forests

MDPI

Article

Ten-Year Responses of Underplanted Northern Red Oak to Silvicultural Treatments, Herbivore Exclusion, and Fertilization

Graham S. Frank [1,2,*], Ronald A. Rathfon [1] and Michael R. Saunders [1]

[1] Department of Forestry and Natural Resources, Purdue University, 715 W. State Street, West Lafayette, IN 47907, USA; ronr@purdue.edu (R.A.R.); msaunder@purdue.edu (M.R.S.)

[2] Department of Forest Ecosystems and Society, Oregon State University, 252 Richardson Hall, Corvallis, OR 97331, USA

* Correspondence: graham.frank@oregonstate.edu or frankg@purdue.edu; Tel.: +1-971-533-4433

Received: 12 August 2018; Accepted: 11 September 2018; Published: 15 September 2018

Abstract: Establishing adequate advanced oak reproduction prior to final overstory removal is crucial for regenerating oak forests in the eastern U.S. Many management approaches exist to this end, but benefits associated with any individual technique can depend on the suite of techniques employed and the geographic location. At four mixed-hardwood upland forest sites in central and southern Indiana, we tested factorial combinations of deer fencing, controlled-release fertilization, and various silvicultural techniques (midstory removal, crown thinning, and a shelterwood establishment cut) for promoting the growth and survival of underplanted red oak seedlings. Crown thinning resulted in slow growth and low survival. Midstory removal and the shelterwood establishment cut were nearly equally effective for promoting seedling growth. Seedling survival was strongly influenced by fencing, and differences in survival between silvicultural treatments were minimal when fencing was employed. Fertilization had minimal effects overall, only increasing the probability that unfenced seedlings were in competitive positions relative to surrounding vegetation. We suggest that underplanting oak seedlings can augment natural reproduction, but the practice should be accompanied by a combination of midstory removal and fencing, at a minimum, for adequate growth and survival.

Keywords: *Quercus rubra*; oak regeneration; Central Hardwood Forest region; shelterwood; deer herbivory

1. Introduction

Oaks (*Quercus* spp.) have been a foundational species in forests of eastern North America, but have been failing to regenerate in recent decades [1,2]. Forests dominated by oaks are ecologically and economically valuable as a source of timber, as a food source and habitat for wildlife, and for relatively open stand characteristics that promote diverse understory flora [3]. These forests were historically maintained by a frequent fire regime, and current oak dominance often reflects legacies of heavy logging, burning, and grazing by early European settlers [2]. However, fire suppression, land use changes, and the expansion of deer populations have dramatically altered disturbance regimes, shifting forests towards less open stand conditions and resulting in a lack of large advance oak reproduction in the understory to take advantage of periodic canopy openings [4,5]. Oak declined in importance across 81% of forested area in the Central Hardwood Forest Region between 1980–2008 [6], and oak regeneration becomes increasingly challenging as forest compositions shift towards more shade-tolerant species, reducing light penetration to the forest floor, and further suppressing fire [7].

An array of silvicultural practices has been developed to counter the numerous obstacles to oak regeneration. Oak are only moderately shade tolerant, and seedlings beneath dense midstory canopies grow slowly and have high mortality rates [8]. Moreover, single-tree selection and other partial cutting practices favor the growth of shade-tolerant advance regeneration [9–11]. Conversely, oaks are slow-growing and can be outcompeted in high light environments on productive sites following more intensive harvests, such as commercial or silvicultural clearcuts [12,13]. Shelterwood techniques have been used successfully, providing adequate light for oak growth and survival, while reducing the advantage of shade-intolerant competitors [14–17].

Despite the relative effectiveness of shelterwood techniques, examples of regeneration failure in shelterwoods still exist [13,18], and can be influenced by deer herbivory, site quality, and competitive pressure [19]. The relative importance of these factors can vary geographically, causing uncertainty in the outcomes of prescriptions designed to promote oak regeneration [20]. For example, stronger understory competition on productive sites may make regeneration failure more likely in Indiana than in Missouri [21]. Deer herbivory pressure can vary according to landscape-level factors, including the amount of surrounding forest acreage [22].

Management context can be as important as geographic context for determining the effectiveness of any single management action for promoting oak regeneration. Deer herbivory pressure on hardwood seedlings can depend on the size of canopy gaps following different silvicultural treatments [23], the amount of early successional habitat created by harvest openings [24,25], or the application of understory competition control [18]. Fertilization improved height growth of planted red oak seedlings in one study where those seedlings were protected from herbivory, particularly in conjunction with understory competition control, but fertilization was confounded with lime application [26]. However, red oak plantings do not always respond to nitrogen fertilization [27,28], and fertilization can increase herbivory damage when seedlings are not protected, eliminating any potential benefits to growth [29]. Interactive effects of different treatments coupled with geographic variability in treatment effects make studies that examine multiple treatments in combination particularly important, and such studies should be implemented in a variety of locations and conditions [20].

Temporal variability in acorn production creates an additional source of uncertainty when developing prescriptions for oak regeneration [30], and asynchrony between management actions and acorn mast crop can result in limited oak reproduction present to take advantage of release [31]. Underplanting oak seedlings (i.e., artificial regeneration, enrichment planting) may be a viable approach to supplement poor natural reproduction and allow managers to precisely plan the timing of silvicultural practices [19], but the approach increases the costs of securing oak regeneration. This greater investment increases the economic consequences for managers and family forest landowners in the event of regeneration failure.

