to belowground than aboveground structures, the root:shoot ratio for the two hickories were approximately 33% greater than white oak and 150% greater than northern red oak and chestnut oak. In contrast, sugar maple (*Acer saccharum* Marshall) and yellow-poplar (*Liriodendron tulipifera* L.) allocated more to aboveground structures. The mean light compensation point of mockernut hickory was 8.371 ± 0.297 μmol·m⁻²·s⁻¹, with a quantum efficiency of 0.0343 ± 0.001 μmol·μmol⁻¹, a maximum carbon exchange rate of 8.87 ± 0.35 μmol CO₂·m⁻²·s⁻¹, a dark respiration of -0.822 ± 0.34, and a stomatal conductance of 0.208 ± 0.015 mol·m⁻²·s⁻¹ (Fig. 3). The light compensation point of mockernut hickory was similar to published values for white oak, but lower than other oaks and yellow-poplar (Table 3). Mockernut hickory had the highest maximum carbon exchange rate of the species examined.

3.2. Reproduction response to overstory manipulation

Our analysis of the shelterwood study, which included overstory reductions to 40–60% stocking, showed those differences in residual

Table 2

Size and mass metrics (mean ± standard deviation) for bitternut hickory (*C. cordiformis*) and mockernut hickory (*C. tomentosa*) nut-origin seedlings after one growing season under greenhouse conditions in Delaware, OH. Biomass includes weight (g) and proportion (%) of total seedling biomass in parentheses.

Species	Size			
	Stem Height (cm)	Stem Diameter (mm)	Root Collar Diameter (mm)	Taproot Length (cm)
Bitternut hickory	16.0 ± 3.9	2.6 ± 0.8	4.5 ± 0.8	37.0 ± 2.7
Mockernut hickory	14.5 ± 3.7	4.2 ± 1.0	7.0 ± 1.6	33.6 ± 7.1
Species	Biomass			
	Leaf (g)	Stem (g)	Taproot (g)	Total (g)
Bitternut hickory	0.92 ± 0.49 (11.9%)	0.69 ± 0.37 (9.5%)	5.41 ± 2.42 (73.8%)	7.39 ± 3.38
Mockernut hickory	1.98 ± 1.40 (11.1%)	1.67 ± 0.86 (10.0%)	12.73 ± 6.39 (75.1%)	17.0 ± 8.53

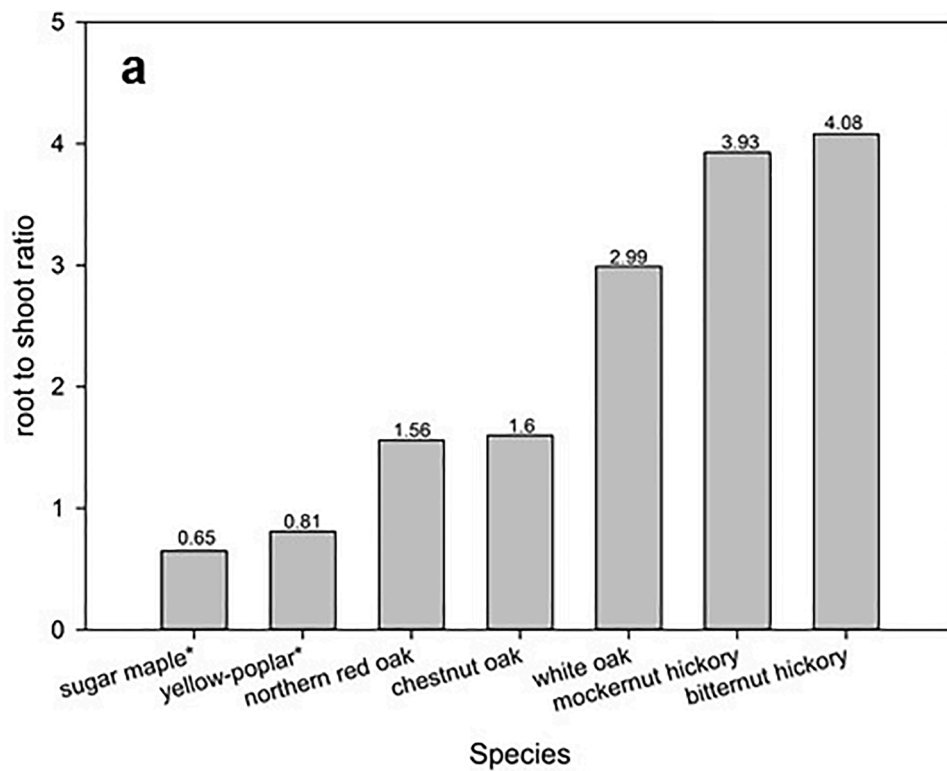


Fig. 2. (a) Root:shoot for mockernut hickory (*C. tomentosa*), bitternut hickory (*C. cordiformis*) and associated species grown under greenhouse conditions. Sugar maple (*A. saccharum*) and yellow-poplar (*L. tulipifera*), root:shoot are from Tjoelker and Luxmore (1991), Tjoelker et al. (1993). (b) Three randomly selected mockernut hickory seedlings harvested following one growing season under greenhouse conditions. Centimeter scale placed for reference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



stocking level were not important for the mean abundance of reproduction in any circumstance examined. Reproduction abundance of hickories and oaks were much greater on Average sites than Good sites, though we note the two sites were analyzed independently (Fig. 4). This reduction in reproduction density between sites is likely due to increased competition from other species on higher quality sites (Appendix A). For both site productivity types, there were differences in the response of species group by height class since the initial shelterwood harvest, but the importance of these effects varied by site (Appendix B).

Generally, on both sites, hickories had consistent abundance across height classes through time (Fig. 4). However, red oaks accumulated individuals into the next tallest size class as time progressed. White oaks

responded immediately to overstory reductions with increases in the abundance of reproduction across height classes, but these gains were lost as time continued. Large-sized reproduction was present for all species and time periods on Average sites with no general trends. However, on Good sites, large reproduction of hickories and red oaks increased through time, whereas large reproduction of white oaks increased initially and then declined.

3.3. Midstory persistence

The mean and median ages of sapling and pole-sized hickories harvested at VFEF were 77 and 73 years, respectively, indicating a capacity

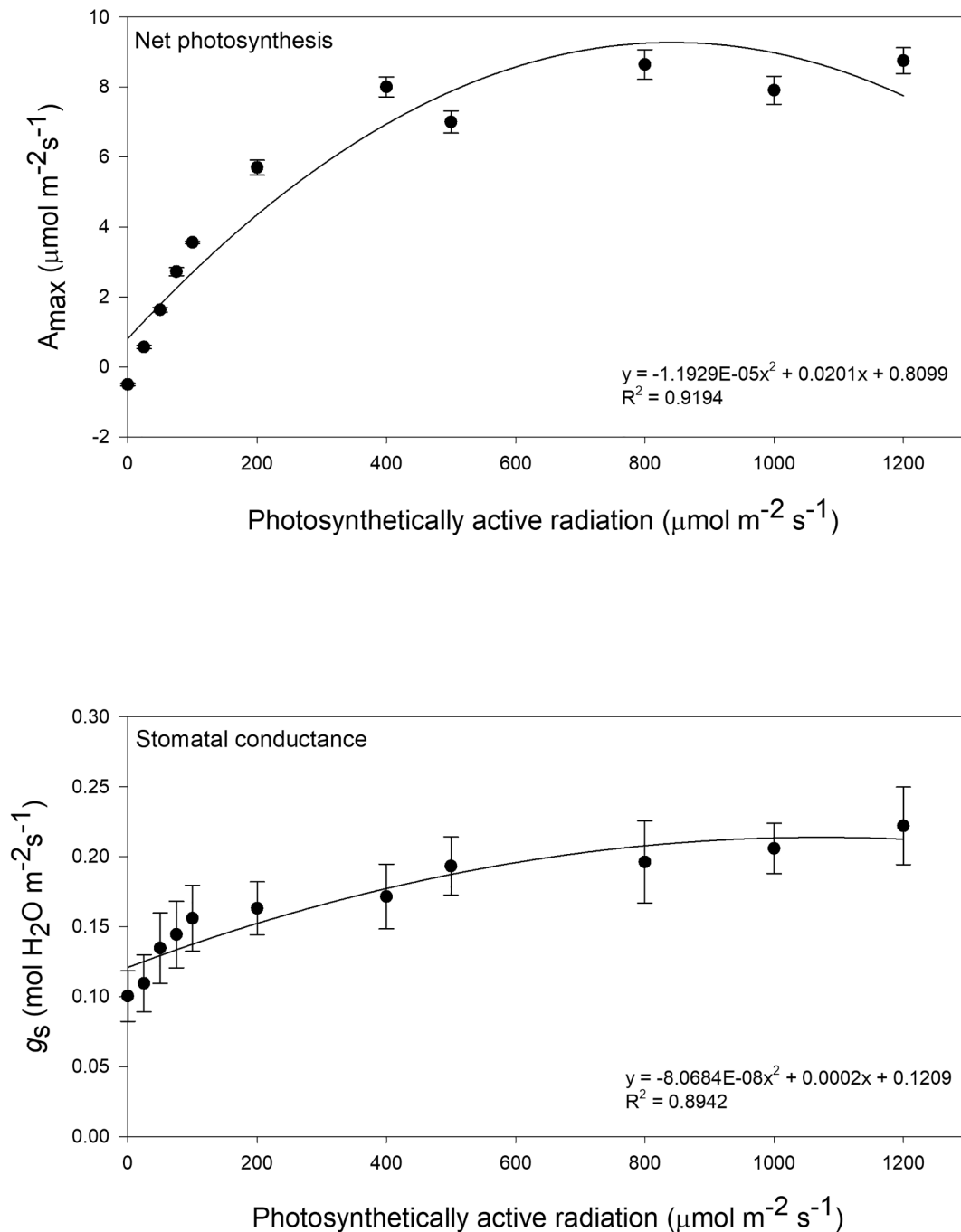


Fig. 3. Photosynthetic light response curves of mockernut hickory (*C. tomentosa*) seedlings grown under greenhouse conditions. Mean estimates of light compensation point, maximum carbon exchange rate, quantum efficiency, and dark respiration were derived from these curves (see Table 3).

for long-persistence in the understory and midstory (Fig. 5). The oldest sampled midstory hickories (>130 years) were found at the most xeric collection site (the Demo Burn site).

