Canadian Journal of
Forest Research

Research Article

Effects of silvicultural release on artificial oak regeneration in bottomland hardwood forests in northern Missouri

Isaac Hayford[a,b], **Benjamin O. Knapp**[b], **Jeffrey D. Wood**[b], **Alba Argerich**[b], **John M. Kabrick**[c], **Grant P. Elliott**[d], **and Matthew G. Olson**[e]

[a]Department of Agriculture and Environmental Sciences, Lincoln University of Missouri, Jefferson City, MO 65101, USA; [b]School of Natural Resources, University of Missouri, Columbia, MO 65211, USA; [c]USDA Forest Service, Northern Research Station, Columbia, MO 65211, USA; [d]Department of Geography, University of Missouri, Columbia, MO 65211, USA; [e]School of Natural Sciences and Mathematics, Stockton University, Galloway, NJ 08205, USA

Corresponding author: **Isaac Hayford** (email: hayfordi@lincolnu.edu)

Abstract

In bottomland forests, managing oak regeneration is challenging due to competition with other species. Low understory light levels in mature stands favor more shade-tolerant tree species, whereas harvest often results in release of fast-growing competitors. In the late 1990s, a study was initiated in northeastern Missouri to evaluate the effects of overstory harvests on stand development of bottomland forests, with particular interest in oak regeneration. Canopy removal resulted in rapid growth of undesired soft-mast species without increasing the abundance of oak reproduction. In 2017, bare-rooted pin oak (*Quercus palustris* Muenchh.) and swamp white oak (*Quercus bicolor* Willd.) seedlings were planted, to increase the oak component through enrichment planting in the stands that had previously been harvested and underplanting in the stands that had received no regeneration harvest. For all planted seedlings, three levels of midstory release treatments were applied after planting in 2017, including a control (no release), and light release, and a heavy release. This study tested the effects of the original overstory harvests and the subsequent midstory release on survival and development of planted oak advance reproduction over 5 years. Our results suggest that establishing oak advance reproduction prior to overstory harvest is more efficient than enrichment planting after overstory harvest. A prior midstory release is important to develop competitive oak advance reproduction before a later overstory harvest to ensure successful oak regeneration.

Key words: enrichment planting, underplanting, midstory release, overstory harvest, oak advance reproduction

1. Introduction

Bottomland hardwood forests occur along floodplains of streams and rivers and are transitional habitats between permanently flooded swamps and drier upland forests (Collins and Battaglia 2008). They are highly productive sites that provide important ecological and economic benefits within the midwestern and southern United States, including timber production, wildlife habitat, carbon and water storage, nutrient cycling, erosion control, enhanced water quality through filtering of nutrients, and recreational purposes (Kellison and Young 1997; Yin et al. 1997). Forest managers are commonly interested in maintaining oaks (*Quercus* spp.) within bottomland forests because they provide favorable habitat for wildlife and are often preferred for timber production (Johnson 1994; Olson et al. 2015*b*).

Historically (ca 1780s), Missouri had an estimated 1.9 million hectares of bottomland forests and riparian areas, much of which were bottomland forests that included oaks (Frazier and Galat 2009). These bottomland forests and riparian areas decreased by 14 000 ha per year during 1940–1980, largely due to conversion to croplands, representing a total loss of 560 000 ha over the 40-year period (Abernethy and Turner 1987). Currently, less than 13% of the historical bottomland forests and riparian areas remain in the state (Frazier and Galat 2009). With increased demands for resources within the remaining forests, a clear understanding of how management programs impact them is imperative.

Managing for oaks in competition with faster growing tree species is challenging. The low understory light levels associated with mature bottomland forests favor more shade-tolerant tree species over oaks, which are classified as intermediate to very intolerant of shade (Hodges and Gardiner 1993). Due to the high potential productivity of bottomland hardwood forests, very high light availability tends to release fast-growing, shade-intolerant species that can outcompete oaks, especially for newly germinated oak seedlings that have slow initial shoot growth (Motsinger et al. 2010; Miller et al. 2017; Hayford et al. 2023). Thus, midstory release that provides an intermediary level of light, generally 10%–20% of full sunlight, is often used to increase the initial survival and growth of oak seedlings as they develop into larger advance reproduction (Lhotka and Loewenstein 2009; Motsinger et al. 2010; Brose and Rebbeck 2017; Miller et al. 2017). However, to achieve maximum growth in the long term, subsequent reductions in overstory density are required to increase the light levels up to 50% of full sunlight (Gottschalk 1994; Gardiner and Hodges 1998; Brose 2008).

Bottomland oaks are prolific acorn producers and consequently are capable of producing a large number of seedlings following abundant acorn crops (Johnson et al. 2019). However, the dense shade found in the understory of bottomland forests reduces oak seedling survival, preventing the accumulation of advance reproduction (Motsinger et al. 2010). Successful oak regeneration in bottomland hardwood forests is usually dependent on an adequate population of large oak advance reproduction prior to overstory release. Some bottomland and upland studies have demonstrated that the survival and subsequent recruitment of oak advance reproduction following release improve with the size of the individual (Belli et al. 1999; Spetich et al. 2002; Gardiner et al. 2009; Miller et al. 2017; Hayford et al. 2023). Smaller oak seedlings cannot compete effectively with larger seedlings of shade-tolerant species or fast-growing, shade-intolerant competitors following release. Past studies have suggested that advance reproduction of at least 122 cm in height should be present before overstory release (Sander et al. 1976; Vickers et al. 2011). Hayford et al. (2023) observed that basal diameter > 1.4 cm at planting was needed for at least 60% probability of survival 15 years after planting bare-rooted pin oak (*Quercus palustris* Muenchh.). The lack of sufficient numbers of large oak advance reproduction is often attributed to excessive shade and competition from undesired vegetation (Rives et al. 2020; Hayford et al. 2023).

Forest management to sustain oak populations requires attention to regeneration and recruitment processes, often requiring timely silvicultural release from competition in the midstory and the overstory layers, in the proper sequence to first allow development of large advance reproduction and then provide sufficient release for recruitment. This challenge is particularly acute within productive bottomland hardwood forests, where cutting too heavy or with improper timing could release competitors and shift composition away from oaks (Rives et al. 2020). In such cases, enrichment planting, defined as artificial regeneration carried out to increase the proportion of desired species after harvest has resulted in poor regeneration (Schuler and Robison 2010), may be an option for maintaining even a low level of oak composition in the developing stand. In contrast, deferring overstory harvest until large advance reproduction develops may be more effective for reaching long-term goals. In these cases, underplanting, defined as artificial regeneration in mature stands before harvest to start advance regeneration (Dey et al. 2012), may be useful.

This study was designed to investigate the effects of a series of silvicultural practices on oak regeneration in bottomland forests. In the late 1990s, a study was initiated at Deer Ridge Conservation Area (DRCA) in Lewis County, MO to evaluate effects of overstory harvests on stand development of bottomland forests, with particular interest in natural oak regeneration. The regeneration harvests resulted in rapid growth of soft-mast species without increasing the abundance of oak reproduction (Rives et al. 2020). These early results suggested that additional treatments were needed for maintaining or increasing the abundance of oak in the developing stands. The study design provided an opportunity to compare planting with pin oak and swamp white oak (*Quercus bicolor* Willd.) seedlings in harvested and unharvested stands with three levels of midstory release to evaluate effects on oak regeneration. The objectives of this study were to determine the effects of silvicultural removal of overstory and midstory trees on (1) forest stand structure (basal area per hectare, trees per hectare); (2) survival of planted pin oak and swamp white oak seedlings; and (3) size and growth of planted pin oak and swamp white oak seedlings. Results from this study can inform the practicality of enrichment planting after overstory harvest fails to regenerate oak species and evaluate effectiveness of midstory release with enrichment planting and underplanting approaches.

2. Materials and methods

2.1. Study area

The study was conducted on a 220 ha mixed bottomland hardwood forest at DRCA (40°10′30″N, 91°48′0″W), adjacent to a channelized segment of the North Fabius River in Lewis County of northeastern Missouri. DRCA has one of the largest tracts of remnant bottomland forest in northeastern Missouri (Gwaze and Elliott 2011). This site was selected for the study because it had not been harvested for more than five decades, it contained contiguous bottomland forest blocks >20 ha, and state ownership facilitated long-term access and control of management activities. The soils of the study area were dominated by Blackoar silt loam (fine-silty, mixed, superactive, mesic Fluvaquentic Hapludolls), Fatima silt loam (fine-silty, mixed, superactive, mesic Fluvaquentic Hapludolls), and Kickapoo fine sandy loam (coarse-loamy, mixed, superactive, nonacid, mesic Typic Udifluvents), with each formed in alluvium, with slopes between 0 and 2 degrees but varying in drainage class. The site was prone to annual flooding, with patches of low-lying areas permanently inundated with water. The mean annual temperature and precipitation for the area over a 30-year period (1991–2020) were 11.7 °C and 1007 mm, respectively (PRISM Climate Group, prism.oregonstate.edu). The tree species in the area were predominantly silver maple (*Acer saccharinum* L.), American elm (*Ulmus americana* L.), American sycamore (*Platanus occidentalis* L.), green ash (*Fraxinus pennsylvanica* Marsh.), boxelder (*Acer negundo* L.), eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall), pin oak, bur oak (*Quercus macrocarpa* Michx.), and swamp white oak (Rives et al. 2020).

2.2. Experimental design and treatments of the original overstory harvests

The original study used a completely randomized design, with one of three overstory harvest treatments randomly assigned to 20 stands varying in size from 2.6 to 3.2 ha. The three treatments included clearcut with reserves (CCR; canopy retention of up to 2.3 m^2/ha); basal area retention, an irregular shelterwood method where the overwood is retained indefinitely (BAR; canopy retention of 4.6–6.9 m^2/ha); and uncut control (CON; no harvest; canopy 32.0 m^2/ha). The treatments were applied as a commercial harvest operation from fall 1999 to spring 2000. All cutting was done with chainsaw and yarding with a grapple skidder. The CCR treatment included cutting almost all trees > 2.54 cm dbh, except for some cavity and hard mast trees, principally oaks, left to provide food and shelter for wildlife or serve as seed trees. The prescription for the BAR treatment called for cutting all trees > 11.43 cm dbh and retaining enough dominant and codominant trees to meet the residual basal area requirement. The criteria for retaining trees for BAR were similar to CCR, except larger oaks were favored for retention to serve as seed source to encourage oak regeneration. Some large soft-mast species were also retained in the BAR to maintain tree species diversity, benefit wildlife, and meet residual basal area targets. In both the CCR and BAR treatments, the remaining trees of 2.54–20.3 cm dbh after the commercial harvest not marked for retention were cut down, and those >20.3 cm dbh were killed by double girdling with a chainsaw (Gwaze and Elliott 2011; Olson et al. 2015*a*; Rives et al. 2020).