The economic efficiency of planting oak seedlings depends upon not only the cost of planting and other silvicultural treatments, but also the survival and competitive ability of those seedlings during early stages of stand development [32]. In this study, we aimed to improve oak regeneration prescriptions by directly testing the utility of commonly prescribed management actions for promoting competitive advance oak reproduction, in combination with one another and at an operational scale in central and southern Indiana. We expected that (1) a shelterwood establishment cut coupled with deer exclusion fencing would be the most effective approach for promoting growth and survival of natural and underplanted oak seedlings; (2) fertilization would increase growth and survival of underplanted seedlings; and (3) the strength of any individual treatment effect would depend upon the combination of treatments applied.

2. Materials and Methods

2.1. Site Descriptions

We conducted this study at four mature, mixed-oak forest sites in central and southern Indiana, US. Study sites had no evidence of recent (at least 40–50 years) major disturbance, based on observations of stand condition and ground evidence (i.e., lack of recent stumps, slash, etc.; RAR, pers. obs.). All sites had a well-developed midstory canopy of tree species dominated by sugar maple (*Acer saccharum* Marshall), red maple (*A. rubrum* L.), and American beech (*Fagus grandifolia* Ehrh.). Three sites were selected from properties managed by The Nature Conservancy (TNC) in southern Indiana: (1) Wulfman Tract, a dry-mesic forest located in southeastern Harrison County; (2) Knapp Tract, a dry-mesic forest located in north central Washington County; and (3) McKinney Tract, a dry to dry-mesic forest located in eastern Brown County. The first two sites are located in the Mitchell Karst Plain Section of the Highland Rim Natural Region of Indiana. The McKinney Tract is located in the Brown County Hills Section of the same natural region [33]. These three sites are all located within the unglaciated region of the state. A fourth site was located on the Purdue University Nelson-Stokes property in northern Putnam County on the Tipton Till Plain Section of the Central Till Plain Natural Region. Soils at Nelson-Stokes are formed in deep glacial till supporting densely stocked mesic to dry-mesic forest.

Study sites represented a range of basal areas (BA), stocking levels, and overstory oak abundance. Pre-treatment BA ranged from 23.9 m^2/ha on the McKinney tract to 34.7 m^2/ha on the Nelson-Stokes tract (Table 1). Stocking levels at these sites ranged from 89% full stocking on the McKinney tract to 121% full stocking on the Nelson-Stokes tract. Oak abundance ranged from 21% of the total BA on the Wulfman tract to 49% on the Knapp tract. Beech and maple accounted for 27% of the BA across all tracts.

Table 1. Mean ± SE basal area (BA) estimates for silvicultural treatments in each sampling year. Initial BA change was calculated as the percent change between Y0 and Y2 sampling periods for each plot. Therefore, values displayed in the Initial BA Change column reflect means of the percent change in BA, rather than the percent change in the means.

Treatment	Basal Area				Initial BA Change
	2007 (Y0) (m^2 ha^{-1})	2009 (Y2)	2011 (Y4) †	2018 (Y10)	Percent
Control	26.7 ± 3.2	28.5 ± 3.0	28.4 ± 2.7	23.9 ± 2.0	+7.0 ± 5.3 ^{a}
Midstory Removal	27.4 ± 3.1	21.3 ± 2.8	21.2 ± 2.6	20.8 ± 1.9	−24.1 ± 5.0 ^{b}
Thinning	30.1 ± 3.4	20.4 ± 3.2	20.7 ± 2.9	19.3 ± 2.1	−29.2 ± 5.7 ^{b}
Shelterwood	30.0 ± 3.1	20.2 ± 2.8	19.9 ± 2.6	17.9 ± 1.8	−36.1 ± 5.0 ^{b}

Letters indicate significant differences at α = 0.05; only pretreatment BA and percent change tested; † Nelson-Stokes site re-measured 2010 (Y3).

2.2. Experimental Design

At each site, three to four plots, each ranging in size from 0.6 to 1.1 ha (1.5 to 2.7 acres) in size, were randomly assigned one of three silvicultural treatments or as a control. The first treatment, a light crown thinning with a residual stocking target of 70%–80% full stocking, was accomplished through a marked commercial timber harvest followed by timber stand improvement to remove non-commercial trees. Crown thinning removed lower-value timber and late successional species, and retained oak species. The second treatment, a midstory removal treatment, removed all trees from 5.1 cm dbh (diameter at breast height) (2.0 inches) to 20.3 to 30.5 cm (8.0 to 12.0 inches) dbh using chainsaw felling, girdling, and herbicide application. Oaks and other desirable species were coppiced. The third treatment was a shelterwood establishment cut that included light crown thinning to 70%–80% full stocking, followed by the removal of all non-merchantable-sized trees down to 5.1 cm (2.0 inches) dbh. Controls received no silvicultural treatment. All sites, other than the Knapp Tract, included each treatment; the Knapp Tract did not include the light crown thinning treatment because a midstory removal treatment had been previously implemented across the entire site, and addition of the light crown treatment would have been akin to a second replication of the shelterwood establishment cut at the site. In addition, control plots for the Knapp Tract were included on adjacent private land to avoid the previous midstory removal treatment, prohibiting the inclusion of a fenced control plot.