3.4. Stand dynamics in mature, unmanaged forests

In mature, unmanaged forests at VFEF, the size distribution of hickories showed no change over time, but red oaks and white oaks had a significant shift into the larger size classes (Fig. 6a). Over time, hickories continued to occupy small size classes (Fig. 6a). For small trees, hickories had higher relative growth rates than white oaks (Fig. 6b; $F_{2,65} = 4.1$, $P = 0.02$), but, there was no difference in relative growth rates for large trees (Fig. 6c; $F_{2,189} = 0.23$, $P = 0.80$). However, it is important to

note the rarity of large hickories and small red oaks at this site. The shift demonstrated for oaks is typical of an even-aged maturation process where oaks move into larger size classes with a lack of new recruits (Fig. 6d, e). Hickories, in contrast, had higher absolute recruitment numbers (Fig. 6d) and higher recruitment rates (Fig. 6e), although the difference in recruitment rates was not statistically significant ($F_{2,9} = 3.2$, $P = 0.09$). Mortality rates for hickories also did not significantly differ from the oaks (Fig. 6f; $F_{2,9} = 0.36$, $P = 0.70$). Red oaks recruited a single stem into the tree size class during the forty years examined. Most of the new recruits were shade-tolerant species; red maple (*Acer rubrum* L., 57% of all new recruits), blackgum (*Nyssa sylvatica* Marshall, 14%) and sourwood [*Oxydendrum arboreum* (L.) DC., 8%] (Appendix C). Collectively, these results are indicative of an on-going self-thinning

Table 3
Photosynthetic light response parameter estimates for selected upland hardwood seedlings.

Species	Light compensation point ³ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Maximum carbon exchange rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$)	Dark respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$)	Quantum efficiency ⁴ (μmol^{-1})
Mockernut hickory	8.37 ± 0.30	8.87 ± 0.35	-0.82 ± 0.34	0.034 ± 0.001
Chestnut oak ¹	19.92 ± 2.31	5.73 ± 0.50	-1.13 ± 0.15	0.062 ± 0.002
Northern red oak ¹	15.72 ± 1.83	6.44 ± 0.25	-0.74 ± 0.08	0.054 ± 0.007
White oak ¹	7.16 ± 1.39	7.03 ± 0.40	-0.32 ± 0.07	0.047 ± 0.001
Yellow-poplar ²	43.30 ± 9.90	5.33 ± 0.92	0.77 ± 0.14	0.022 ± 0.002

¹ Rebbeck et al. 2012 CJFR 42:1025-1037.

² Rebbeck and Loats 1997 CJFR 27:1595-1605.

³ Light compensation point – Light level at which photosynthesis (carbohydrate gain) equals respiration (carbohydrate loss). Note: Photosynthetically active radiation in undisturbed stands is approximately 30–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

⁴ Quantum efficiency – the molar ratio between oxygen released in photosynthesis (or carbon assimilated) to photons absorbed in the process.

process for oaks, but one that is progressing more rapidly for red oaks than white oaks.

For KEF, all three groups showed a significant shift in size distributions (Fig. 7a) although hickories still had a higher density of small-sized trees compared to red and white oaks. Hickories and white oaks had similar growth rates, while red oaks had significantly higher relative growth rates in both small trees (Fig. 7b; $F_{2,167} = 9.16, P < 0.01$) and large trees (Fig. 7c; $F_{2,65} = 28.9, P < 0.01$). Mortality rates were similar (Fig. 7f; $F_{2,21} = 0.67, P = 0.52$) as were recruitment rates (Fig. 7e; $F_{2,21} = 1.58, P = 0.23$). Recruitment at KEF has generally been low for

hickories and oaks, with red oaks having 0 new recruits recorded in these plots for 77 years (Fig. 7d). Recruitment at this site was dominated by sugar maple (56% of all new recruits), and white ash (*Fraxinus americana* L.; 18%) (Appendix C).

3.5. Region-wide contemporary demographics

Across mature oak-hickory forests in the Central Hardwood Region, hickories are less abundant on average than oaks in virtually all crown classes (Fig. 8a). Hickories more closely approximate the classic ‘reverse j’ size structure decreasing in abundance with increasing size (represented by crown class) and are remarkably consistent in relative abundance across crown classes at 6–11% (Fig. 8b). In contrast, codominant oaks were highly abundant; there were nearly 3 times as many codominant oaks per hectare compared to intermediate oaks and 1.5 times more codominant oaks than overtopped oaks. Differences between oak and hickory abundance generally increased with advancing crown class, with oaks being 4–5 times more abundant than hickories in dominant and codominant positions.

Differences in mortality rates between oaks and hickories also varied across crown classes in mature stands, with oak mortality rates becoming increasingly greater in both absolute terms and relative to hickory with decreasing canopy position (Fig. 8c). Generally, hickories had lower rates of mortality, and this difference was most pronounced in overtopped stems where oaks displayed much greater rates of mortality. The hickory mortality rate was lower than other species in codominant and intermediate positions and nominally so in overtopped positions. In contrast, oaks, with a mortality rate over 4.0% for overtopped trees, were markedly less persistent than hickories or other species which averaged 1.3% and 1.6% trees·ha⁻¹·yr⁻¹, respectively.

Not only were overtopped hickories more persistent survivors than oaks, their recruitment rate (into the 12.7 cm size class) was also more than twice that of oaks (1.74% vs 0.73% trees·ha⁻¹·yr⁻¹, Fig. 8d). Comparative demographics indicate that oaks in mature forests are a

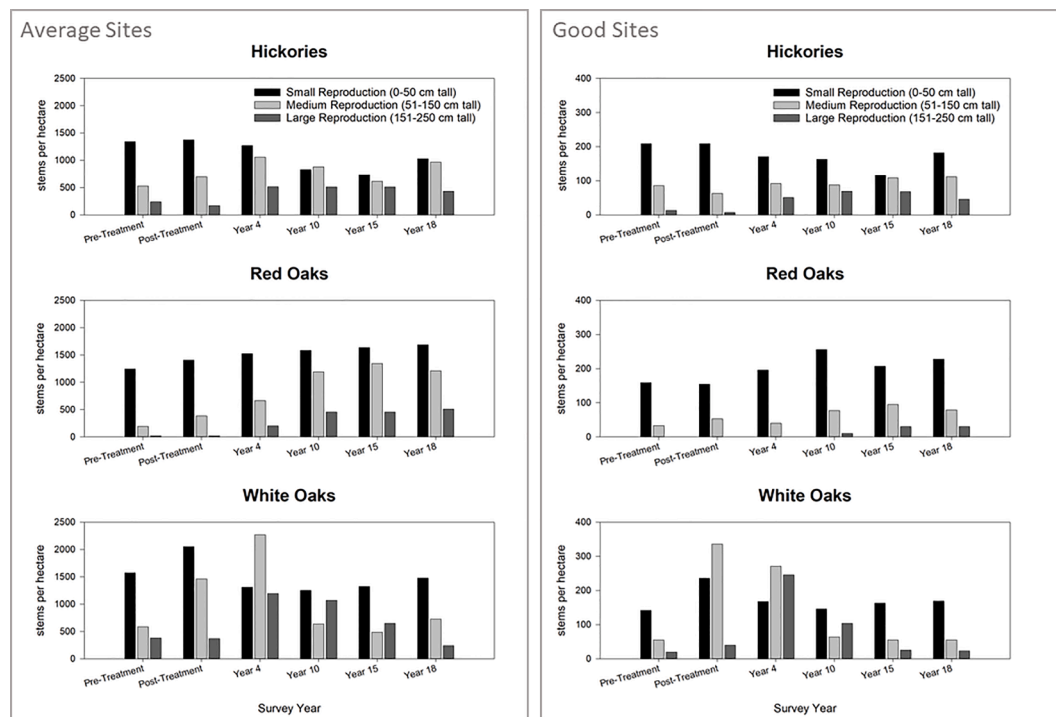


Fig. 4. Density of reproduction by height class (small: 0–50 cm tall, black bars; medium: 51–150 cm tall, light grey bars; large: 151–250 cm tall, dark grey bars) through time following shelterwood (reductions to 40–60% stocking) establishment cuts on Average (SI: 18 m) and Good (SI: 23 m) sites on the Sinkin Experimental Forest (SEF). Pre-treatment data are prior to establishment cut, post-treatment is one growing season following establishment cut, and year 18 is one growing season following the final overstory removal.