2.3. Midstory release

In 2017, midstory release treatments were added to the experimental design to release planted oak advance reproduction in a completely randomized split-plot design. The main-plot treatments were the original harvests (CON, BAR, CCR), and the split-plot treatments included three levels of midstory release: light release, heavy release, and no treatment (i.e., the untreated control). The main-plots were each replicated in five stands (15 main plot units total), and each was subdivided into three split-plots (45 split-plot experimental units total). Each split-plot experimental unit was 0.40 ha and oriented either as a square (63 × 63 m) or a rectangle (80 × 50 m). Within each split-plot unit, 25–40 planting locations were established in a grid at approximately 9 m spacing, with each planting location including both a pin oak and a swamp white oak as a pair for release and subsequent measurement. Each seedling pair consisted of one swamp white oak and one pin oak planted adjacent to one another at 1 m spacing. Seedlings were 1-0 bare-rooted stock produced by the George O. White State Nursery in Licking, Missouri.

The light and heavy release treatments depended on the main plot treatment. For the CON stands, a uniform, area-based approach was used to reduce stand basal area by 30% and 65% in the light and heavy release treatments, respectively. For the BAR and CCR stands, the light and heavy release treatments were applied using a crop-tree release approach for the 25–40 oak seedling pairs. A light release radius of 3.10 m and heavy release radius 4.57 m around oaks resulted in approximately 30% and 65% reduction in stand density, respectively. Within each crop tree release treatment area, all competing woody stems > 2.54 cm dbh were treated with a hack-and-spray treatment to kill them. We applied one hack per approximately 2.54 cm of dbh, using a solution of 50% triclopyr, 3% imazapyr, and the remainder water. Prescriptions for light and heavy release treatments differed in CON from CCR and BAR to reflect the inherent structural differences between both original harvest treatments and the control. We consider CON to represent an underplanting approach and CCR and BAR to represent enrichment planting.

2.4. Data collection

2.4.1. Overstory and midstory trees

In each split-plot, we established one 0.08 ha circular plot (16 m radius; overstory plot) centered in the middle of the split-plot for fixed-area sampling of vegetation. Within each overstory sampling plot, trees ≥ 11.43 cm dbh and rooted within the sampling plot were identified to species, and dbh was recorded in summer 2021. The species and dbh for each midstory tree ≥ 3.81 cm dbh but <11.43 cm were recorded in four circular 0.01 ha plots (5.67 m radius), with the center of each midstory plot located on the boundary of the overstory plot at each of the cardinal directions from plot center.

We grouped species into eight species groups in accordance with the rules of Rives et al. (2020) determined by species abundance and management objectives, including American elm, American sycamore, eastern cottonwood, green ash, hickories, oaks, silver maple, and "other species". The hickories group included bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch) and shellbark hickory (*Carya laciniosa* (Michx. f.) Lould.), and the oaks group included pin oak, bur oak, and swamp white oak. The "other species" group included boxelder, honey locust (*Gleditsia triacanthos* L.), hackberry (*Celtis occidentalis* L.), black walnut (*Juglans nigra* L.), river birch (*Betula nigra* L.), willows (*Salix* spp.), Ohio buckeye (*Aesculus glabra* Willd.), American basswood (*Tilia americana* L.), and eastern redbud (*Cercis canadensis* L.).

2.4.2. Oak seedlings

Each planted oak seedling pair was tagged for identification throughout the study period. The basal diameter at the root collar and height of each seedling were measured at the time of planting in March 2017. All surviving seedlings were re-measured following the first (2017), second (2018), third (2019), fourth (2020), and fifth (2021) growing seasons. For the basal diameter of each seedling, two measurements were taken in perpendicular directions to account for irregularity in the root collar form, and the average of the two measurements was used for analyses.

2.5. Statistical analyses

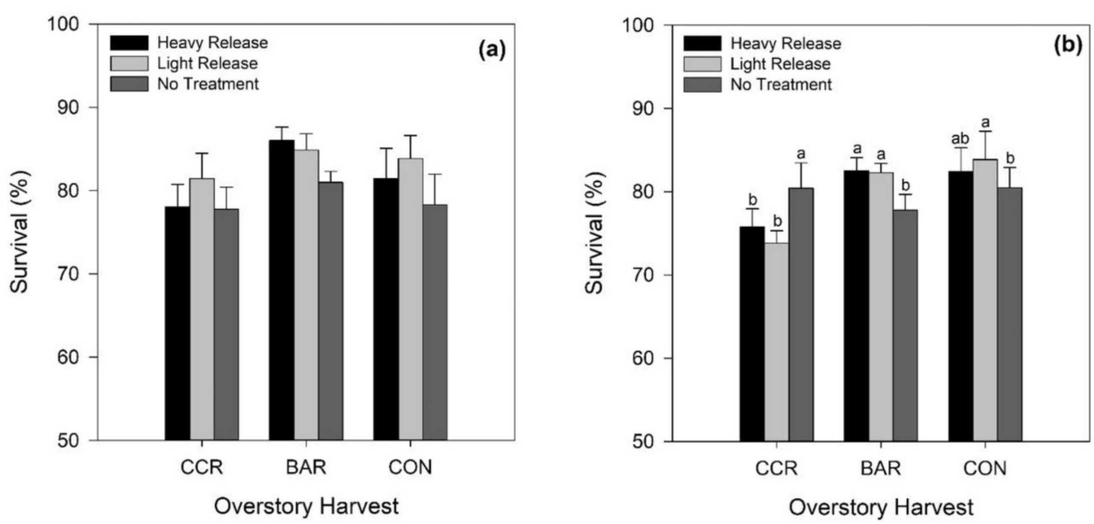
We tested the effects of overstory and midstory release on forest stand structure (basal area per hectare, trees per hectare) (Objective 1) with split-plot Analysis of variance (ANOVA) using the MIXED procedure of SAS (version 9.3; SAS Institute, Inc., Cary, NC). The analysis was conducted separately with basal area and trees per hectare as dependent

Table 1. Treatment effects on basal area (m^2/ha) and trees per hectare of overstory trees (trees ≥ 11.43 cm dbh) and midstory trees (3.81 ≤ dbh < 11.43 cm) sampled in 2021.

	Overstory trees (trees ≥ 11.43 cm dbh)				Midstory trees (3.81 ≤ dbh < 11.43 cm)			
	Basal area (m^2/ha)		Trees per hectare		Basal area (m^2/ha)		Trees per hectare	
Treatment	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Overstory harvest								
Clearcut with reserves	17.98b	2.36	471.15a	45.24	0.67	0.13	145.79	29.89
Basal area retention	23.08ab	1.54	334.42b	18.34	0.52	0.07	122.73	16.95
Uncut control	27.17a	2.42	205.10c	7.75	0.35	0.07	93.90	20.73
p-value	0.03		<0.01		0.10		0.32	
Midstory release								
Heavy release	20.86	1.92	299.82b	44.73	0.26b	0.04	70.84c	11.28
Light release	23.69	2.30	323.71ab	37.19	0.45a	0.11	108.73b	26.93
No treatment	23.68	2.24	387.13a	31.34	0.83a	0.11	182.86a	19.75
p-value	0.44		0.04		<0.01		<0.01	

Note: Different lowercase letters within a treatment effect indicate significant difference at $\alpha = 0.05$. SE = standard error of the mean.

Fig. 1. Percent survival (mean ± 1 SE) of pin oak (*a*) and swamp white oak (*b*) compared among midstory release within each overstory harvest treatments. Overstory harvest treatments included clearcut with reserves (CCR), basal area retention (BAR), and uncut control (CON). For each overstory harvest, different letters indicate significant differences among midstory release treatments ($p < 0.05$).