Half of each silvicultural treatment plot, including the control, was fenced to exclude deer using an eight-feet-high polypropylene woven fence, resulting in a split-plot design (Figure 1). Within each split plot, 100 1-0 northern red oak (*Quercus rubra* L.) seedlings were hand planted using KBC bars on a grid with approximately 9.1 m × 9.1 m (30 ft × 30 ft) spacing. Immediately after planting, every other seedling was fertilized with 60 g (2.1 oz) of Osmocote® Exact Lo-Start 15N-9P-10K plus minors, 16- to 18-month release fertilizer (ICL Specialty Fertilizers—North America: Dublin, OH, US), resulting in 50 fertilized and 50 unfertilized seedlings per split-plot. Fertilizer was applied directly adjacent to seedling roots using a Pottiputki seedling planter (BAP Equipment, Ltd.: Baileyville, ME, US). Fences were routinely maintained throughout the first 10 years of the study on the three TNC properties. The fence on the Nelson-Stokes property was maintained through the fifth year.

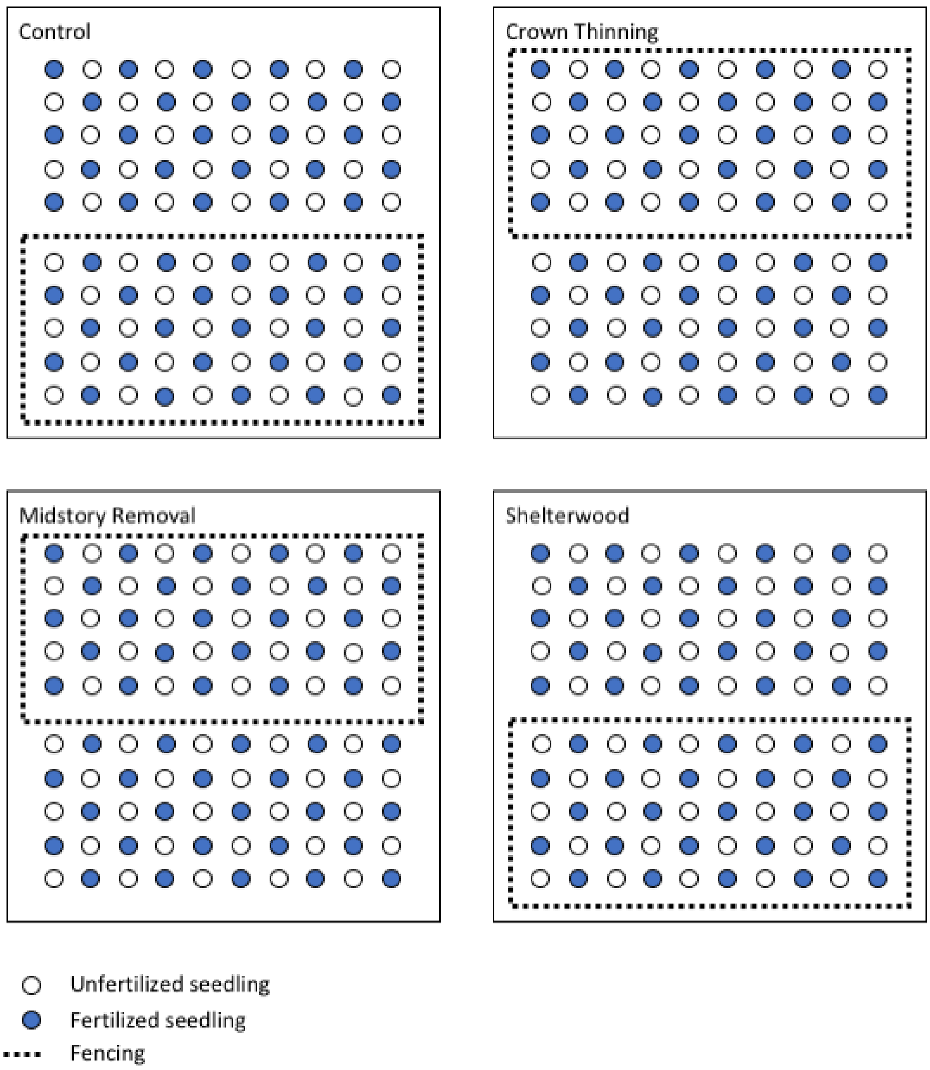

Figure 1. Schematic layout of a single study site, showing the split-plot design created by fencing half of the seedlings underplanted beneath each silvicultural treatment. We applied fertilizer to every other seedling at planting.

2.3. Data Collection

Overstory composition and BA were sampled using four 405-m^2 (0.1-acre) circular plots placed systematically within each silvicultural treatment plot, with two in each fenced or unfenced split-plot. Within 405-m^2 plots, we measured diameter and recorded the species of all trees ≥5.1 cm (2.0 inches) dbh. At the same plot center points, a 40.5-m^2 (0.01-acre) circular plot was used to tally all tree saplings ≥1 m (3.3 ft) tall and <5.1 cm (2.0 inches) dbh. Four 1-m^2 (10.8-ft^2) quadrats were permanently marked 3.6 m (11.8 ft) in cardinal directions from plot center to sample all tree seedlings <1 m (3.3 ft) tall. Sampling occurred prior to treatment and again at years 2, 4, and 10.

Data on planted red oak seedlings were collected at year 10. We measured height to the nearest 1 cm (0.4 inch) using a height pole and measured ground line diameter (GLD) to the nearest 1 mm (0.04 inch) using calipers for all surviving seedlings. We also assessed the competitive status of surviving seedlings by recording the crown class of each seedling, relative to the same cohort of woody regeneration, as well as its free-to-grow status. Free-to-grow status was assessed by projecting a 90-degree cone from the apical bud of each seedling 1.2 m (4.0 ft) upwards and counting the number of cone quadrants occupied by a woody competitor [34].