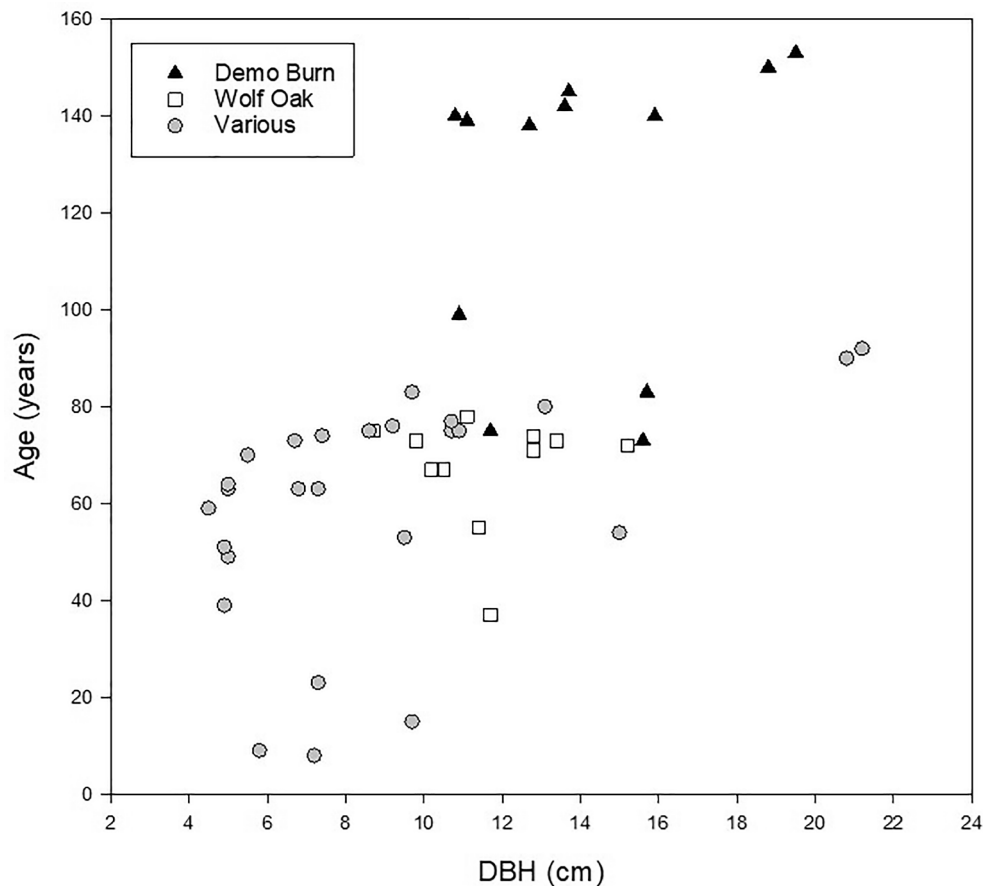


Fig. 5. Diameter at breast height (DBH) and age (ring counts from basal cross-sections) of 49 midstory hickory saplings and poles, collected from the Vinton Furnace Experimental Forest (VFEF) in southeastern Ohio.

much more dynamic population than hickories, but one that, by net abundance, declines without disturbance. Average annual recruitment of oaks replaced only about half of the trees lost to mortality (Fig. 8e) while hickory recruitment was net positive, on average, and nearly 2.5 times that of oak species.

4. Discussion

Our study highlights that hickories exhibit some life history traits that are distinct from oaks, notably in terms of growth and recruitment. As seedlings, (1) the root-centered growth of hickories is comparable and may exceed that of oaks and (2) physiologically, mockernut hickory is as shade tolerant as white oak and has traits that infer its high adaptability to changes in the light environment. Following reductions in overstory stocking, (3) the reproduction of hickories across height classes was stable in comparison to the initial flush of white oaks or the site-dependent accumulation of large red oak reproduction through time. Midstory hickories were remarkably persistent (4), especially on drier sites, with some individuals less than 18 cm in diameter over 140 years in age. As highlighted by both long-term studies and contemporary Central Hardwood Region-wide assessments, (5) the diameter distribution of hickories suggests a slow and protracted recruitment to the mid and overstory, whereas oaks exhibit a well-documented recruitment bottleneck. Further, across the landscape, (6) the recruitment rates and mortality rates of hickories greatly contrasts with that of oaks; and although less abundant, hickories displayed greater recruitment rates from saplings to trees with lower rates of mortality than their oak counterparts.

4.1. Regenerative attributes and seedling dynamics of hickories

Our results confirm that the seedlings of hickories examined exhibit conservative developmental strategies, perhaps even more so than associated oaks. This was evidenced by greater biomass allocation to roots for mockernut and bitternut hickories when compared to oaks (Rebbeck et al., 2011). Some advantages in persistence for large-seeded hickories when compared to smaller seeded oaks was not surprising; though conventional seed size-juvenile survival expectations have not proven consistent (Saverimuttu and Westoby 1996; Walters and Reich 2000; Moles and Westoby 2004). In the case of hickories, our results indicate more efficient recruitment into successive size classes than oaks on a per seedling basis and greater persistence beyond the seedling stage, especially in shaded understories.

Seedling establishment, which is driven, in part, by requirements for synchronous occurrence of a good mast year and favorable environmental conditions for germination (Frey et al. 2007) may be more consistent for hickories than the periodicity exhibited by oaks (Lefland et al. 2018). One reason hickories may be less abundant in Central Hardwood forests than oaks is simple differences in seed production arising from seed mass-seed abundance trade-offs (Leishman 2001). When hickories are compared to oaks, the age to reproductive maturity is longer for hickories (oaks: 20–25 years, hickories 25–40 years), with shorter seed-bearing intervals (oaks: 3–10 years, hickories: 1–3 years) but smaller seed yields (oaks: 250–900 acorns/kg, hickories: 200–440 seeds/kg) (Young and Young 1992). From our examination of long-term and contemporary datasets, juvenile hickories are present in the smallest size classes at levels consistent or somewhat less abundant than smaller seeded red and white oaks. Further, at small spatial scales, the foraging

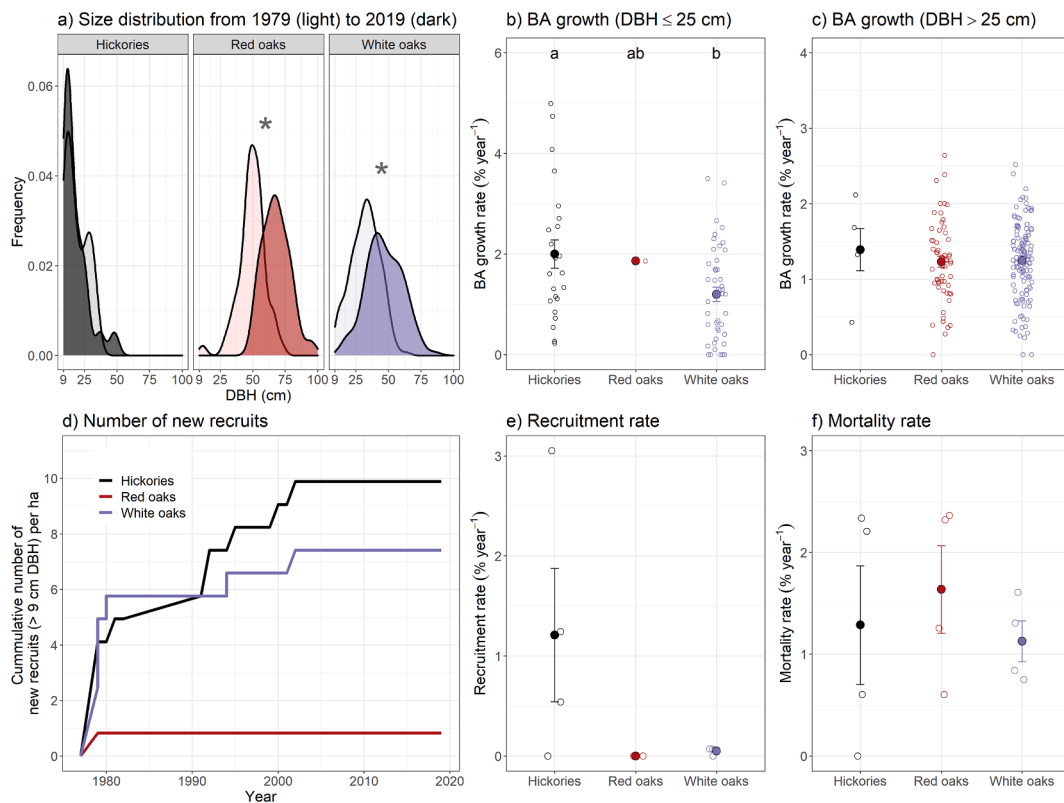


Fig. 6. Demographics of the species groups at the Vinton Furnace Experimental State Forest (VFEF) including (a) diameter (cm) distribution; (b) basal area growth for stems less than 25 cm DBH at first measurement; (c) basal area growth for stems less than 25 cm DBH at first measurement; (d) number of new recruits; and (e) recruitment and (f) mortality rates. Asterisk (*) denotes statistically significant difference, while contrasting letters show significant differences between species groups.

ecology of rodents and squirrels may influence the clustering of hickories (Lefland et al. 2018).