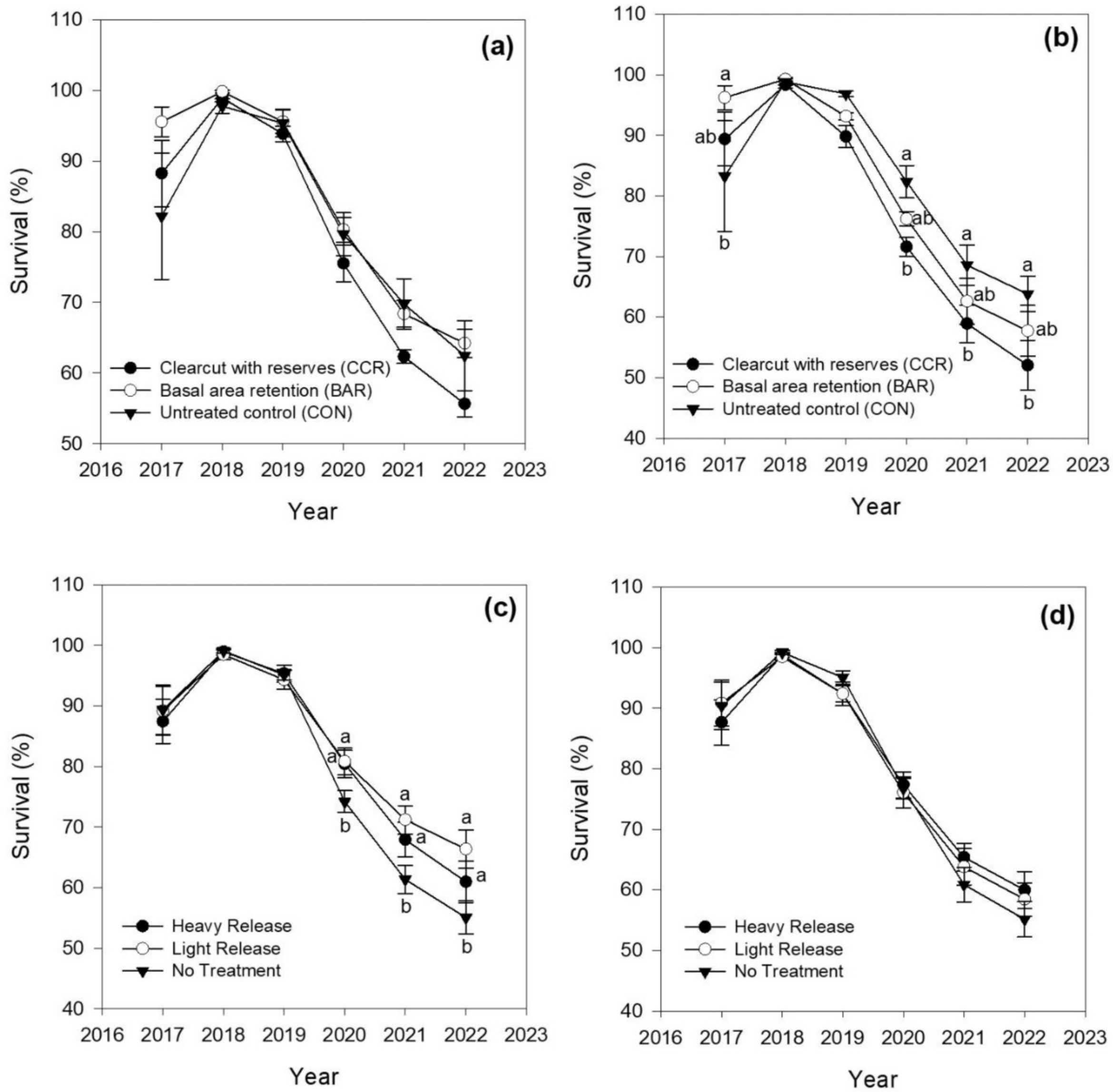
variables based on measurements collected in 2021. We calculated mean values of basal area and trees per hectare for overstory and midstory trees at the split-plot level. The effects of overstory harvest, midstory release, year, and their interactions on survival, size (height and basal diameter), and growth of planted pin oak and swamp white oak seedlings (Objectives 2 and 3) were tested with repeated measures split-plot ANOVA using the MIXED procedure of SAS (version 9.3; SAS Institute, Inc., Cary, NC). Overstory harvest was modeled as the whole-plot effect, and midstory release as the split-plot effect. We used overstory harvest, midstory release, year of measurement, and their interactions as fixed effects and the random effects were stand, stand × overstory harvest, and stand × overstory harvest × year interactions. Percent survival was estimated at the split-plot level. Annual growth of the oaks was calculated as the difference in height or basal diameter between two consecutive sampling years. All pairwise comparisons were evaluated with Tukey's honestly significant difference adjustment. We used $\alpha = 0.05$ to determine statistical significance for all analyses.

3. Results

3.1. Overstory and midstory density

The basal area of overstory trees was lower in CCR compared to CON ($p = 0.03$; Table 1; Table A1). However, the number of overstory trees per hectare was greatest in the CCR, followed by BAR, and the CON ($p < 0.01$). Overstory harvest had no effect on the basal area ($p = 0.10$) and number of trees per hectare ($p = 0.32$) of midstory trees. The basal area ($p < 0.01$) and number of trees per hectare ($p < 0.01$) were reduced in the

Fig. 2. Percent survival (mean ± 1 SE) of pin oak (*a* and *c*) and swamp white oak (*b* and *d*) by overstory harvest and midstory release at the end of each growing season. Different letters within a given year indicate significant differences among overstory harvest and midstory release treatments ($p < 0.05$).



heavy release compared to no release. The number of overstory trees per hectare was also reduced in the heavy release compared to no release ($p = 0.04$). Silver maple was the dominant species in the BAR and CCR stands, accounting for over 27% of the basal area in each treatment (Table A5). The most dominant species based on basal area in the CON stands was eastern cottonwood (29%), followed by silver maple (27%). The basal area contribution of oaks was less than 8% in each overstory treatment.

3.2. Survival of oak reproduction

Midstory release showed no effect on survival of pin oak within any of the overstory harvest treatments ($p = 0.40$) but affected survival of swamp white oak ($p < 0.01$) (Fig. 1; Table A2). Within the CCR treatment, survival of swamp white oak following light (73.83%) and heavy midstory release (75.76%) were lower than no release (80.43%). Within the BAR treatment, survival of swamp white oak following light (82.29%) and heavy midstory release (82.51%) were higher than no release (77.79%). The survival of swamp white oak after light release (83.87%) was higher than no release (80.48%) within the CON overstory treatment, but survival did not differ between heavy release (82.47%) and no release.

Overstory harvest treatments showed no effect on survival of pin oak in any year ($p = 0.21$) but affected survival of swamp white oak in 2020, 2021, and 2022 ($p = 0.03$) (Fig. 2; Table A2). The CCR treatment reduced survival of swamp white oak compared to CON in 2020, 2021, and 2022, but survival was not different between BAR and CON. Midstory release showed no effect on survival of swamp white oak in all years ($p = 0.21$) but affected survival of pin oak ($p = 0.03$;

Fig. 3. Effects of overstory harvest and midstory release on height (mean ± 1 SE) of swamp white oak through time. Overstory harvest treatments included clearcut with reserves (CCR), basal area retention (BAR), and uncut control (CON). Different uppercase letters above bars indicate significant differences among overstory harvest treatments within a given midstory release treatment. Different lowercase letters above bars indicate significant differences among midstory release treatments within a given overstory harvest treatment.