2.4. Statistical Analysis

We used generalized linear mixed-effects models (GLMMs) to analyze differences in height, GLD, survival, and competitiveness of planted seedlings, as well as density of naturally regenerated oak seedlings and saplings. Height and GLD were analyzed with a linear link (Gaussian distribution); competitiveness and survival were analyzed with a logistic link (binomial distribution); and counts of naturally regenerated seedlings and saplings were analyzed with a log link (Poisson distribution). Competitiveness was treated as binary, and planted seedlings were considered competitive if their crown class position was dominant or co-dominant, or if their crown class position was intermediate, but they were free-to-grow (i.e., zero competitors in cone) because of sparse local competition. GLMMs were initially fit with all possible two-way interactions, which were tested individually for inclusion in each model using likelihood ratio tests ($\alpha = 0.05$). GLMMs for the effects of treatments on planted seedlings included random site intercepts as well as random treatment effects for each site. To account for pretreatment differences between treatment plots, seedling densities were analyzed with a repeated-measures approach. Limited numbers of sapling-size oak in earlier sampling years restricted our analysis of naturally regenerated sapling densities to year 10. To test for significant differences between treatment effects, we used planned contrasts with adjusted p-values for multiple comparisons ($\alpha = 0.05$). All analyses were conducted with R programming software, version 3.4.4 [35], using the packages lme4 to build and run GLMMs [36] and multcomp to test planned contrasts [37]. R code and input data used in analyses can be found in Supplementary Materials.

3. Results

3.1. Overstory Conditions

Initial stand BA was slightly higher in plots randomly selected for crown thinning and shelterwood treatments, but these differences were not statistically significant ($F3,51.8 = 0.53$, $p = 0.66$; Table 1). Mean percent BA reductions between pretreatment values and the first post-treatment sampling year were greatest for the shelterwood treatment, intermediate for the thinning treatment, and lowest for the midstory removal treatment (Table 1). After initial treatments, stand BA declined further during the interval between 2011 and 2017 samples, primarily due to storm damage (RAR, personal observation). The greatest reductions in overstory BA during this interval occurred in control plots (Table 1). Despite the similarities in total BA between thinning and midstory removal treatments at all sampling periods following initial treatments, overstory size class distributions between these treatments were markedly different both before and after perceived storm damage (Figure 2).