The shade tolerance of hickories has been debated (Cowden et al. 2014b), with classifications varying from intolerant (Zon and Graves 1911) to very tolerant of shade (Boisen and Newlin 1910) depending on species and maturity. In a study of mature trees, net assimilation rates were highest in scarlet oak ($10.3 \mu\text{mol m}^{-2} \text{s}^{-1}$), northern red oak ($8.9 \mu\text{mol m}^{-2} \text{s}^{-1}$), and lower in white oak ($7.6 \mu\text{mol m}^{-2} \text{s}^{-1}$) and pignut hickory ($7.2 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Sullivan et al. 1996). In the case of mockernut hickory seedlings, the light compensation point (LCP) was similar to that reported by Rebbeck et al. (2012) for seedlings of white oak but less than that of northern red oak. The estimated LCP of mockernut was the equivalent of natural ambient light levels found in undisturbed hardwood forest stands (Hudson et al. 2017). This result indicates the light level at which photosynthesis (carbohydrate gain) equals respiration (carbohydrate loss) is lower for mockernut hickory and white oak than northern red oak, suggesting greater tolerance to shade and capacity to persist as seedlings under relatively low light conditions (Rebbeck et al. 2012). However, this contrasts with summary data from Niinemets and Valladares (2006) suggesting less shade tolerance for mockernut hickory than either white oak or northern red oak.

4.2. Recruitment of hickories to the overstory

Extended advantages in recruitment and persistence for understory hickories over oaks probably cannot be wholly attributed to similarities in shade tolerance and greater adaptive physiology as seedlings. Continued physiological plasticity as trees age can be an important strategy when resource availability is variable (Rice and Bazzaz 1989; Latham 1992; Sultan 2000; Meilhac et al. 2020). Although we did not attempt to empirically test factors that lead to niche differentiation

between oaks and hickories, ontogenetic drift and associated environmental factors likely contribute to interspecific differences in growth and persistence through development (Bond 2000; Wright and McConaughay 2002; Weiner 2004; Geng et al. 2007). Mockernut saplings have a high degree of phenotypic plasticity. This plasticity to a broad range of environmental conditions as stems age is expressed by large relative differences between sun and sunfleck leaves in net photosynthesis, leaf conductance, water vapor diffusion, leaf thickness, guard cell length, and leaf mass area (Abrams and Mostoller 1995). These mechanisms may be key for extended persistence and overstory recruitment of hickories under a range of environmental conditions.

Hickories exhibit a high degree of persistence as seedlings and saplings. Seedlings have been reported to be as old as 21–42 years of age in undisturbed forests (Monk 1981; Lefland et al. 2018). Further, our data suggest that saplings of hickories can persist for over a century under the forest canopy and that this persistence may be greatest on drier sites. In a study by Parker et al. (1985), saplings of hickories had reduced mortality rates in smaller size classes, similar to that of sugar maple. While hickories are generally less abundant than oaks, their lower mortality rates maintain their ubiquitous presence in the forest midstory. Our long-term and region-wide assessments of the demographic trends in hickories and oaks in the Central Hardwood Region suggest that they differ markedly in their successional pathways through recruitment and mortality patterns. Lefland et al. (2018) contended that hickory presence across all height and diameter classes in the northeastern US could reflect a protracted recruitment into the canopy, with a high proportion of stems in intermediate or suppressed canopy positions where they stay for decades, contrary to single-cohort recruitment often reported for oaks where diameter distributions are skewed towards larger size classes (Larsen and Johnson 1998; Liptzin and Ashton 1999; Allison et al. 2003). This is further supported by our assessments. For both oak

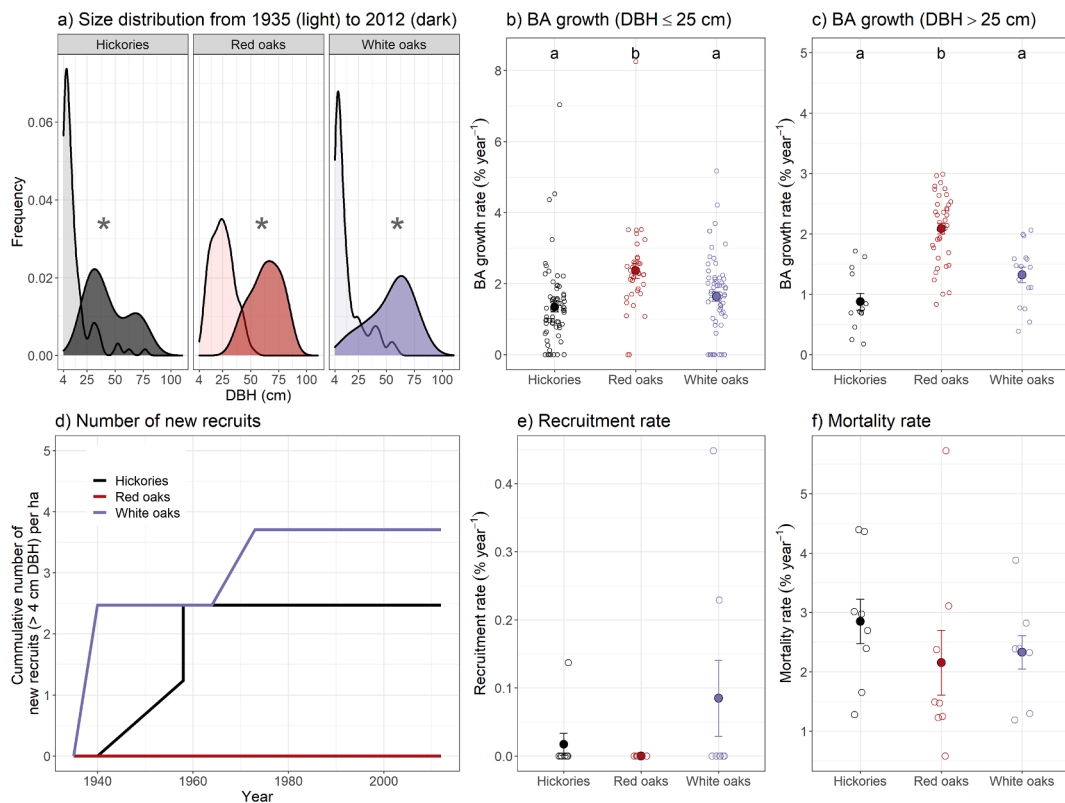


Fig. 7. Demographics for species groups at Kaskaskia Experimental Forest (KEF) including (a) diameter (cm) distribution; (b) basal area growth for stems less than 25 cm DBH at first measurement; (c) basal area growth for stems less than 25 cm DBH at first measurement; (d) number of new recruits; and (e) recruitment and (f) mortality rates. Asterisk (*) denotes statistically significant difference, while contrasting letters show significant differences between species groups.