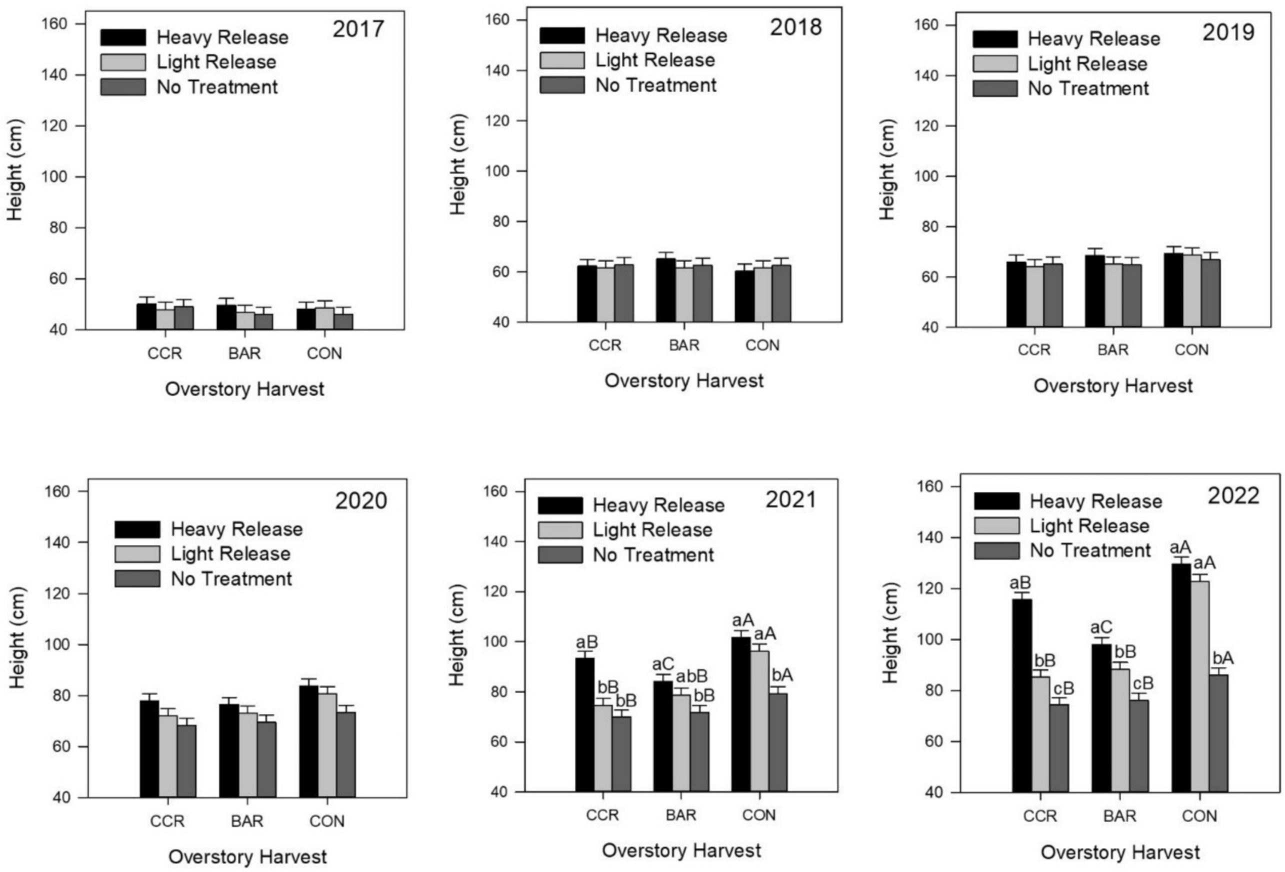


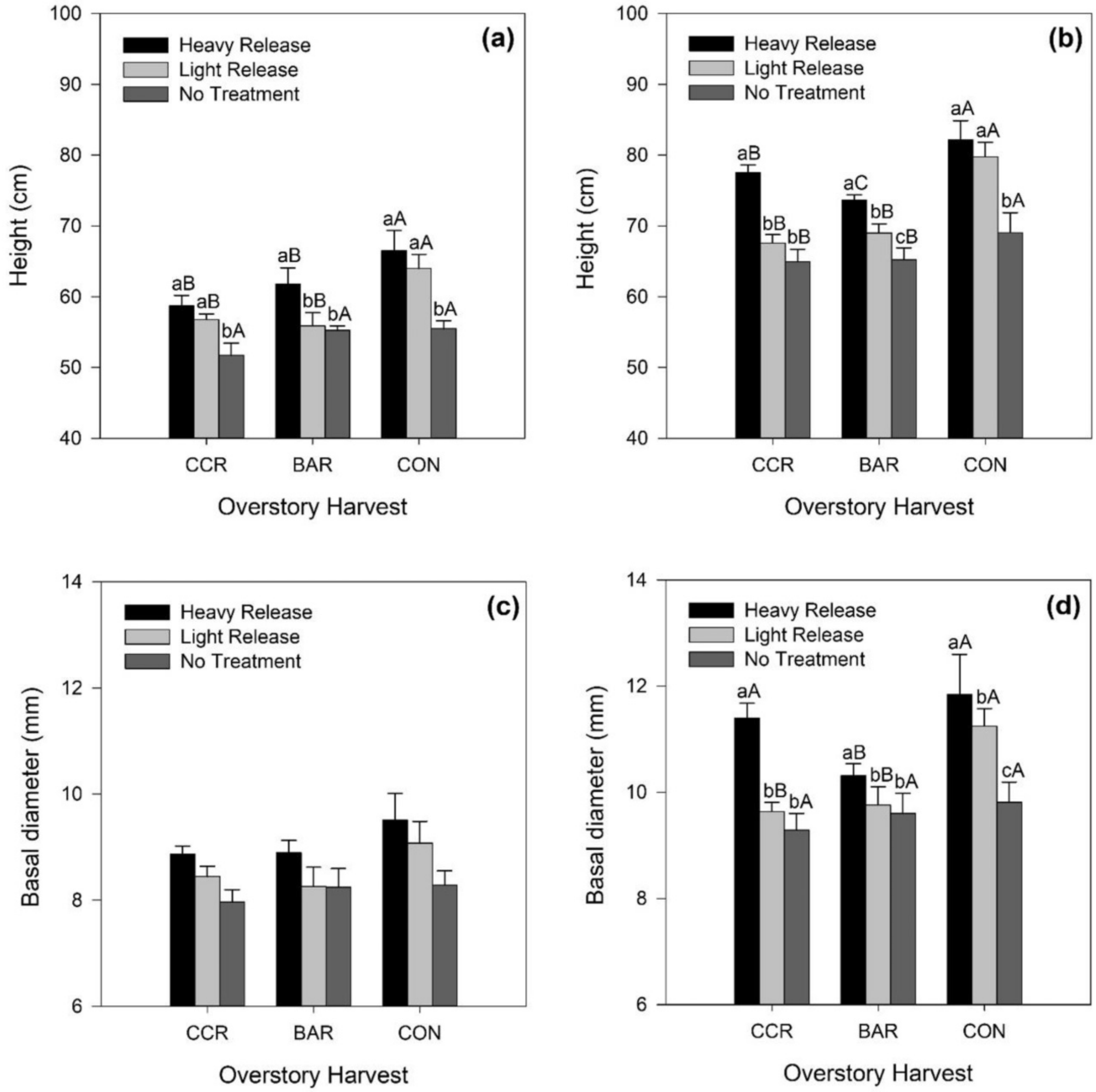
Fig. 2; Table A2). The light and heavy release treatments increased survival of pin oak compared to no release in 2020, 2021, and 2022. However, pin oak seedling survival in light release did not differ from heavy release in those years.

3.3. Size of oak reproduction

The heavy midstory release increased the heights of both pin oak and swamp white oak compared to no midstory release treatment within all the overstory harvest treatments ($p < 0.01$; Figs. 3 and 4; Table A3). Within the CON overstory treatment, the mean heights of pin oak and swamp white oak were 66.52 and 82.16 cm, respectively, following heavy midstory release, and 55.49 and 69.10 cm in the no release (Fig. 4). Mean height of pin oak in heavy midstory release and no midstory release were, respectively, 61.79 and 55.26 cm in BAR, and 58.70 and 51.72 cm in CCR (Fig. 4). The mean height of swamp white oak in heavy midstory release and no midstory release were 73.65 and 65.22 cm in BAR, and 77.52 and 64.95 cm in CCR, respectively (Fig. 4). The heights of both oak species following the heavy midstory release were greater in CON overstory treatment than BAR and CCR (Fig. 4). The heavy midstory release increased the basal diameter of swamp white oak compared to light release and no release within all the overstory harvest treatments ($p < 0.01$) but had no effect on pin oak ($p = 0.11$; Fig. 4; Table A3). The mean basal diameter of swamp white oak following heavy midstory release was greater in CON overstory treatment (11.84 mm) than BAR (10.31 mm) and CCR (11.40 mm). The light midstory release consistently increased the heights of both oak species, and basal diameter of swamp white oak within the CON overstory treatment (Fig. 4).

The treatments had no effects on the oaks until after the fourth and fifth growing seasons for height and basal diameter, respectively (Figs. 5 and 6; Table A3). When the treatments started showing effects, the heights and basal diameters of both oak species were greater in CON treatment than in BAR and CCR in all years (Fig. 5). However, the heights and basal diameters of both oak species were not different between BAR and CCR in most years. The heights of pin oak and swamp white oak 6 years after planting were 88.59 and 112.91 cm in CON, 73.36 and 87.58 cm in BAR, and 70.57 and 91.81 cm in CCR, respectively. Basal diameters of pin oak and swamp white oak following the sixth year were 10.99 and 14.76 mm in CON, 9.30 and 11.50 mm in BAR, and 9.42 and 12.40 mm in CCR, respectively. The light and heavy release

Fig. 4. Effects of overstory harvest and midstory release on height (mean ± 1 SE) and basal diameter (mean ± 1 SE) of pin oak (*a* and *c*) and swamp white oak (*b* and *d*). Overstory harvest treatments included clearcut with reserves (CCR), basal area retention (BAR), and uncut control (CON). Different uppercase letters above bars indicate significant differences among overstory harvest treatments within a given midstory release treatment. Different lowercase letters above bars indicate significant differences among midstory release treatments within a given overstory harvest treatment.

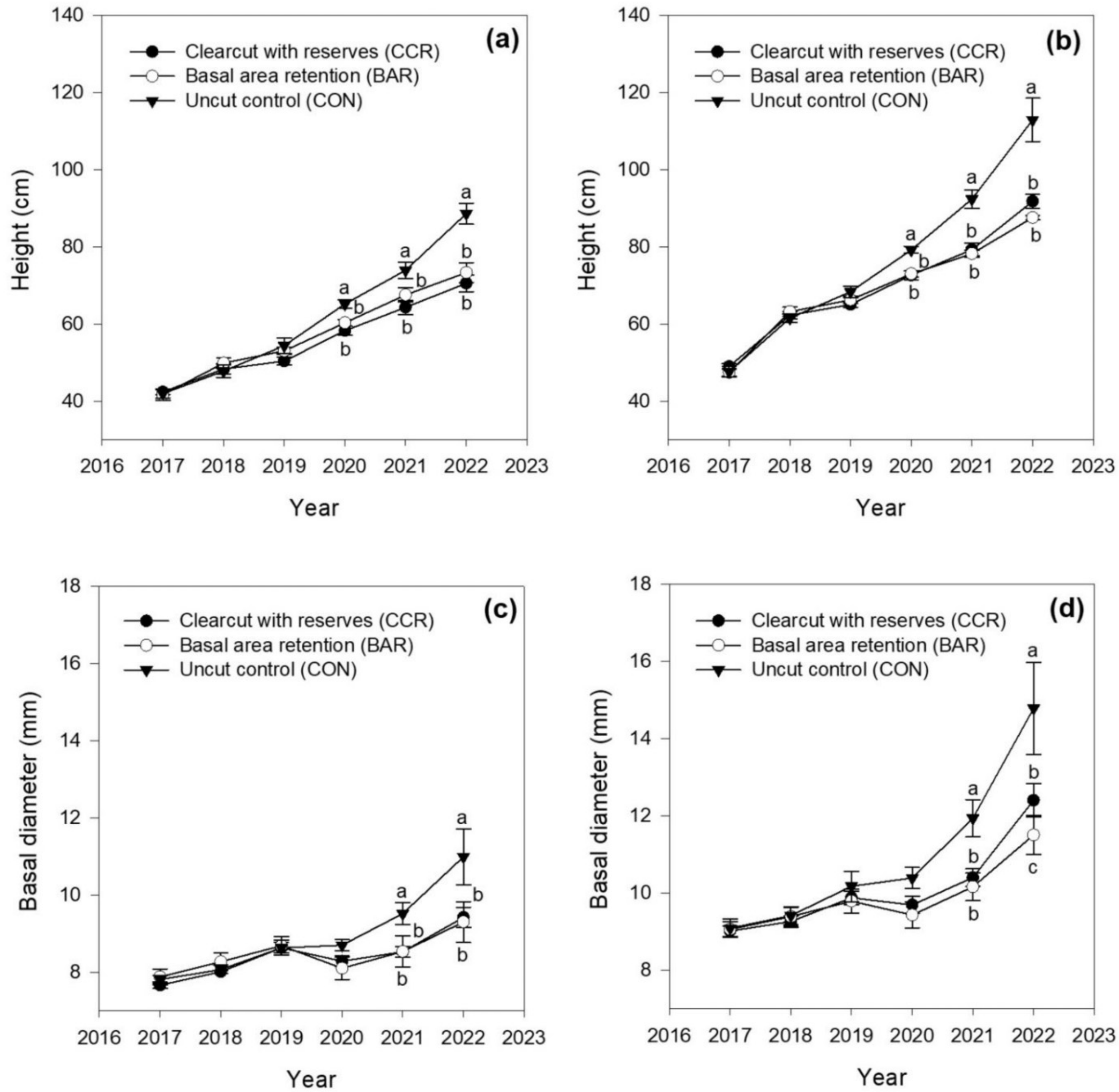


treatments increased the heights and basal diameters of both pin oak and swamp white oak compared to no release (Fig. 6; Table A3). The heights of pin oak and swamp white oak were, respectively, 87.77 and 114.52 cm in the heavy midstory release, compared to 65.23 and 78.95 cm in the no release 6 years after planting. Basal diameters of pin oak and swamp white oak 6 years following planting were, respectively, 11.13 and 15.50 mm in the heavy midstory release, and 8.69 and 10.42 mm in the no release.

3.4. Growth of oak reproduction

The heavy midstory release applied within each overstory harvest treatment increased the height growth of both pin oak (p = 0.01) and swamp white oak (p < 0.01) compared to no release (Fig. 7; Table A4). Within the CON overstory treatment, the mean height growth of pin oak and swamp white oak following heavy midstory release were 10.41 and 15.27 cm/year, respectively, compared to 3.98 and 7.00 cm/year in the no release. The mean height growth of pin oak and swamp white oak after heavy midstory release were, respectively, 7.23 and 8.59 cm/year in BAR, and 6.58 and 11.45 cm/year in CCR, compared to no release within BAR and CCR that ranged from 2.97 to 4.80 cm/year for both species. Within the CON overstory treatment, both light and heavy release treatments increased the height growth of pin oak and swamp white oak. The light and heavy release treatments applied within the CON overstory treatment resulted in greater height growth of pin oak and swamp white oak compared to light and heavy release applied within BAR and CCR. The heavy release applied within all the overstory harvest treatments increased only basal diameter growth of swamp white oak compared to no midstory release (p = 0.01) but had

Fig. 5. Height (mean ± 1 SE) and basal diameter (mean ± 1 SE) of pin oak (*a* and *c*) and swamp white oak (*b* and *d*) compared among overstory harvest treatments at the end of each growing season. Different letters within each year indicate significant differences among overstory harvest treatments.