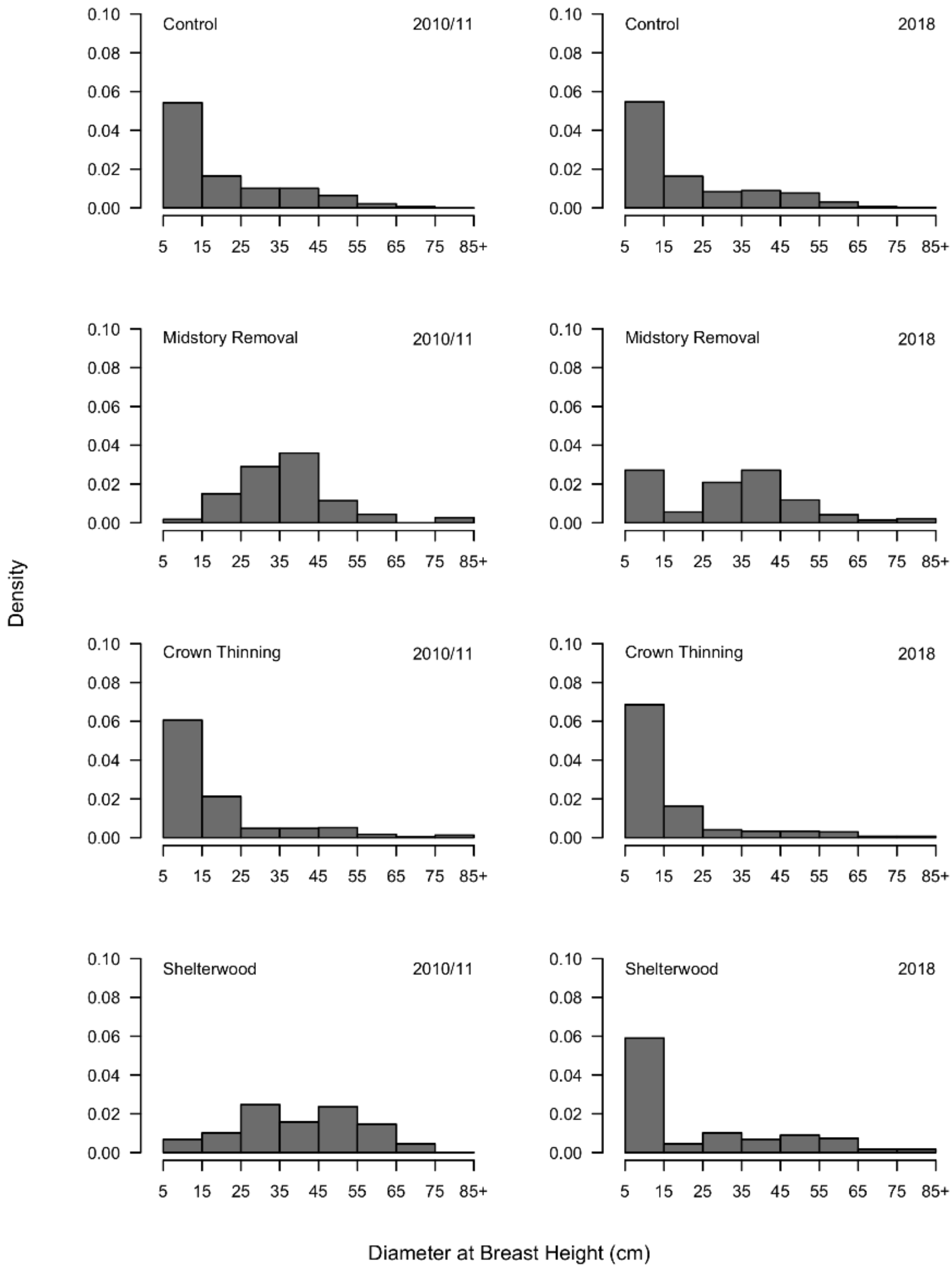

Figure 2. Size class distributions for all trees 5.1 cm dbh (diameter at breast height) and greater, three to four years and ten years after implementation of silvicultural treatments.

3.2. Artificial Regeneration

Of the 2900 seedlings planted at the commencement of this study in 2007, 866 survived to March 2018 across all study sites and treatments. All silvicultural treatments increased seedling survival relative to the control. With no additional treatments, midstory removal and the shelterwood increased the odds of survival 3.9 and 4.7 times more than the thinning treatment, respectively (Table 2). Compared to the crown thinning treatment alone, deer fencing had the strongest effect of any additional treatment on seedling survival, including the effect of the shelterwood cut (Figure 3a). However, a significant interaction between fencing and silvicultural treatment indicated that the strength of this fencing effect varied depending on the treatment combination ($\chi^2_3 = 27.03$, $p < 0.001$). Fencing was less consequential in the shelterwood than in the thinning treatment and had intermediate effects when paired with midstory removal (Table 2). Fertilizing planted seedlings did not affect their odds of surviving to 10 years ($\chi^2_1 = 0.03$, $p = 0.86$). Overall, 10-year survival approached or exceeded 50 percent in all treatment combinations that included deer fencing and some silvicultural treatment (Table 3).

Table 2. Results of mixed-effects logistic regression analyzing the effects of silvicultural treatments, fencing, and fertilization on 10-year survival and competitiveness of underplanted northern red oak (*Quercus rubra* L.) seedlings. Coefficients are presented on the log-odds scale.

Response	Fixed Effects	Estimate	SE	*z* Value	Significance	95% Conf. Int.	
						Lower	Upper
Survival							
	Silvicultural Treatment						
	Midstory Removal	3.817 [a]	0.630	6.055	***	2.233	5.401
	Thinning	2.781 [b]	0.659	4.218	***	1.125	4.438
	Shelterwood	4.317 [a]	0.629	6.865	***	2.737	5.897
	Fencing	2.838	0.686	4.136	***	1.114	4.562
	Fertilization	0.015	0.092	0.160		−0.217	0.246
	Silvi. × Fence						
	MR × Fn	−1.328 [a]	0.641	−2.071		−2.939	0.283
	TH × Fn	−0.712 [a]	0.663	−1.075		−2.377	0.952
	SW × Fn	−1.968 [b]	0.639	−3.082	*	−3.572	−0.364
Competitiveness							
	Silvicultural Treatment						
	Midstory Removal †	-	-				
	Thinning	−2.000 [a]	0.820	−2.439	·	−4.181	0.181
	Shelterwood	0.341 [b]	0.437	0.780		−0.821	1.503
	Fencing	1.790	0.401	4.464	***	0.724	2.856
	Fertilization	0.974	0.313	3.106	*	0.140	1.807
	Silvi × Fence						
	TH × Fn	1.831 [a]	0.778	2.353		−0.238	3.899
	SW × Fn	−0.318 [b]	0.358	−0.890		−1.269	0.633
	Fert × Fence	−0.795	0.357	−2.227		−1.744	0.154

† Reference level; Superscripts indicate significant differences at $\alpha = 0.05$ between levels of a factor. Significance levels are displayed as $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 3. Predicted probabilities of seedling survival and competitiveness generated from the most parsimonious mixed-effects logistic regression models for each response after ten years. Probability of competitiveness is relative to the number of seedlings initially planted. Treatments are listed in descending order by predicted probability of competitiveness. *MR* midstory removal; *TH* thinning; *SW* shelterwood.

Silvicultural Treatment	Fence	Fertilized	Predicted Probability of Survival	Predicted Probability of Competitiveness
SW	Y	Y	0.531	0.161
MR	Y	Y	0.565	0.158
SW	Y	N	0.527	0.138
TH	Y	Y	0.461	0.137
MR	Y	N	0.562	0.135
TH	Y	N	0.457	0.117
SW	N	Y	0.321	0.089
MR	N	Y	0.223	0.065
SW	N	N	0.318	0.035
MR	N	N	0.220	0.025
TH	N	Y	0.092	0.009
TH	N	N	0.091	0.004
Control	Y	Y	0.097	–
Control	Y	N	0.096	–
Control	N	Y	0.006	–
Control	N	N	0.006	–