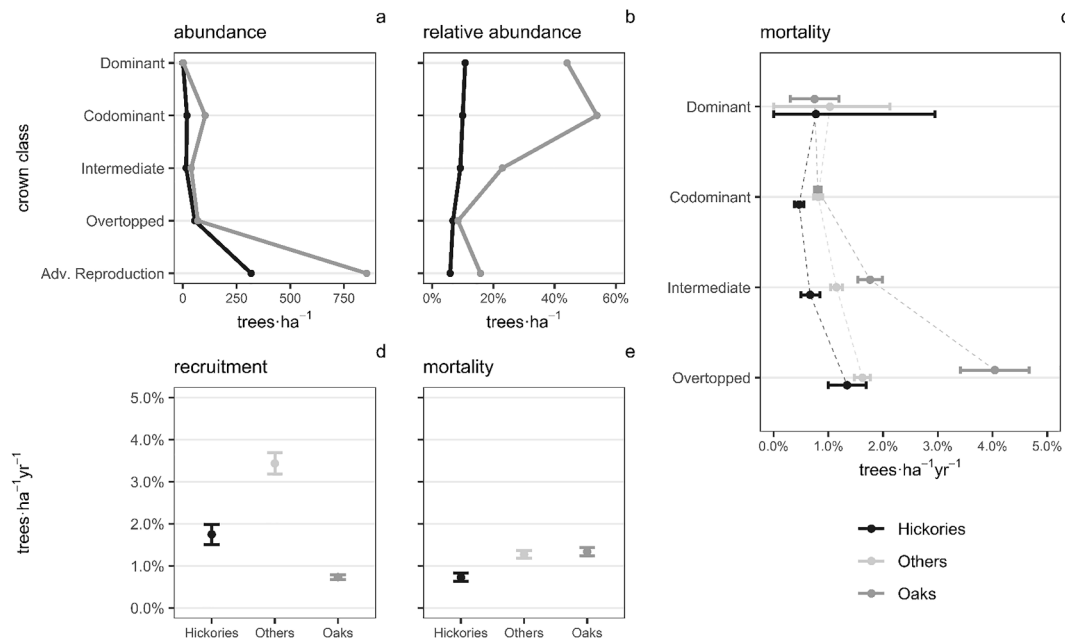


Fig. 8. Selected demographics for hickories, oaks, and other species in mature, oak-hickory central hardwood forests. a) abundance by crown class ($\text{trees}\cdot\text{ha}^{-1}$); b) relative abundance by crown class ($\% \text{ trees}\cdot\text{ha}^{-1}$); c) annual mortality rates by crown class ($\% \text{ trees}\cdot\text{ha}^{-1}$); d) annual recruitment rates ($\% \text{ trees}\cdot\text{ha}^{-1}$); e) overall annual mortality rates ($\% \text{ trees}\cdot\text{ha}^{-1}$). Note: crown classes are applicable to stems with $\text{DBH} \geq 2.5$ cm and advance reproduction abundances include stems with $\text{DBH} < 2.5$ cm, but total height ≥ 30.5 cm. All mortality and recruitment estimates are applicable to stems with $\text{DBH} \geq 12.7$ cm. Data from USDA Forest Service Forest Inventory and Analysis program. Error bars depict 95% confidence intervals around the mean.

groups, recruitment bottlenecks are apparent, with few individuals entering the smallest size classes while the distribution shifts to larger and, presumably, older trees. This is in direct contrast to the hickories,

which continue to recruit new individuals. Parker et al. (1985) reported that over a 50-year period in an old growth forest in Indiana, hickories increased in abundance and basal area whereas oaks decreased in

abundance but increased in basal area. Further, in a study by [Sork \(1983\)](#) in undisturbed forests in the upper Midwest, canopy and sub-canopy hickories are similar in age but differ in size and growth rate. However, the diameters of hickory increased the least in comparison to the other species with mean growth rates less than red and white oaks ([Parker et al. 1985](#)). In our long-term studies, even though growth and mortality rates of hickories, red oaks, and white oaks differed by location, hickories continued to recruit more individuals than oaks at both sites.

Successional patterns in the Missouri Ozarks indicate that even intermediate and suppressed hickories and white oaks are more likely to survive than dominant and co-dominant red oaks ([Fan et al. 2006](#)). [Boisen and Newlin \(1910\)](#) noted the capacity for highly suppressed hickories to respond to release even after 60–100 years. Further, [Cowden et al. \(2014a\)](#) report the establishment and recruitment of hickories is possible in both low and high light environments. From our region-wide assessment, hickories differed in their ability to persist in subordinate canopy positions in comparison to the oaks. Mortality of oaks was greatest in the overtopped, intermediate, and codominant canopy positions, whereas hickories had mortality rates less than 2% even when overtopped.

4.3. Influence of disturbance and management on hickories

It is worth noting, that although hickories are common associates but seldom dominant in oak-hickory forests, past land practices, may have allowed more hickories to recruit into the overstory than would generally occur today. For example, pre-settlement estimates of hickory suggest that they represented only 2% of the witness trees compared to 56% oak in the Midwest Broadleaf Forest Province (see [McNab et al. \(2007\)](#)). The greatest proportion of witness trees reported as hickories (13%) was

recorded in the Prairie Parkland Province ([Hanberry and Nowacki 2016](#)). Based on witness tree data in southern Ohio, prior to settlement, hickories were relatively abundant (14% of trees) on the landscape but significantly smaller than the oaks, similar to today's dominance pattern ([Rentch and Hicks, 2005](#); [Dyer and Hutchinson 2019](#)). Following European settlement, land-use practices, including excessive and intensive grazing or browsing by domesticated livestock may have favored contemporary forest compositions, especially at small-scales ([Apsley et al. 1984](#); [Glitzenstein et al. 1990](#)). Hickories are one of the least preferred browsing species by domesticated livestock including cattle ([Boisen and Newlin, 1910](#)) and goats ([Beebe 2021](#)). Historic accounts suggest that even following several years of intensive browsing pressure, the stems of hickories persist primarily because of their reduced palatability when compared to other hardwood species ([Fig. 9](#)). Further, following even minimal browse pressure, the root-centered growth of hickories may contribute to greater survival.

It has been reported that overstory disturbance events can release the layer of hickory saplings ([Rebertus and Meier 2001](#); [Cowden et al. 2014b](#)). However, contrary to our findings of continued recruitment without large-scale disturbance, it has been suggested by [McCarthy and Wistendahl \(1988\)](#) that small scale disturbances such as the removal or death of a single tree (gap-phase replacement) will not facilitate the recruitment of hickories to the overstory. For example, [Parker et al. \(1985\)](#) documented no hickory or oak recruited within a 5-m radius after the mortality of a single dominant or co-dominant tree in Indiana. [Vickers et al. \(2014; 2017\)](#) found that post-disturbance establishment and height growth of hickory, red oak, and white oak saplings all increased with decreasing residual overstory densities. In our shelterwood study, pretreatment densities of hickory were similar to those of white oaks and red oaks among sites and treatments. However, reproduction densities of hickories remained relatively consistent across



Fig. 9. Historic depiction of browsing by domesticated goats in the Ozark Highlands region of Missouri. Picture caption reads: 5/14/51 Along Highway 63 opposite Freeburg Fire Tower. Goats in this pasture are eating hickory sprouts. Hickory is less palatable than most other hardwoods; hence, it is one of the last to be killed by goating. This pasture has been goated for several years. – Martin.

height classes for each site, whereas white oaks and red oaks were more dynamic and responsive to changes in light availability. This supports the idea that hickories maintain a more constant recruitment than oaks, but often at lower levels over decades (Lefland et al. 2018). Kabrick et al. (2008b) also documented dynamic responses in red and white oak reproduction populations in response to changes in overstory density over a ten-year period post-disturbance. Our shelterwood results indicated the level of residual stocking was not important for the abundance of reproduction for any of the three height classes. The disparity in results may be attributable, in part, to three complementary characteristics of our shelterwood study. First, the residual overstory treatments were similar, representing canopies slightly below or equal to full stocking (i.e., crown closure). Second, it would be expected that even the sparsest overstory would return to a fully-stocked condition within ten years (Ginrich 1967). Third, the extended period before complete overstory removal, approximately 18 years likely negated any initial differences from the overstory treatments that were likely subtle and fleeting. For example, Vickers et al. (2014) showed that red oak saplings can outgrow both white oaks and hickories in height at low residual overstory densities but those differences decrease with increasing overstory density and are indistinguishable at levels below even the sparsest shelterwood treatment in this study.

Several recent studies have shown that regeneration of oak-hickory forests is imperiled in many places (McEwan et al. 2011; Miller and McGill 2019; Vickers et al. 2019). Oak and, to a lesser degree, hickory regeneration success has been shown to be affected by interactions of management and site factors (Kabrick et al. 2008b; Iverson et al. 2017). For example, on southwest-facing slopes in Central Missouri, clearcutting produced stands in which oaks and hickories comprised 60% of the canopy dominant stems 30 years after harvesting (Knapp et al. 2019). However, on northeast-facing slopes and ridges, clearcutting produced stands with oaks and hickories comprising fewer than 25% of the dominant stems. Crop tree release treatments are recommended following a stand-initiating disturbance prior to 20 years of age for hickories with follow up release treatments to reduce faster growing competition (Nixon et al. 1983), which may be more important on more productive sites. Less productive sites within the Central Hardwood Region are thought to allow more flexibility in oak management (Johnson et al. 2019). Especially in the Missouri Ozarks where successful even and uneven-aged management for oaks has been demonstrated (Kabrick et al. 2008b; Fan et al. 2014). Whether this axiom holds for hickories specifically is less clear. We did not observe obvious site differences in reproduction abundance for hickories in our shelterwood results, but when we compared dynamics at larger spatial and temporal scales, site differences in hickory mortality were apparent.

Interestingly, several of the most common oak species within the Central Hardwood Region exhibit notable spatial variation in importance values across their range, usually with greater importance in areas of relatively poor site productivity (Peters et al. 2020). In contrast, importance values for hickories are generally more diffuse. Future investigations into the ecology and silviculture of hickory at local and range-wide scales are needed. While current landscape-scale climate and management trends are generally conducive to declining oak importance in future forests (Fei et al. 2011; Shifley et al. 2014; Dey et al. 2019), our results suggest a potential for hickory to fare better than oaks in some cases as contemporary disturbance regimes, that is, a lack of disturbance, favors hickories over oaks to some degree. However, both genera benefit from appropriate active management and therefore, some management is necessary to maintain the oak-hickory forest type across the landscape. Similar to oaks, root-centered growth in hickory aids in their persistence under low light conditions but also provides necessary reserves for resprouting in disturbed environments (Crow 1988). This is an especially important mechanism for survival in frequent surface fire regimes (Brose et al. 2014). However, we have limited understanding on the association of hickories with fire.