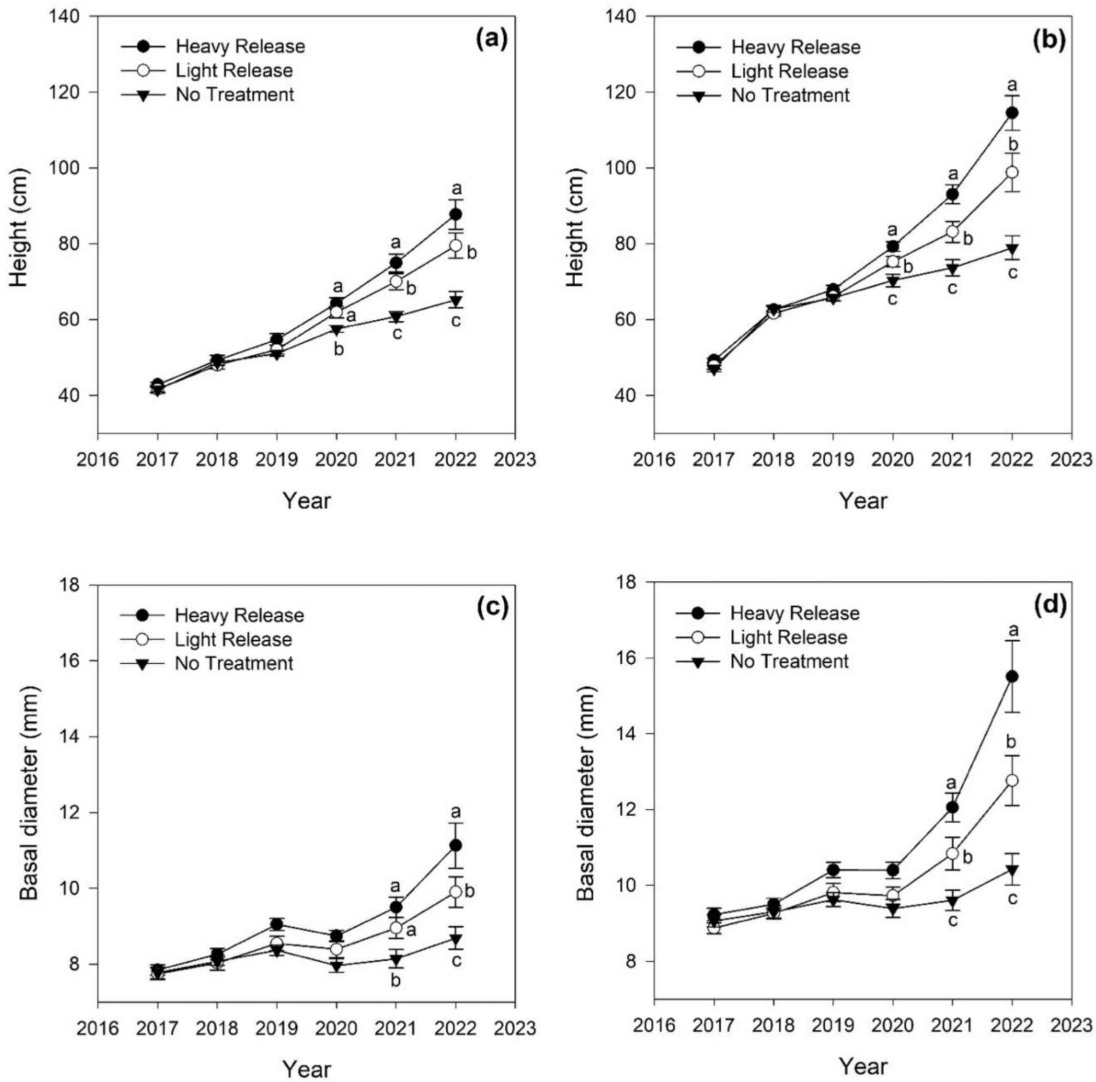
no effect on basal diameter growth of pin oak ($p = 0.20$) (Fig. 7). The light release applied within CON overstory treatment resulted in greater basal diameter growth of swamp white oak compared to light release applied within BAR and CCR.

The mean height growth of both pin oak and swamp white oak increased in CON overstory treatment compared to BAR and CCR treatments (Fig. 8; Table A4). However, the height growth of both oak species was not different between BAR and CCR in all years. The mean height growth of pin oak and swamp white oak during the fifth growing season were, respectively, 12.31 and 19.99 cm/year in CON, 5.34 and 7.93 cm/year in BAR, and 5.47 and 10.92 cm/year in CCR. The light and heavy release treatments increased height growth and basal diameter growth of both pin oak and swamp white oak compared to no release (Fig. 9; Table A4). The heavy release resulted in greater height growth and basal diameter growth of both pin oak and swamp white oak compared to light release in most years. The mean annual height growth of pin oak and swamp white oak following heavy midstory release during the fifth growing season were 11.45 and 19.65 cm/year, respectively, compared to 3.10 and 4.56 cm/year in the no release.

4. Discussion

In general, we found that seedlings established through enrichment planting after failed methods to regenerate oaks had inferior performance compared to seedlings established under an uncut overstory. The regeneration harvests that were intended to promote oak regeneration, applied in 1999 or 2000 using either the CCR or the BAR method, resulted in

Fig. 6. Height (mean ± 1 SE) and basal diameter (mean ± 1 SE) of pin oak (*a* and *c*) and swamp white oak (*b* and *d*) compared among midstory release at the end of each growing season. Different letters within each year indicate significant differences among midstory release treatments.

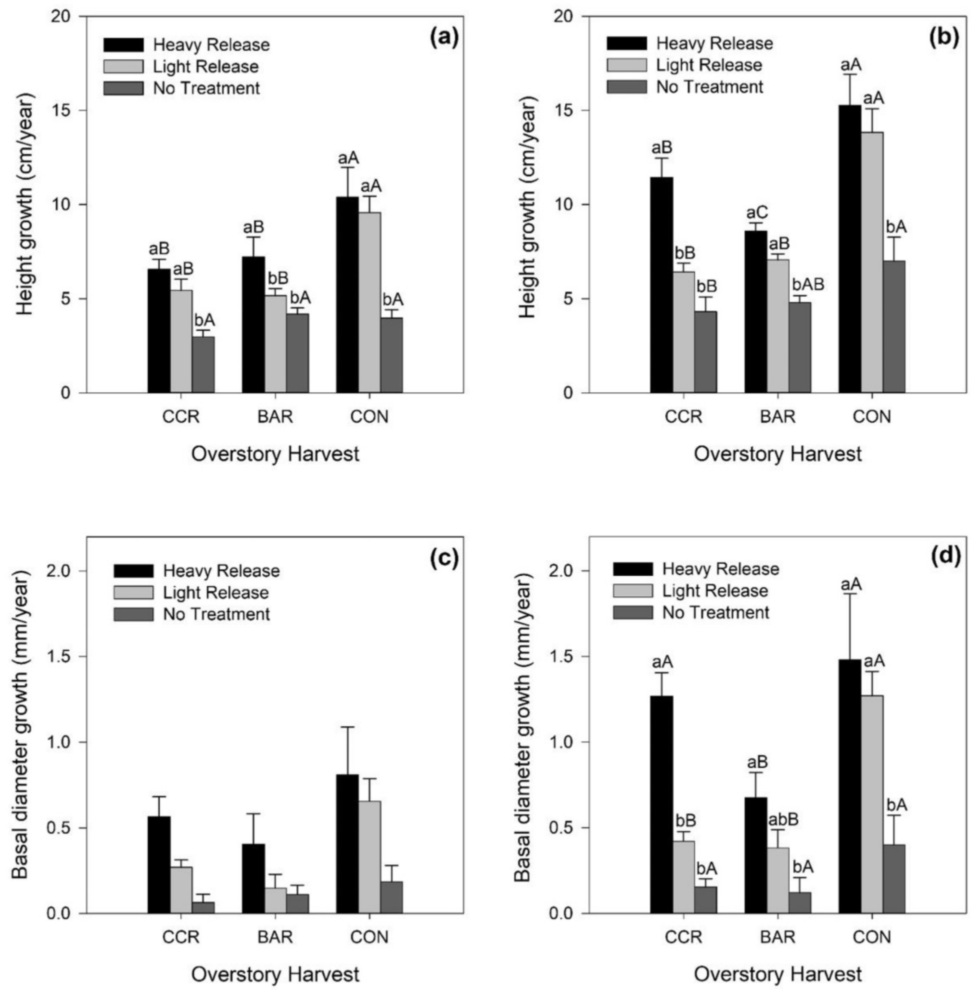


aggressive regeneration of fast-growing species that created a highly competitive environment, consistent with reports in other bottomland studies (Oliver et al. 2005; Rives et al. 2020). Despite the CON stands having higher overstory basal area, these results suggest greater midstory competitive pressure in the previously harvested stands.

Developing competitive oak advance reproduction prior to overstory harvest is important for successful oak regeneration (Lorimer 1993; Rives et al. 2020; Hayford et al. 2023). Furthermore, our findings demonstrate the difficulty of achieving successful enrichment planting following overstory harvest due to competition. Oaks have a growth strategy that promotes initial root growth at the expense of shoot growth, while most of their competitors (e.g., silver maple, green ash) prioritize shoot over root growth (Lorimer et al. 1994). These different growth strategies enable higher shoot growth in competitors relative to oaks, especially in full sunlight conditions in bottomland forests. However, large oak advance reproduction with well-developed root systems can effectively compete with other species following overstory harvests.