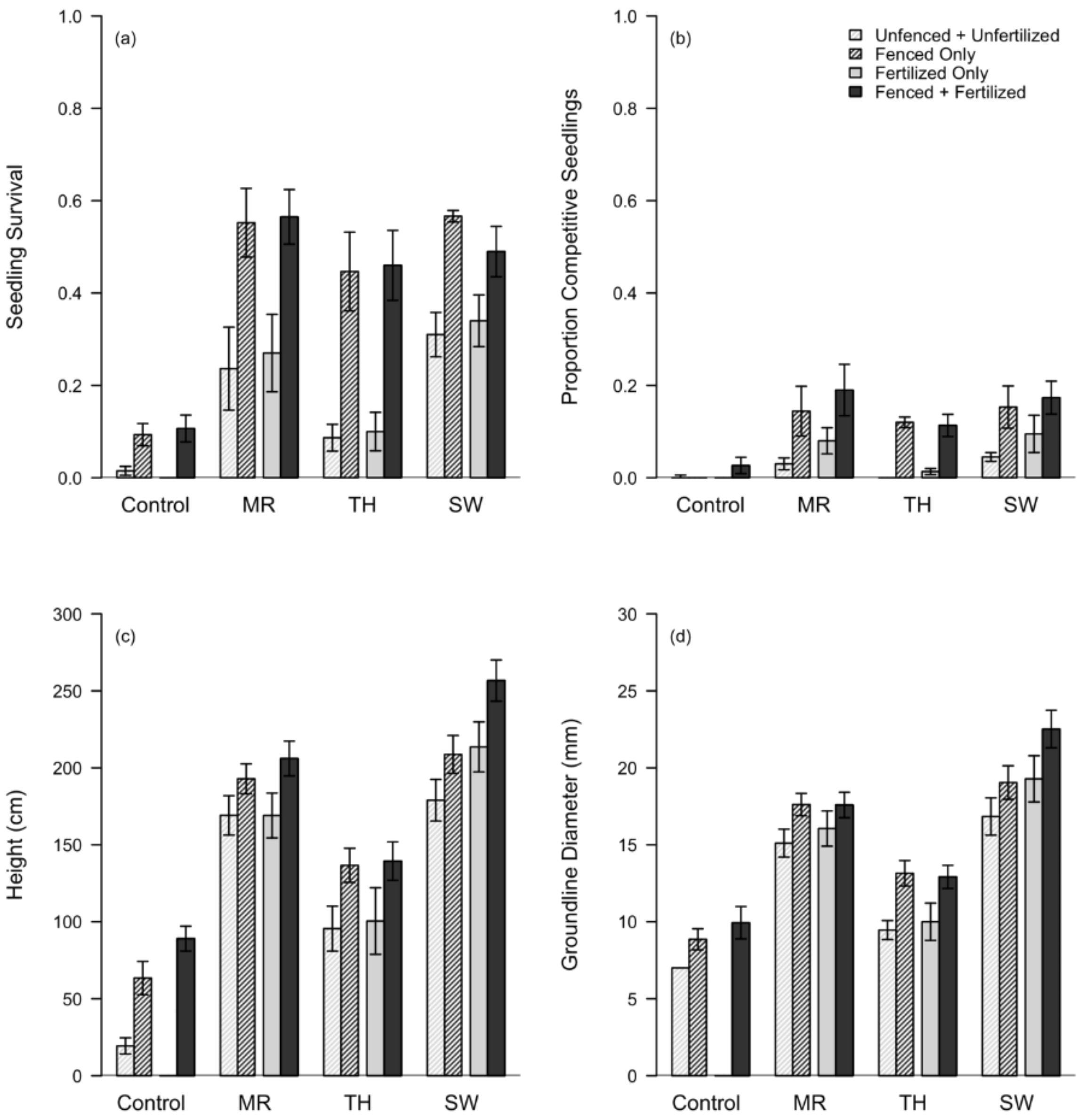

Figure 3. Mean (±SE) survival (**a**), competitiveness (**b**), height (**c**), and ground-line diameter (**d**) of underplanted northern red oak (*Quercus rubra* L.) seedlings ten growing seasons after planting with different silvicultural, fencing, and fertilization treatments. *MR* midstory removal; *TH* light crown thinning; *SW* shelterwood establishment cut.

In addition to increasing survivorship, deer fencing resulted in significantly greater height and diameter growth of surviving seedlings, and the absence of significant interactions between fencing and other treatments indicated that these effects were consistent across treatment combinations (Table 4). Mean increases in 10-year height and diameter growth attributable to fencing ranged from 24–43 cm (9.4–16.9 inches) and 1.5–3.6 mm (0.06–0.14 inches), respectively, in different treatment combinations. The effect of fencing on seedling height varied between study sites, but was consistently positive. Mean heights of all surviving seedlings planted in fenced areas relative to unfenced areas ranged from 13.5 cm (6.6%) greater at the Nelson-Stokes tract to 50.1 cm (81.8%) greater at the McKinney tract and 55.8 cm (31.3%) greater at the Knapp tract. The shelterwood resulted in the greatest height and diameter growth of any silvicultural treatment and had stronger effects on growth than fencing alone, relative to thinning (Figure 3c,d). Fertilized seedlings were larger than unfertilized seedlings in the control, but this may have been an artifact of low survival, as this effect was not evident in any of the treatment plots (Table 4). The combination of fencing and either midstory removal or the shelterwood treatment—which also included a midstory removal component—resulted in 10-year seedling heights of approximately 2 m (6.6 ft) or more (Figure 3c).