Finally, our understanding of hickories could be greatly improved by

differentiating species when conducting plant censuses for research and monitoring. Even in our study, species differences were recorded for oaks but were not attempted for hickories, therefore limiting our ability to determine species level demographic patterns and treatment responses. Although hickories are difficult to identify, especially as juveniles, as are the oaks, but effort is often taken to differentiate oak species even as seedlings. Managing for resilience, especially with increased stressors from invasive insects, pathogens and plants in eastern North America will require increasing our understanding about species that are less abundant but are also incredibly important contributors to ecological goods and services.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119513>.

References

- Abrams, M.D., Mostoller, S.A., 1995. Gas exchange, leaf structure and nitrogen in contrasting successional tree species growing in open and understorey sites during a drought. *Tree Physiol.* 15, 361–370. <https://doi.org/10.1093/treephys/15.6.361>.
- Aldrich, P.R., Parker, G.R., Romero-Severson, J., Michler, C.H., 2005. Confirmation of oak recruitment failure in Indiana old-growth forest: 75 years of data. *Forest Science* 51, 406–416. <https://doi.org/10.1093/forests/51.5.406>.
- Alexander, H. D., C. Siegert, J. S. Brewer, J. Kreye, M. A. Lashley, J. K. McDaniel, A. K. Paulson, H. J. Renninger, and J. M. Varner. 2021. Mesophication of oak landscapes: evidence, knowledge gaps, and future research. *BioScience* biaa169. <https://doi.org/10.1093/biosci/biaa169>.
- Allison, T.D., Art, H.W., Cunningham, F.E., Teed, R., 2003. Forty-two years of succession following strip clearcutting in a northern hardwoods forest in northwestern Massachusetts. *For. Ecol. Manage.* 182, 285–301. [https://doi.org/10.1016/S0378-1127\(03\)00066-5](https://doi.org/10.1016/S0378-1127(03)00066-5).
- Apsley, D.K., Leopold, D.J., Parker, G.R., 1984. Tree species response to release from domestic livestock grazing. In: *Proceedings of the Indiana Academy of Science*, pp. 215–226.
- Arner, S.L., Westfall, J.A., Scott, C.T., 2004. Comparison of annual inventory designs using Forest Inventory and Analysis Data. *Forest Science* 50, 188–203. <https://doi.org/10.1093/forests/50.2.188>.
- Baker, F.S., 1949. A revised tolerance table. *J. Forest.* 47, 179–181. <https://doi.org/10.1093/jof/47.3.179>.
- Barnes, T.A., Van Lear, D.H., 1998. Prescribed fire effects on advanced regeneration in mixed hardwood stands. *South. J. Appl. For.* 22, 138–142. <https://doi.org/10.1093/sjaf/22.3.138>.
- Bechtold, W. A., and P. L. Patterson. 2005. The enhanced forest inventory and analysis program—national sampling design and estimation procedures. USDA Forest Service, Southern Research Station.
- Beebe, G.R., 2021. Smole, goats, and oaks: The effects of targeted goat browsing and prescribed fire on woody regeneration and ground flora in Ozark woodlands. University of Missouri, Columbia, MO.
- Boisen, A., and J. Newlin. 1910. The commercial hickories. Page 64. USDA Forest Service.
- Bond, B.J., 2000. Age-related changes in photosynthesis of woody plants. *Trends Plant Sci.* 5, 349–353. [https://doi.org/10.1016/S1360-1385\(00\)01691-5](https://doi.org/10.1016/S1360-1385(00)01691-5).
- Brandt, L., H. He, L. Iverson, F. R. Thompson, P. Butler, S. Handler, M. Janowiak, P. D. Shannon, C. Swanston, M. Albrecht, R. Blume-Weaver, P. Deizman, J. DePuy, W. D. Dijk, G. Dinkel, S. Fei, D. T. Jones-Farrand, M. Leahy, S. Matthews, P. Nelson, B. Oberle, J. Perez, M. Peters, A. Prasad, J. E. Schneiderman, J. Shuey, A. B. Smith, C. Studvin, J. M. Tirkak, J. W. Walk, W. J. Wang, L. Watts, D. Weigel, and S. Westin. 2014. Central Hardwoods ecosystem vulnerability assessment and synthesis: a report from the Central Hardwoods Climate Change Response Framework project. Northern Research Station, Gen. Tech. Rep. NRS-124. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 254 p.
- Braun, E. 1950. Eastern deciduous forests of North America, Blakiston, Philadelphia.
- Brose, P., Van Lear, D., Cooper, R., 1999a. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. *For. Ecol. Manage.* 113, 125–141. [https://doi.org/10.1016/S0378-1127\(98\)00423-X](https://doi.org/10.1016/S0378-1127(98)00423-X).
- Brose, P.H., Dey, D.C., Phillips, R.J., Waldrop, T.A., 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in Eastern North America? *Forest Science* 59, 322–334. <https://doi.org/10.5849/forsci.12-039>.