Regardless of the prior overstory treatment, we found that midstory release can be an effective approach to improve growth of planted oak reproduction in bottomland forests, consistent with previous work (Lockhart et al. 2000; Lhotka and Loewenstein 2009; Motsinger et al. 2010). Interestingly, work on upland oak species has also found increased growth following midstory release when compared to control treatments (Parrott et al. 2012; Craig et al. 2014; Hackworth et al. 2020). Consequently, midstory release treatments have been proposed as a method to develop competitive advance reproduction prior to overstory removal by favoring oak growth while limiting the release of competitors (Loftis 1990). However, the long-term effectiveness of release treatments with enrichment planting are not known. Given the height disadvantage and slow initial growth of planted oak seedlings

Fig. 7. Interaction effects of overstory harvest and midstory release on height growth (mean ± 1 SE) and basal diameter growth (mean ± 1 SE) of pin oak (*a* and *c*) and swamp white oak (*b* and *d*). Overstory harvest treatments included clearcut with reserves (CCR), basal area retention (BAR), and uncut control (CON). Different uppercase letters above bars indicate significant differences among overstory harvest treatments within a given midstory release treatment. Different lowercase letters above bars indicate significant differences among midstory release treatments within a given overstory harvest treatment.



relative to competitors, it is likely that they will remain vulnerable to competition through stand development.

The impact of midstory release on seedling development was influenced by the intensity of overstory harvest. Our results suggested that applying either level of midstory release (light or heavy release) in the previously unharvested stands increases height growth of both pin oak and swamp white oak. However, in the BAR or CCR stands, only the heavy midstory release consistently enhanced the development of oak reproduction. Moreover, we observed that a combination of underplanting and midstory release in previously unharvested stands generally ensured greater oak seedling growth compared to a combination of enrichment planting and midstory release in harvested stands. This underscores the importance of using an initial midstory release to develop competitive oak advance reproduction prior to overstory harvest to improve oak regeneration success in bottomland forests. The timing of future overstory release is contingent on the size of oak reproduction with at least 122 cm height considered to be the minimum release height needed to achieve oak regeneration success (Sander et al. 1976; Vickers et al. 2011). Although swamp white oak appeared to grow taller than pin oak, neither species had attained 122 cm in height following the fifth growing season.

Our results indicate a 4 year time lag for planted oak seedlings to show a growth response to midstory release. Delays in seedling growth response to release have been documented for other oak species, including cherrybark oak (*Quercus pagoda* Raf.) (Lockhart et al. 2000), black oak (*Quercus velutina* Lam.) (Parrott et al. 2011), and white oak (*Quercus alba* L.) (Dillaway et al. 2007; Parrott et al. 2011), as well as other tree species such as lodgepole pine (*Pinus contorta* Douglas ex Louden) (Kneeshaw et al. 2002), eastern white pine (*Pinus strobus* L.) (Bebber et al. 2004), and black spruce (*Picea mariana* (Mill) Britton, Sterns & Poggenb.) (Girona et al. 2016). The delay in growth to silvicultural release could be attributed to transplant shock commonly associated with post-planting moisture/nutrient stress or acclimatization of the seedlings

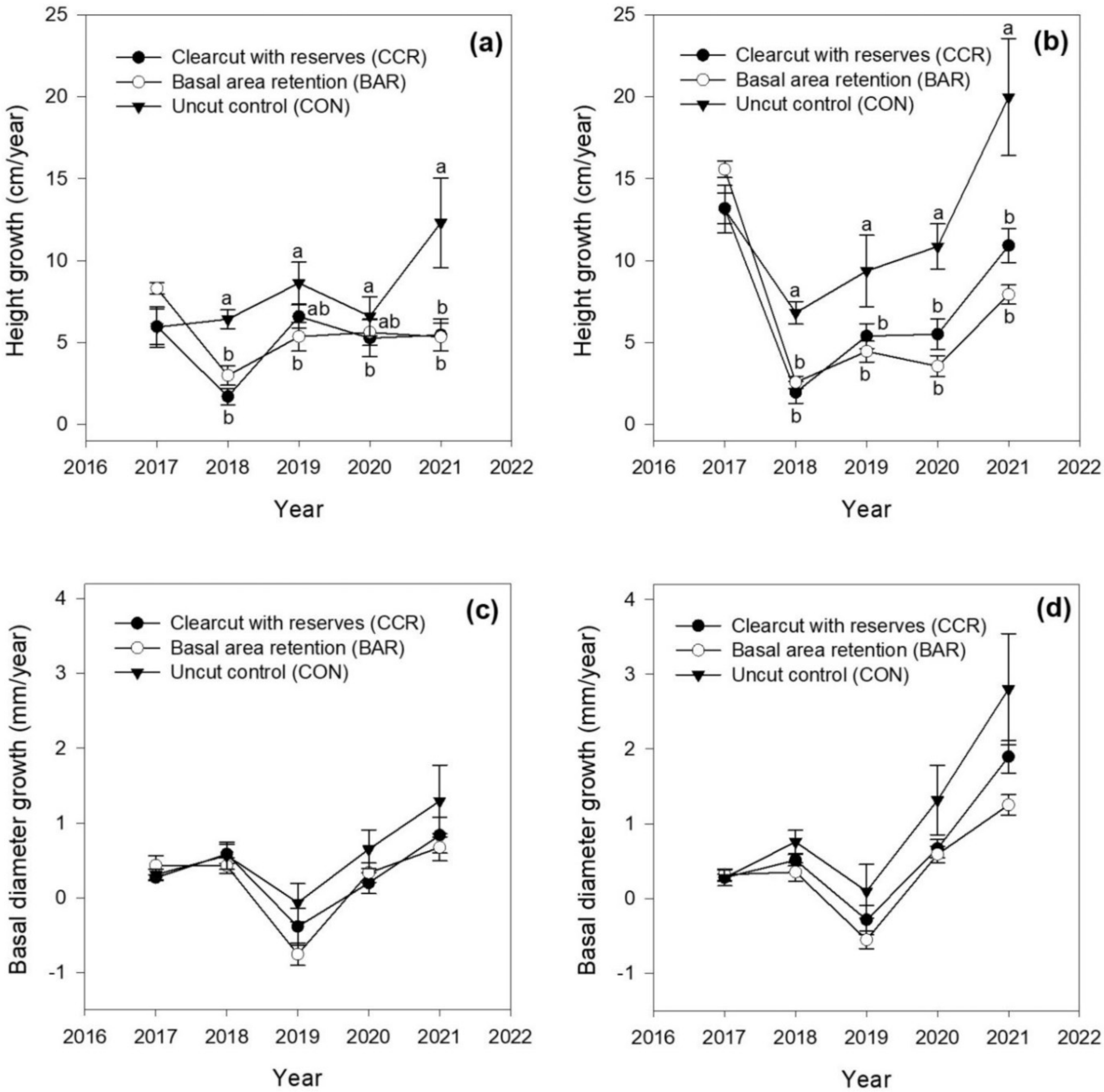
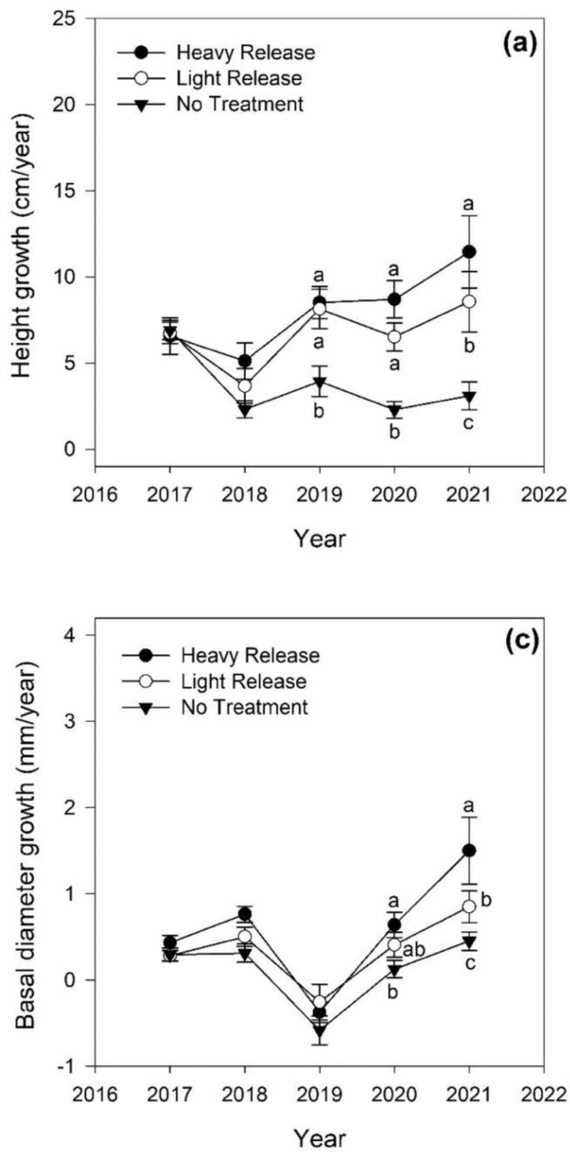


Fig. 8. Height growth (mean ± 1 SE) and basal diameter growth (mean ± 1 SE) of pin oak (*a* and *c*) and swamp white oak (*b* and *d*) compared among overstory harvest treatments at the end of each growing season. Different letters within each year indicate significant differences among overstory harvest treatments.

to the new environmental conditions (Close et al. 2005; Jacobs et al. 2009). Other possible causes include initial root growth at the expense of shoot growth (Kabrick et al. 2015), and inadequate hydraulic structures in seedlings for the increased demand for resources following release (Lockhart et al. 2000).

We found that growth differences between midstory release and control treatments became more pronounced through time for both pin oak and swamp white oak. Previous studies have reported magnified height growth response between midstory release and control treatments over time in bottomland forests for other plantings such as cherrybark oak (Lockhart et al. 2000; Lhotka and Loewenstein 2013), water oak (*Quercus nigra* L.) (Lhotka and Loewenstein 2013), and yellow poplar (*Liriodendron tulipifera* L.) (Lhotka and Loewenstein 2013). The conservative initial growth strategy of oaks that allocates higher proportion of biomass to its root system might contribute to the slower height growth response to treatments in the early stages of development. As root systems of oaks develop through time, the potential for increased height growth becomes higher in the future growing seasons, accounting for the magnified height growth response over time. However, the magnified growth rate in response to midstory release through time peaks and starts to decline when further release is warranted. Lhotka and Loewenstein (2013) reported that mean annual height growth following complete midstory release peaked during the fifth growing season at 20.2 cm/year for cherrybark oak and 18.5 cm/year for water oak. The rate of height growth in that study subsequently declined 2 years later to 17.3 cm/year for cherrybark oak and 14.5 cm/year for water oak. In our study, the mean annual height growth following heavy mid-

Fig. 9. Height growth (mean ± 1 SE) and basal diameter growth (mean ± 1 SE) of pin oak (*a* and *c*) and swamp white oak (*b* and *d*) compared among midstory release at the end of each growing season. Different letters within each year indicate significant differences among midstory release treatments.



story release during the fifth growing season (when the last monitoring was done) was 11.5 cm/year for pin oak and 19.7 cm/year for swamp white oak. Continued monitoring of the oak seedlings will be necessary to provide more insight into when growth following midstory release will peak and necessitate the need for subsequent release to facilitate recruitment.