Table 4. Results of mixed-effects linear regression analyzing the effects of silvicultural treatments, fencing, and fertilization on 10-year height and ground line diameter (GLD) growth of underplanted northern red oak (*Quercus rubra* L.) seedlings. Responses were transformed with natural log prior to analysis.

Response	Fixed Effects	Estimate	SE	*t* Value	Signif.	95% Conf. Int.	
						Lower	Upper
Height (cm)							
	Silvicultural Treatment						
	Midstory Removal	1.135	0.218	5.205	***	0.560	1.710
	Thinning	0.877	0.226	3.881	***	0.282	1.472
	Shelterwood	1.288	0.217	5.929	***	0.715	1.860
	Fencing	0.299	0.068	4.379	***	0.119	0.479
	Fertilization	0.537	0.228	2.357		−0.063	1.138
	Silvi. × Fert.						
	MR × Fert.	−0.502	0.227	−2.215		−1.100	0.095
	TH × Fert.	−0.539	0.235	−2.289		−1.160	0.081
	SW × Fert.	−0.310	0.226	−1.370		−0.907	0.286
GLD (mm)							
	Silvicultural Treatment						
	Midstory Removal	0.516 [ab]	0.117	4.416	***	0.214	0.818
	Thinning	0.282 [a]	0.121	2.336		−0.030	0.595
	Shelterwood	0.664 [b]	0.117	5.692	***	0.363	0.965
	Fencing	0.184	0.045	4.054	***	0.067	0.301
	Fertilization	0.049	0.050	0.979		−0.081	0.179

Superscripts indicate significant differences at $\alpha = 0.05$ between levels of a factor. Significance levels are displayed as $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Of the 866 seedlings surviving after 10 years, 226 maintained potentially competitive positions, only one of which occurred in control plots and two of which occurred in unfenced plots beneath crown thinning (Figure 3b). Without fencing, the odds of a planted seedling being in a competitive position after 10 years were 8.0- and 10.4-fold higher in midstory removal and shelterwood treatments than in the thinning treatment ($p = 0.04$ and $p = 0.01$, respectively). Reflecting the interactive effects between fencing and silvicultural treatments on seedling survival, the odds of competitiveness did not differ between silvicultural treatments within deer fencing (Figure 3b). Among surviving seedlings only, the odds of being in a competitive position were no different between silvicultural treatments, but were increased 94 ± 24 percent (mean ± standard error) by fencing and 65 ± 18 percent by fertilization at planting (Table 3).

3.3. Natural Regeneration

Oak seedling densities were affected little by silvicultural treatments or fencing in this study (Figure 4). Overall, treatments explained less than 10% of the variation in oak seedling densities (marginal $R^2 = 0.062$), whereas location (site and plot) effects were much more important and explained well over half the variation (conditional $R^2 = 0.653$). As individual factors, neither fencing ($z = -0.08$, $p > 0.99$) nor the implementation of silvicultural treatments ($z = 1.62$, $p = 0.20$) had any detectable effect on the change in oak seedling density.

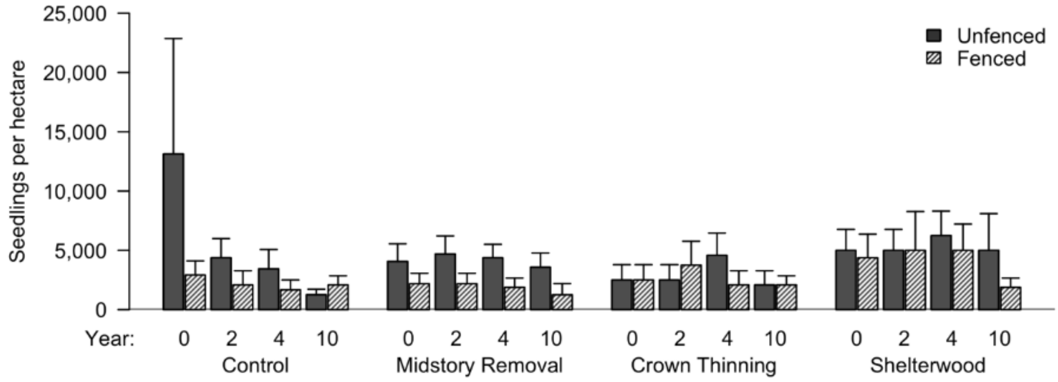

Figure 4. Mean (+SE) density of oak (*Quercus* spp.) seedlings per hectare in response to silvicultural treatments and deer fencing. Year 0 represents pretreatment data.

The density of naturally regenerated oak saplings greater than 1 m tall after 10 growing seasons was generally low across all treatments and was highly variable, with no clear effect of fencing ($\chi^2_1 = 1.71$, $p = 0.19$; Figure 5). The shelterwood treatment had the most oak saplings, with an average of 41 ± 12 per ha across fenced and unfenced plots. There were more naturally regenerated oak saplings in the shelterwood and midstory removal treatments than the control ($p < 0.01$, $p = 0.03$). Considered in terms of stocking (i.e., whether a 40.5 m^2 plot contained at least one naturally regenerated sapling), both midstory removal and shelterwood treatments increased the odds of a stocked plot 2.5-fold over the control (both $z = 2.91$, $p < 0.05$), whereas thinning alone increased those same odds only 1.4-fold, which was not statistically different from the control ($z = 1.62$, $p = 0.4$).