- Brose, P. H., D. C. Dey, and T. A. Waldrop. 2014. The fire-oak literature of eastern North America: synthesis and guidelines. Page 98. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.
- Brose, P.H., Van Lear, D.H., Keyser, P.D., 1999b. A shelterwood—burn technique for regenerating productive upland oak sites in the Piedmont Region. *South. J. Appl. For.* 23, 158–163. <https://doi.org/10.1093/sjaf/23.3.158>.
- Burrill, E.A., Wilson, A.M., Turner, J.A., Pugh, S.A., Menlove, J., Christiansen, G., Conkling, B.L., Winnie, D., 2017. The forest inventory and analysis database: database description and user guide version 7.2 for Phase 2. USDA For. Serv. 946p, [Online].
- Cleland, D. T., J. A. Freeouf, J. E. Keys, G. J. Nowacki, C. A. Carpenter, and W. H. McNab. 2007. Ecological subregions: sections and subsections for the conterminous United States. Gen. Tech. Report WO-76D [Map on CD-ROM] (A.M. Sloan, cartographer).
- Cowden, M.M., Hart, J.L., Buchanan, M.L., 2014a. Canopy accession strategies and climate responses for three *Carya* species common in the Eastern Deciduous Forest. *Trees* 28, 223–235. <https://doi.org/10.1007/s00468-013-0944-3>.
- Cowden, M.M., Hart, J.L., Schweitzer, C.J., Dey, D.C., 2014b. Effects of intermediate-scale wind disturbance on composition, structure, and succession in *Quercus* stands: Implications for natural disturbance-based silviculture. *For. Ecol. Manage.* 330, 240–251. <https://doi.org/10.1016/j.foreco.2014.07.003>.
- Crow, T.R., 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*) - a review. *Forest Science* 34, 19–40. <https://doi.org/10.1093/forestscience/34.1.19>.
- Dey, D.C., Knapp, B.O., Battaglia, M.A., Deal, R.L., Hart, J.L., O'Hara, K.L., Schweitzer, C. J., Schuler, T.M., 2019. Barriers to natural regeneration in temperate forests across the USA. *New Forest* 50, 11–40. <https://doi.org/10.1007/s11056-018-09694-6>.
- Dionisio, L. F. S., G. Schwartz, J. d. C. Lopes, and F. d. A. Oliveira. 2018. Growth, mortality, and recruitment of tree species in an Amazonian rainforest over 13 years of reduced impact logging. *Forest Ecol. Manage.* 430:150–156. Doi: 10.1016/j.foreco.2018.08.024.
- Dyer, J.M., Hutchinson, T.F., 2019. Topography and soils-based mapping reveals fine-scale compositional shifts over two centuries within a central Appalachian landscape. *For. Ecol. Manage.* 433, 33–42. <https://doi.org/10.1016/j.foreco.2018.10.052>.
- Fan, Z., Kabrick, J.M., Shifley, S.R., 2006. Classification and regression tree based survival analysis in oak-dominated forests of Missouri's Ozark highlands. *Can. J. For. Res.* 36, 1740–1748. <https://doi.org/10.1139/x06-068>.
- Fan, Z., Yao, Q., Dey, D., Spetich, M., Ezell, A., Shifley, S., Kabrick, J., Jensen, R., 2014. Efficacy and associated factors of even- and uneven-aged management to promote oak regeneration in the Missouri Ozarks. *Forest Sci.* 61, 397–408. <https://doi.org/10.5849/forsci.13-069>.
- Fei, S., Kong, N., Steiner, K.C., Moser, W.K., Steiner, E.B., 2011. Change in oak abundance in the eastern United States from 1980 to 2008. *For. Ecol. Manage.* 262, 1370–1377. <https://doi.org/10.1016/j.foreco.2011.06.030>.
- Frey, B.R., Ashton, M.S., McKenna, J.J., Ellum, D., Finkral, A., 2007. Topographic and temporal patterns in tree seedling establishment, growth, and survival among masting species of southern New England mixed-deciduous forests. *For. Ecol. Manage.* 245, 54–63. <https://doi.org/10.1016/j.foreco.2007.03.069>.
- Geng, Y.-P., Pan, X.-Y., Xu, C.-Y., Zhang, W.-J., Li, B., Chen, J.-K., 2007. Plasticity and ontogenetic drift of biomass allocation in response to above- and below-ground resource availabilities in perennial herbs: a case study of *Alternanthera philoxeroides*. *Ecol. Res.* 22, 255. <https://doi.org/10.1007/s11284-006-0017-9>.
- Ginrich, S.F., 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. *Forest Sci.* 13, 38–53. <https://doi.org/10.1093/forestscience/13.1.38>.
- Glitzenstein, J.S., Canham, C.D., McDonnell, M.J., Streng, D.R., 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. *Bull. Torrey Bot. Club* 117, 106–122. <https://doi.org/10.2307/2997050>.
- Goodrum, P.D., Reid, V.H., Boyd, C.E., 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. *J. Wildl. Manage.* 35, 520–532. <https://doi.org/10.2307/3799707>.
- Greenberg, C.H., Keyser, C.E., Rathbun, L.C., Rose, A.K., Fearer, T.M., McNab, W.H., 2013. Forecasting long-term acorn production with and without oak decline using forest inventory data. *Forest Science* 60, 222–230. <https://doi.org/10.5849/forsci.12-106>.
- Hanberry, B.B., Nowacki, G.J., 2016. Oaks were the historical foundation genus of the east-central United States. *Quat. Sci. Rev.* 145, 94–103. <https://doi.org/10.1016/j.quascirev.2016.05.037>.
- Hudson, J.E., Levina, D.F., Hudson, S.A., Bais, H.P., Legates, D.R., 2017. Phenoseasonal subcanopy light dynamics and the effects of light on the physiological ecology of a common understory shrub, *Lindera benzoin*. *Plos One* 12, e0185894. <https://doi.org/10.1371/journal.pone.0185894>.
- Hunt, R. 1982. *Plant Growth Curves. The Functional Approach to Plant Growth Analysis.* Edward Arnold Ltd, London, UK.
- Iverson, L.R., Hutchinson, T.F., Peters, M.P., Yaussy, D.A., 2017. Long-term response of oak-hickory regeneration to partial harvest and repeated fires: influence of light and moisture. *Ecosphere* 8, e01642. <https://doi.org/10.1002/ecs2.1642>.
- Iverson, L.R., Hutchinson, T.F., Prasad, A.M., Peters, M.P., 2008. Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern US: 7-year results. *For. Ecol. Manage.* 255, 3035–3050. <https://doi.org/10.1016/j.foreco.2007.09.088>.
- Johnson, P.S., Shifley, S.R., Rogers, R., Dey, D.C., Kabrick, J.M., 2019. *The Ecology and Silviculture of Oaks.* 3rd Edition edition. Cabi, Boston, MA.
- Kabrick, J.M., Dey, D.C., Jensen, R.G., Wallendorf, M., 2008a. The role of environmental factors in oak decline and mortality in the Ozark Highlands. *For. Ecol. Manage.* 255, 1409–1417. <https://doi.org/10.1016/j.foreco.2007.10.054>.
- Kabrick, J.M., Zenner, E.K., Dey, D.C., Gwaze, D., Jensen, R.G., 2008b. Using ecological land types to examine landscape-scale oak regeneration dynamics. *For. Ecol. Manage.* 255, 3051–3062. <https://doi.org/10.1016/j.foreco.2007.09.068>.
- Knapp, B.O., Anderson, S.E., Curtin, P.J., Ghilardi, C., Rives, R.G., 2019. Can clearcutting reset successional trajectories in upland oak-hickory forests? A case study from Mid-Missouri. *J. Forest.* 117, 435–442. <https://doi.org/10.1093/jofore/fvz041>.
- Larsen, D.R., Johnson, P.S., 1998. Linking the ecology of natural oak regeneration to silviculture. *For. Ecol. Manage.* 106, 1–7. [https://doi.org/10.1016/S0378-1127\(97\)00233-8](https://doi.org/10.1016/S0378-1127(97)00233-8).
- Latham, R.E., 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. *Ecology* 73, 2129–2144. <https://doi.org/10.2307/1941461>.
- Lecoutre, B., 1991. A correction for the epsilon approximate test with repeated measures design with two or more independent groups. *J. Educat. Statist.* 16, 371–372.
- Lefland, A.B., Duguid, M.C., Morin, R.S., Ashton, M.S., 2018. The demographics and regeneration dynamic of hickory in second-growth temperate forest. *For. Ecol. Manage.* 419–420, 187–196. <https://doi.org/10.1016/j.foreco.2018.03.027>.
- Leishman, M.R., 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93, 294–302. <https://doi.org/10.1034/j.1600-0706.2001.930212.x>.
- Liptzin, D., Ashton, P.M.S., 1999. Early-successional dynamics of single-aged mixed hardwood stands in a southern New England forest, USA. *For. Ecol. Manage.* 116, 141–150. [https://doi.org/10.1016/S0378-1127\(98\)00448-4](https://doi.org/10.1016/S0378-1127(98)00448-4).
- Loftis, D.L., 1990. A shelterwood method for regenerating red oak in the Southern Appalachians. *Forest Science* 36, 917–929. <https://doi.org/10.1093/forestscience/36.4.917>.
- McCarthy, B.C., Small, C.J., Rubino, D.L., 2001. Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. *For. Ecol. Manage.* 140, 193–213. [https://doi.org/10.1016/S0378-1127\(00\)00280-2](https://doi.org/10.1016/S0378-1127(00)00280-2).
- McCarthy, B.C., Wistendahl, W.A., 1988. Hickory (*Carya* spp.) distribution and replacement in a second-growth oak hickory forest of southeastern Ohio. *The American Midland Naturalist* 119, 156–164. <https://doi.org/10.2307/2426064>.
- McEwan, R.W., Dyer, J.M., Pederson, N., 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34, 244–256. <https://doi.org/10.1111/j.1600-0587.2010.06390.x>.
- McNab, W.H., 2011. Subregional Variation in Upland Hardwood Forest Composition and Disturbance Regimes of the Central Hardwood Region. Pages 11–26 in C. Greenberg, B. Collins, and F. Thompson Iii, editors. *Sustaining Young Forest Communities: Ecology and Management of early successional habitats in the central hardwood region*, U.S. Springer Netherlands, Dordrecht.
- McNab, W.H., Cleland, D.T., Freeouf, J.A., Keys, J.E., Nowacki, G.J., Carpenter, C.A., 2007. Description of ecological subregions: sections of the conterminous United States. Gen. Tech. Report WP-76B.
- Meilhac, J., Deschamps, L., Maire, V., Flajoulot, S., Litrico, I., 2020. Both selection and plasticity drive niche differentiation in experimental grasslands. *Nat. Plants* 6, 28–33. <https://doi.org/10.1038/s41477-019-0569-7>.
- Miller, K.M., McGill, B.J., 2019. Compounding human stressors cause major regeneration debt in over half of eastern US forests. *J. Appl. Ecol.* 56, 1355–1366. <https://doi.org/10.1111/1365-2664.13375>.
- Moles, A.T., Westoby, M., 2004. Seedling survival and seed size: a synthesis of the literature. *J. Ecol.* 92, 372–383. <https://doi.org/10.1111/j.0022-0477.2004.00884.x>.
- Monk, C.D., 1981. Age structure of *Carya tomentosa* (Poir.) Nutt. in a young oak forest. *The American Midland Naturalist* 106, 189–191. <https://doi.org/10.2307/2425148>.
- Monk, C.D., Donald, W.L., Potter, R.L., 1990. Oak forests of eastern North America. *Castanea* 55, 77–96.
- Moser, W.K., Fan, Z., Hansen, M.H., Crosby, M.K., Fan, S.X., 2016. Invasibility of three major non-native invasive shrubs and associated factors in Upper Midwest U.S. forest lands. *For. Ecol. Manage.* 379, 195–205. <https://doi.org/10.1016/j.foreco.2016.07.043>.
- Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547. [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2).
- Nixon, C.M., McClain, M.W., Landes, R.K., Hansen, L.P., Sanderson, H.R., 1983. Response of suppressed hickories to release cutting. *Wildl. Soc. Bull.* 1973–2006 (11), 42–46.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the Eastern United States. *Bioscience* 58, 123–138. <https://doi.org/10.1641/b580207>.
- Parker, G.R., Leopold, D.J., Eichenberger, J.K., 1985. Tree dynamics in an old-growth, deciduous forest. *For. Ecol. Manage.* 11, 31–57. [https://doi.org/10.1016/0378-1127\(85\)90057-X](https://doi.org/10.1016/0378-1127(85)90057-X).
- Peet, R.K., Christensen, N.L., 1980. Succession: a population process. Pages 131–140 in E. van der Maarel, editor. *Succession: Symposium on advances in vegetation sciences*, Nijmegen, The Netherlands, May 1979. Springer Netherlands, Dordrecht.
- Peters, M.P., Prasad, A.M., Matthews, S.N., Iverson, L.R., 2020. *Climate change tree atlas*, Version 4. U.S. Forest Service, Northern Research Station and Northern Institute of Applied Climate Science, Delaware, OH.
- Pommerening, A., Muszta, A., 2016. Relative plant growth revisited: towards a mathematical standardisation of separate approaches. *Ecol. Model.* 320, 383–392. <https://doi.org/10.1016/j.ecolmodel.2015.10.015>.
- Pugh, S.A., Turner, J.A., Burrill, E.A., David, W., 2018. *The Forest Inventory and Analysis Database: Population Estimation User Guide.* USDA Forest Service, Washington DC, USA, URL <https://www.fia.fs.fed.us/library/database-documentation/current/ver80/FIADB>.