The swamp white oak seedlings were taller and larger in basal diameter than the pin oak through six growing seasons. Shade-intolerant species, like pin oak, generally exhibit greater growth in response to increased light availability than shade-tolerant species. Thus, we expected pin oak to show greater growth in response to the midstory release treatments compared to swamp white oak, that is intermediate in shade tolerance. The growth disparities between the two oak species can be attributed in part to differences in their flood tolerance and initial planting size. Swamp white oak, which is classified as flood-tolerant, can thrive and grow under persistent flooded conditions during the growing season, whereas pin oak is moderate in flood-tolerance. In a flood experiment conducted by Kabrick et al. (2012) in Missouri, it was reported that swamp white oak maintained a high growth rate following flooding, while pin oak suffered significant growth reductions with increased flooding. Our study site is prone to annual flooding, and this may have provided swamp white oak with a growth advantage over pin oak. In addition, the survival and growth of artificial oak reproduction increase with initial planting size (Belli et al. 1999; Spetich et al. 2002; Hayford et al. 2023). The initial size (height and diameter) of swamp white oak at planting in 2017 was greater than the pin oak, which likely contributed to the observed higher growth rate in swamp white oak.

5. Conclusions

We found that the survival and growth of planted oak reproduction were inversely related to the intensity of overstory harvest, with the greatest survival and growth observed in untreated control, followed by BAR, and CCR. However, the opposite pattern was observed for the post-planting midstory release, with the greatest growth in heavy release, followed by light release, and no release. These results are encouraging for establishing oak advance reproduction prior to overstory harvest and demonstrate the difficulty of getting successful enrichment planting following overstory harvest. A prior midstory release is important to develop competitive oak advance reproduction before a later overstory harvest to ensure successful oak regeneration. Overstory harvests performed prior to enrichment planting of oaks promote the development of fast-growing vegetation that often outcompete and preclude the development of large oak advance reproduction capable of recruiting into the overstory. Our results suggested that applying either level of midstory release (light or heavy release) in the previously unharvested stands will increase growth of oak reproduction. However, only the heavy midstory release consistently promoted the development of oak reproduction in the previously harvested stands.

Acknowledgements

Funding for this study was provided by the Missouri Department of Conservation through cooperative agreement number 371 under agreement MCC-01-01-00. Additional support was provided by the United States Department of Agriculture, National Institute of Food and Agriculture, McIntire-Stennis program. We are also grateful to Jennifer Weaver, Brad Graham, Chad Runco, Bob Rives, Dacoda Maddox, Hope Fillingim, Alexander Bross, Carlee Steppe, Spencer Lamb, Jacob Hart, Kaitlyn Rankin, Shasta Brymner, Kaley Henderson, and many others who have supported the project through time.

Article information

History dates

Received: 19 March 2024
Accepted: 21 June 2024
Accepted manuscript online: 26 June 2024
Version of record online: 1 October 2024

Copyright

Data availability

Data will be made available upon request.

Author information

Author ORCIDs

Isaac Hayford https://orcid.org/0000-0002-5876-0542
Jeffrey D. Wood https://orcid.org/0000-0001-6422-2882
Alba Argerich https://orcid.org/0000-0001-6430-0449
Grant P. Elliott https://orcid.org/0000-0002-4642-8673

Author contributions

Conceptualization: IH, BOK, MGO
Formal analysis: IH, BOK
Funding acquisition: BOK, MGO
Investigation: IH, BOK
Methodology: BOK, MGO
Supervision: BOK, JDW, AA, JMK, GPE
Writing – original draft: IH
Writing – review & editing: IH, BOK, JDW, AA, JMK, GPE, MGO

Competing interests

The authors declare there are no competing interests.

References

Abernethy, Y., and Turner, R.E. 1987. U.S. forested wetlands: 1940-1980. Bioscience, **37**: 721–727. doi:10.2307/1310469.

Bebber, D.P., Thomas, S.C., Cole, W.G., and Balsillie, D. 2004. Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. Trees Struct. Funct. **18**: 29–34. doi:10.1007/s00468-003-0274-y.

Belli, K.L., Hart, C.P., Hodges, J.D., and Stanturf, J.A. 1999. Assessment of the regeneration potential of red oaks and ash on minor bottoms of Mississippi. South. J. Appl. For. **23**: 133–138. doi:10.1093/sjaf/23.3.133.

Brose, P.H. 2008. Root development of acorn-origin oak seedlings in shelterwood stands on the Appalachian Plateau of northern Pennsylvania: 4-year results. For. Ecol. Manag. **255**: 3374–3381. doi:10.1016/j.foreco.2008.02.021.

Brose, P.H., and Rebbeck, J. 2017. A comparison of the survival and development of the seedlings of four upland oak species grown in four different understory light environments. J. For. **115**: 159–166. doi:10.5849/jof.15-155.

Close, D.C., Beadle, C.L., and Brown, P.H. 2005. The physiological basis of containerised tree seedling 'transplant shock': a review. Aust. For. **68**: 112–120. doi:10.1080/00049158.2005.10674954.

Collins, B., and Battaglia, L.L. 2008. Oak regeneration in southeastern bottomland hardwood forest. For. Ecol. Manag. **255**: 3026–3034. doi:10.1016/j.foreco.2007.09.023.

Craig, J.M., Lhotka, J.M., and Stringer, J.W. 2014. Evaluating initial responses of natural and underplanted oak reproduction and a shade-tolerant competitor to midstory removal. For. Sci. **60**: 1164–1171. doi:10.5849/forsci.13-602.

Dey, D.C., Gardiner, E.S., Schweitzer, C.J., Kabrick, J.M., and Jacobs, D.F. 2012. Underplanting to sustain future stocking of oak (*Quercus*) in temperate deciduous forests. New For. **43**: 955–978. doi:10.1007/s11056-012-9330-z.

Dillaway, D.N., Stringer, J.W., and Rieske, L.K. 2007. Light availability influences root carbohydrates, and potentially vigor, in white oak advance regeneration. For. Ecol. Manag. **250**: 227–233. doi:10.1016/j.foreco.2007.05.019.

Frazier, S., and Galat, D.L. 2009. Analysis of Missouri Wetlands Reserve Program easement monitoring data. Final report to Natural Resources Conservation Service, Resource Inventory and Assessment Division. Conservation Effects Assessment Project. University of Missouri, Columbia, MO.

Gardiner, E.S., and Hodges, J.D. 1998. Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. For. Ecol. Manag. **108**: 127–134. doi:10.1016/S0378-1127(98)00220-5.

Gardiner, E.S., Jacobs, D.F., Overton, R.P., and Hernandez, G. 2009. Root collar diameter and third-year survival of three bottomland hardwoods planted on former agricultural fields in the lower Mississippi Alluvial Valley. *In* National Proceedings: Forest and Conservation Nursery Associations-2008. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, RMRS-P-58. pp. 85–89.

Girona, M.M., Morin, H., Lussier, J.M., and Walsh, D. 2016. Radial growth response of black spruce stands ten years after experimental shelterwoods and seed-tree cuttings in boreal forest. Forests, **7**: 1–20. doi:10.3390/f7100240.

Gottschalk, K.W. 1994. Shade, leaf growth and crown development of *Quercus rubra*, *Quercus velutina*, *Prunus serotina* and *Acer rubrum* seedlings. Tree Physiol. **14**(7): 735–749. doi:10.1093/treephys/14.7-8-9.735. PMID: 14967644.

Gwaze, D., and Elliott, A. 2011. Cavity trees, snags, and overstory density in a riparian forest in northeastern Missouri. North. J. Appl. For. **28**: 105–109. doi:10.1093/njaf/28.2.105.

Hackworth, Z.J., Lhotka, J.M., and Stringer, J.W. 2020. Midstory removal facilitates growth but reduces competitiveness of oak reproduction prior to and after shelterwood establishment cutting. For. Sci. **66**: 371–381. doi:10.1093/forsci/fxz083.

Hayford, I., Knapp, B.O., and Kabrick, J.M. 2023. Responses of natural and artificial pin oak (*Quercus palustris*) reproduction to a sequence of silvicultural release treatments in bottomland hardwood forests in southern Missouri. For. Ecol. Manag. **529**: 120699. doi:10.1016/j.foreco.2022.120699.

Hodges, J.D., and Gardiner, E.S. 1993. Ecology and physiology of oak regeneration. *In* Proceedings, Oak Regeneration: Serious Problems, Practical Recommendations. USDA Forest Service, Southern Research Station, Asheville, North Carolina, Gen. Tech. Rep. SE-84. pp. 54–65.

Jacobs, D.F., Francis Salifu, K., and Davis, A.S. 2009. Drought susceptibility and recovery of transplanted *Quercus rubra* seedlings in relation to root system morphology. Ann. For. Sci. **66**: 504–504. doi:10.1051/forest/2009029.

Johnson, P.S. 1994. How to manage oak forests for acorn production. Technical Brief TB-NC-1. USDA Forest Service, Northern Research Station, St. Paul, Minnesota. p. 5.

Johnson, P.S., Shifley, S.R., Rogers, R., Dey, D.C., and Kabrick, J.M. 2019. The ecology and silviculture of oaks. 3rd ed. CABI, Boston, MA. 612p.

Kabrick, J.M., Dey, D.C., van Sambeek, J.W., Coggeshall, M.V., and Jacobs, D.F. 2012. Quantifying flooding effects on hardwood seedling survival and growth for bottomland restoration. New For. **43**: 695–710. doi:10.1007/s11056-012-9331-y.

Kabrick, J.M., Knapp, B.O., Dey, D.C., and Larsen, D.R. 2015. Effect of initial seedling size, understory competition, and overstory density on the survival and growth of *Pinus echinata* seedlings underplanted in hardwood forests for restoration. New For. **46**: 897–918. doi:10.1007/s11056-015-9487-3.

Kellison, R.C., and Young, M.J. 1997. The bottomland hardwood forest of the southern United States. For. Ecol. Manag. **90**: 101–115. doi:10.1016/S0378-1127(96)03905-9.