- R Core Team, 2020. R: a language environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Rebbeck, Joanne, Gottschalk, K., Scherzer, A., 2011. Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? Growth and biomass. *Canadian Journal of Forest Research* 41, 2219–2230. <https://doi.org/10.1139/x11-124>.
- Rebbeck, J., Loats, K.V., 1997. Ozone effects on seedling sugar maple (*Acer saccharum*) and yellow-poplar (*Liriodendron tulipifera*): gas exchange. *Can. J. For. Res.* 27, 1595–1605. <https://doi.org/10.1139/x97-121>.
- Rebbeck, J., Scherzer, A., Gottschalk, K., 2012. Do chestnut, northern red, and white oak germinant seedlings respond similarly to light treatments? II. Gas exchange and chlorophyll responses. *Can. J. For. Res.* 42, 1025–1037. <https://doi.org/10.1139/x2012-057>.
- Rebertus, A.J., Meier, A.J., 2001. Blowdown dynamics in oak-hickory forests of the Missouri Ozarks. *J. Torrey Botanical Soc.* 128, 362–369. <https://doi.org/10.2307/3088668>.
- Rentch, J.S., Hicks Jr., R.R., 2005. Changes in presettlement forest composition for five areas in the central hardwood forest, 1784–1990. *Nat. Areas J.* 25, 228–238.
- Rice, S.A., Bazzaz, F.A., 1989. Quantification of plasticity of plant traits in response to light intensity: comparing phenotypes at a common weight. *Oecologia* 78, 502–507. <https://doi.org/10.1007/BF00378741>.
- Rose, A.K., Rossion, J.F.J., 2007. The importance and distribution of hickory. e-Gen. Tech. Rep. SRS–101. U.S. Department of Agriculture, Forest Service, Southern Research Station: 527-535 [CD-ROM].
- SAS Institute Inc., 2012. SAS Institute Inc., Cary, NC, USA.
- Saverimuttu, T., Westoby, M., 1996. Seedling longevity under deep shade in relation to seed size. *J. Ecol.* 84, 681–689. <https://doi.org/10.2307/2261331>.
- Schlesinger, R.C., Sander, I.L., Davidson, K.R., 1993. Oak regeneration potential increased by shelterwood treatments. *North. J. Appl. For.* 10, 149–153. <https://doi.org/10.1093/njaf/10.4.149>.
- Sheil, D., David, F.R.P.B., Alder, D., 1995. The interpretation and misinterpretation of mortality rate measures. *J. Ecol.* 83, 331–333. <https://doi.org/10.2307/2261571>.
- Shifley, S.R., Moser, W.K., Nowak, D.J., Miles, P.D., Butler, B.J., Aguilar, F.X., DeSantis, R.D., Greenfield, E.J., 2014. Five anthropogenic factors that will radically alter forest conditions and management needs in the Northern United States. *Forest Science* 60, 914–925. <https://doi.org/10.5849/forsci.13-153>.
- Smalley, G.W., 1990. Sweet pignut hickory: *Carya glabra* (Mill.). In: Burns, R.M., Honkala, B.H., editors. *Silvics of North America*. US Department of Agriculture, Forest Service, Washington, DC. Agriculture Handbook 654.
- Smith, H.C., 1990. Mockernut hickory: *Carya tomentosa* (Poir.) Nutt. In: R. M. Burns and B. H. Honkala, editors. *Silvics of North America*. US Department of Agriculture, Forest Service, Washington, DC. Agriculture Handbook 654.
- Sork, V.L., 1983. Distribution of pignut hickory (*Carya glabra*) along a forest to edge transect, and factors affecting seedling recruitment. *Bull. Torrey Bot. Club* 110, 494–506. <https://doi.org/10.2307/2996284>.
- Stanke, H., Finley, A.O., Weed, A.S., Walters, B.F., Domke, G.M., 2020. rFIA: An R package for estimation of forest attributes with the US Forest Inventory and Analysis database. *Environ. Modell. Software* 127, 104664.
- Sullivan, N.H., Bolstad, P.V., Vose, J.M., 1996. Estimates of net photosynthetic parameters for twelve tree species in mature forests of the southern Appalachians. *Tree Physiol.* 16, 397–406. <https://doi.org/10.1093/treephys/16.4.397>.
- Sultan, S.E., 2000. Phenotypic plasticity for plant development, function and life history. *Trends Plant Sci.* 5, 537–542. [https://doi.org/10.1016/S1360-1385\(00\)01797-0](https://doi.org/10.1016/S1360-1385(00)01797-0).
- Swaim, J.T., Dey, D.C., Saunders, M.R., Weigel, D.R., Thornton, C.D., Kabrick, J.M., Jenkins, M.A., 2016. Predicting the height growth of oak species (*Quercus*) reproduction over a 23-year period following clearcutting. *For. Ecol. Manage.* 364, 101–112. <https://doi.org/10.1016/j.foreco.2016.01.005>.
- Tjoelker, M.G., Luxmore, R.J., 1991. Soil nitrogen and chronic ozone stress influence physiology, growth and nutrient status of *Pinus taeda* L. and *Liriodendron tulipifera* L. seedlings. *New Phytol.* 119, 69–81. <https://doi.org/10.1111/j.1469-8137.1991.tb01009.x>.
- Tjoelker, M.G., Volin, J.C., Oleksyn, J., Reich, P.B., 1993. Light environment alters response to ozone stress in seedlings of *Acer saccharum* Marsh, and hybrid *Populus L.* *New Phytol.* 124, 627–636. <https://doi.org/10.1111/j.1469-8137.1993.tb03852.x>.
- Trimble, G.R., 1975. Summaries of some silvical characteristics of several Appalachian hardwood trees. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA.
- USDA Forest Service. 2020. Forest Inventory and Analysis Program Database, Nov. 4, 2020. St. Paul, MN: U.S. Department of Agriculture, Forest Service, Northern Research Station.
- Vickers, L.A., Larsen, D.R., Dey, D.C., Knapp, B.O., Kabrick, J.M., 2017. The impact of overstory density on reproduction establishment in the Missouri Ozarks: models for simulating regeneration stochastically. *Forest Science* 63, 71–86. <https://doi.org/10.5849/forsci.15-183>.
- Vickers, L.A., Larsen, D.R., Knapp, B.O., Kabrick, J.M., Dey, D.C., 2014. The impact of overstory density on sapling height growth in the Missouri Ozarks: implications for interspecific differentiation during canopy recruitment. *Can. J. For. Res.* 44, 1320–1330. <https://doi.org/10.1139/cjfr-2014-0237>.
- Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Dey, D.C., Dickinson, Y.L., Kabrick, J.M., Kenefic, L.S., Kern, C.C., Larsen, D.R., Royo, A.A., Saunders, M.R., Shifley, S.R., Westfall, J.A., 2019. Are current seedling demographics poised to regenerate northern US forests? *J. Forest.* 117, 592–612. <https://doi.org/10.1093/jofore/fvz046>.
- Walters, M.B., Reich, P.B., 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology* 81, 1887–1901. [https://doi.org/10.1890/0012-9658\(2000\)081\[1887:SSNSAG\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1887:SSNSAG]2.0.CO;2).
- Weiner, J., 2004. Allocation, plasticity and allometry in plants. *Perspect. Plant Ecol. Evol. Systemat.* 6, 207–215. <https://doi.org/10.1078/1433-8319-00083>.
- Wood, J.D., Knapp, B.O., Muzika, R.-M., Stambaugh, M.C., Gu, L., 2018. The importance of drought–pathogen interactions in driving oak mortality events in the Ozark Border Region. *Environ. Res. Lett.* 13, 015004 <https://doi.org/10.1088/1748-9326/aa94fa>.
- Wright, S.D., McConaughay, K.D.M., 2002. Interpreting phenotypic plasticity: the importance of ontogeny. *Plant Species Biol.* 17, 119–131. <https://doi.org/10.1046/j.1442-1984.2002.00082.x>.
- Young, J.A., Young, C.G., 1992. *Seeds of woody plants in North America*. Dioscorides Press, Portland, OR.
- Zaczek, J.J., Groninger, J.W., Van Sambeek, J., 2002. Stand dynamics in an old-growth hardwood forest in southern Illinois, USA. *Natural Areas J.* 22 (3).
- Zon, R., and H. Graves. 1911. Light in relation to tree growth. Page 59. Forest Service Bulletin, US Department of Agriculture.