Kneeshaw, D.D., Williams, H., Nikinmaa, E., and Messier, C. 2002. Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting. Can. J. For. Res. **32**: 255–265. doi:10.1139/x01-190.

Lhotka, J.M., and Loewenstein, E.F. 2009. Effect of midstory removal on understory light availability and the 2-year response of underplanted cherrybark oak seedlings. South. J. Appl. For. **33**: 171–177. doi:10.1093/sjaf/33.4.171.

Lhotka, J.M., and Loewenstein, E.F. 2013. Development of three underplanted hardwood species 7 years following midstory removal. South. J. Appl. For. **37**(2): 81–90. doi:10.5849/sjaf.12-001.

Lockhart, B.R., Hodges, J.D., and Gardiner, E.S. 2000. Response of advance cherrybark oak reproduction to midstory removal and shoot clipping. South. J. Appl. For. **24**: 45–50. doi:10.1093/sjaf/24.1.45.

Loftis, D.L. 1990. A shelterwood method for regenerating red oak in the southern Appalachians. For. Sci. **36**(4): 917–929.

Lorimer, C.G. 1993. Causes of oak regeneration problem. *In* Proceedings, Oak Regeneration: Serious Problems, Practical Recommendations. USDA Forest Service, Southern Research Station, Knoxville, Tennessee, Gen. Tech. Rep. SE-84. pp. 66–78.

Lorimer, C.G., Chapman, J.W., and Lorimer, W.D. 1994. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. **82**: 227–237. doi:10.2307/2261291.

Miller, G.W., Brose, P.H., and Gottschalk, K.W. 2017. Advanced oak seedling development as influenced by shelterwood treatments, competition control, deer fencing, and prescribed fire. J. For. **115**: 179–189. doi:10.5849/jof.16-002.

Motsinger, J.R., Kabrick, J.M., Dey, D.C., Henderson, D.E., and Zenner, E.K. 2010. Effect of midstory and understory removal on the establishment and development of natural and artificial pin oak advance reproduction in bottomland forests. New For. **39**: 195–213. doi:10.1007/s11056-009-9164-5.

Oliver, C.D., Burkhardt, E.C., and Skojac, D.A. 2005. The increasing scarcity of red oaks in Mississippi River floodplain forests: influence of the residual overstory. For. Ecol. Manag. **210**: 393–414. doi:10.1016/j.foreco.2005.02.036.

Olson, M.G., Gwaze, D., and Elliott, A.G. 2015a. Fate of live trees retained in mixed bottomland hardwood stands during the first decade after harvest. For. Sci. **61**: 190–196. doi:10.5849/forsci.13-730.

Olson, M.G., Wolf, A.J., and Jensen, R.G. 2015b. Influence of forest management on acorn production in the southeastern Missouri Ozarks: early results of a long-term ecosystem experiment. Open J. For. **05**: 568–583. doi:10.4236/ojf.2015.55051.

Parrott, D.L., Lhotka, J.M., and Stringer, J.W. 2011. Effects of midstory removal on underplanted black oak and white oak in the western Cumberland plateau. *In* Proceedings of the 17th Central Hardwood Forest Conference. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, Gen. Tech. Rep. NRS-P-78. pp. 270–276.

Parrott, D.L., Lhotka, J.M., Stringer, J.W., and Dillaway, D.N. 2012. Seven-year effects of midstory removal on natural and underplanted oak reproduction. North. J. Appl. For. **29**: 182–190. doi:10.5849/njaf.12-001.

Rives, R.G., Knapp, B.O., Olson, M.G., Weegman, M.D., and Muzika, R.M. 2020. Regenerating mixed bottomland hardwood forests in north Missouri: effects of harvest treatment on structure, composition, and growth through 15 years. For. Ecol. Manag. **475**: 118371. doi:10.1016/j.foreco.2020.118371.

Sander, I.L., Johnson, P.S., and Watt, R.F. 1976. A guide for evaluating the adequacy of oak advance reproduction. USDA Forest Service, Northern Research Station, St. Paul, Minnesota, Gen. Tech. Rep. NC-23. p. 7

Schuler, J.L., and Robison, D.J. 2010. Performance of northern red oak enrichment plantings in naturally regenerating southern Appalachian hardwood stands. New For. **40**: 119–130. doi:10.1007/s11056-009-9187-y.

Spetich, M.A., Dey, D.C., Johnson, P.S., and Graney, D.L. 2002. Competitive capacity of *Quercus rubra* L. planted in Arkansas' Boston Mountains. For. Sci. **48**: 504–517. doi:10.1093/forestscience/48.3.504.

Vickers, L.A., Fox, T.R., Loftis, D.L., and Boucugnani, D.A. 2011. Predicting forest regeneration in the Central Appalachians using the REGEN expert system. J. Sustainable For. **30**: 790–822. doi:10.1080/10549811.2011.577400.

Yin, Y., Nelson, J.C., and Lubinski, K.S. 1997. Bottomland hardwood forests along the Upper Mississippi River. Nat. Areas J. **17**: 164–173.

Appendix A

Table A1. Statistical output showing treatment effects on basal area and trees per hectare of overstory (trees ≥ 11.43 cm dbh) and midstory (3.81 ≤ dbh < 11.43 cm) trees (see Table 1).

			Basal area		Trees per hectare	
Effect	Num DF	Den DF	*F* value	*p*-value	*F* value	*p*-value
Overstory trees						
Overstory harvest	2	12	4.60	0.03	21.73	<0.01
Midstory release	2	24	0.84	0.44	3.83	0.04
Overstory harvest × midstory release	4	24	1.82	0.16	1.50	0.23
Midstory trees						
Overstory harvest	2	12	2.87	0.10	1.26	0.32
Midstory release	2	24	12.95	<0.01	11.14	<0.01
Overstory harvest × midstory release	4	24	1.81	0.16	2.23	0.10

Table A2. Statistical output showing treatment effects on the probability of survival of pin oak and swamp white oak (see Figs. 1 and 2).

		Pin oak			Swamp white oak		
Effect	Num DF	Den DF	*F* value	*p*-value	Den DF	*F* value	*p*-value
Overstory harvest	2	12	1.61	0.24	12	2.09	0.17
Midstory release	2	144	7.05	<0.01	144	0.29	0.75
Overstory harvest × midstory release	4	144	1.02	0.40	144	8.65	<0.01
Year	5	60	91.80	<0.01	60.1	98.75	<0.01
Overstory harvest × year	10	60	1.38	0.21	60.1	2.15	0.03
Midstory release × year	10	144	2.06	0.03	144	1.35	0.21
Overstory harvest × midstory release × year	20	144	0.72	0.80	144	1.16	0.30

Table A3. Statistical output showing treatment effects on pin oak and swamp white oak height and diameter (see Figs. 3, 4, 5, and 6).

		Height			Diameter		
Effect	Num DF	Den DF	*F* value	*p*-value	Den DF	*F* value	*p*-value
Pin oak							
Overstory harvest	2	12	7.11	0.01	12	2.03	0.17
Midstory release	2	204	57.97	<0.01	144	29.06	<0.01
Overstory harvest × midstory release	4	204	5.00	<0.01	144	1.91	0.11
Year	5	204	300.18	<0.01	60	34.05	<0.01
Overstory harvest × year	10	204	8.50	<0.01	60	3.40	<0.01
Midstory release × year	10	204	11.07	<0.01	144	4.48	<0.01
Overstory harvest × midstory release × year	20	204	1.29	0.19	144	0.55	0.94
Swamp white oak							
Overstory harvest	2	12	18.26	<0.01	12	3.71	0.06
Midstory release	2	144	18.75	<0.01	144	69.37	<0.01
Overstory harvest × midstory release	4	144	5.96	<0.01	144	9.09	<0.01
Year	5	60	328.13	<0.01	60	59.55	<0.01
Overstory harvest × year	10	60	11.45	<0.01	60	4.38	<0.01
Midstory release × year	10	144	21.40	<0.01	144	15.66	<0.01
Overstory harvest × midstory release × year	20	144	2.19	<0.01	144	1.61	0.06

Table A4. Statistical output showing treatment effects on pin oak and swamp white oak height growth and basal diameter growth (see Figs 7, 8, and 9).

		Height growth			Basal diameter growth		
Effect	Num DF	Den DF	*F* value	*p*-value	Den DF	*F* value	*p*-value
Pin oak							
Overstory harvest	2	12	7.76	0.01	12	2.76	0.10
Midstory release	2	120	34.70	<0.01	120	18.82	<0.01
Overstory harvest × midstory release	4	120	3.60	0.01	120	1.52	0.20
Year	4	48	5.96	<0.01	48	17.13	<0.01
Overstory harvest × year	8	48	3.02	0.01	48	0.87	0.55
Midstory release × year	8	120	4.22	<0.01	120	2.57	0.01
Overstory harvest × midstory release × year	16	120	1.30	0.21	120	1.06	0.40
Swamp white oak							
Overstory harvest	2	12	21.31	<0.01	12	6.60	0.01
Midstory release	2	120	45.29	<0.01	120	39.38	<0.01
Overstory harvest × midstory release	4	120	4.09	<0.01	120	3.56	0.01
Year	4	48	32.93	<0.01	48	29.12	<0.01
Overstory harvest × year	8	48	3.95	<0.01	48	1.25	0.29
Midstory release × year	8	120	9.85	<0.01	120	9.39	<0.01
Overstory harvest × midstory release × year	16	120	1.36	0.17	120	1.19	0.29

Table A5. Mean and percent contribution of basal area (m^2/ha) by species group and treatment of all trees ≥ 3.81 cm dbh sampled in 2021.

	Clearcut with reserves		Basal area retention		Uncut control	
Species group	Mean (m^2/ha)	%	Mean (m^2/ha)	%	Mean (m^2/ha)	%
American elm	2.21	11.85	2.69	11.39	2.28	8.27
American sycamore	2.37	12.71	4.32	18.30	1.53	5.56
Eastern cottonwood	2.43	13.04	2.57	10.90	8.09	29.42
Green ash	2.17	11.64	1.98	8.40	3.48	12.65
Hickories	0.10	0.53	0.27	1.15	0.31	1.14
Oaks	1.46	7.81	1.56	6.60	2.01	7.31
Other species	2.81	15.10	3.32	14.07	2.25	8.16
Silver maple	5.09	27.31	6.89	29.19	7.56	27.49
Total	18.65	100	23.60	100	27.51	100