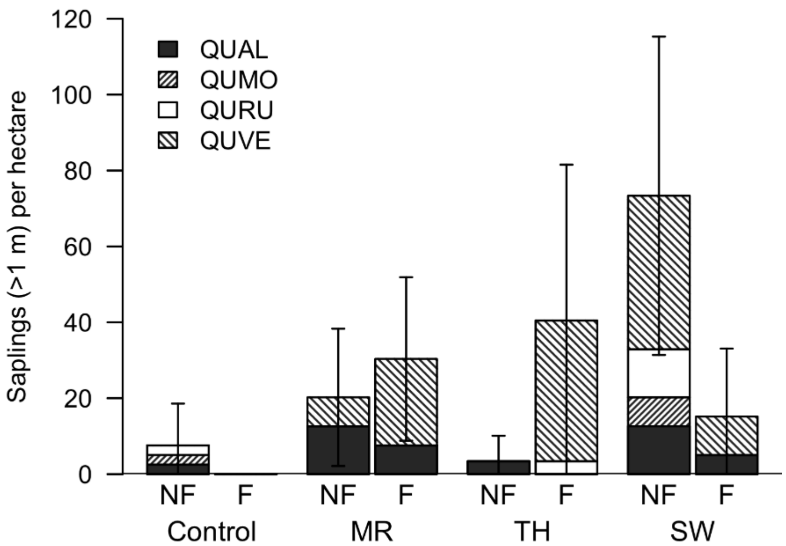

Figure 5. Mean (±SE) density of oak (*Quercus*) saplings (>1 m) per ha, ten growing seasons after midstory removal (MR), crown thinning (TH), and shelterwood (SW) treatments, with deer fencing (F) and without fencing (NF). Only year ten is displayed due to very few oak individuals tall enough to be counted in the sapling plots in previous sampling years.

4. Discussion

Our study sought to determine the best combination of common management approaches for promoting the growth, survival, and competitive status of advance oak reproduction. As we hypothesized, the combination of a shelterwood establishment cut and deer fencing maximized these measures of seedling success, though the effects of midstory removal were generally similar to those of the shelterwood. The benefits of additional treatments are not always additive, and interactive effects between many of the management prescriptions included in this study underscore the need to study them in combination. The numerous management actions commonly recommended to forest landowners for regenerating oak forests can be a deterrent to implementing these practices [38], particularly due to uncertainty surrounding the relative efficiency of different combinations of management actions.

Natural regeneration of oaks was sparse in this study. Sander et al. [39] recommended a minimum of 546 advance oak saplings 1.37 m (4.5 ft) or taller per ha (221 per acre) to obtain 30% oak stocking in the Missouri Ozarks. We only found 67 oak saplings greater than 1 m (3.3 ft) per ha (27 per acre) in our most effective treatment, the shelterwood. Low oak sapling densities may be explained by numerous factors limiting the recruitment of oak seedlings into the sapling layer, including ground-layer competition and browse pressure. Although we did not include understory competition control as a treatment in this study, fencing did not increase oak seedling densities and we found no increases in oak seedling densities even shortly after applying treatments. Acorn production varies dramatically between years and individuals [40], and timing silvicultural treatments to align with years of high acorn production can be critical [31]. Underplanting can help to ensure the presence of oak seedlings and circumvent the need to rigorously structure the timing of silvicultural treatments to coincide with mast years [19].

Underplanting oak seedlings, paired with midstory removal, has been recommended as an initial step in a shelterwood system [41]. Studies consistently show increased height and diameter growth of underplanted oak following midstory removal, and most show increases in survival and competitive ability [34,41], with exceptions likely related to insufficiently large planting stock [42]. Our results are consistent with these findings; mean 10-year heights in all treatment combinations that included midstory removal or shelterwood exceeded the 1.37 m (4.5 ft) minimum recommended by Sander et al. [39] for oaks to be competitive upon release. Notably, overstory BA reductions due to storm damage that affected control plots more than silvicultural treatment plots may have resulted in more conservative comparisons between treatments and the control than would have occurred otherwise. Nonetheless, we expect that comparisons between different silvicultural treatments were affected little due to the relatively small reductions in overstory BA observed between the 2011 and 2018 sampling years.

In addition to midstory removal, further reducing stand density by removing overstory trees is generally recommended as a necessary component of a shelterwood prescription to provide adequate light resources for growth of advance oak reproduction [19]. However, we found no significant differences between midstory removal alone and the shelterwood treatment for any of the metrics examined, suggesting that midstory removal alone may be adequate for underplanted oaks on productive sites. Miller et al. [43] found a shelterwood to be superior to midstory removal alone for survival, growth, and competitiveness of naturally reproduced northern red oak in northcentral Pennsylvania. Despite similar prescriptions for the midstory removal treatments in our study and that of Miller et al. [43], ours resulted in twice the relative BA reduction, 24% compared with 12%. This comparison suggests that complete removal of the midstory may create sufficient growing space for advance red oak reproduction where a dense subcanopy exists, but removal of some larger overstory trees may be necessary where midstory trees make up a smaller proportion of stand BA.

While midstory removal was the most important single treatment for promoting seedling growth, deer fencing was more important for seedling survival, but the strength of this effect varied between silvicultural treatments. Deer are the primary source of browse damage for planted seedlings in the central U.S. [44], and numerous studies have shown the deleterious effects of modern deer abundances on woody reproduction in Indiana [28,45,46]. Northern red oak is highly preferred as browse for deer, relative to co-occurring woody plants in Indiana [47], and seedlings likely lacked the resources necessary to recover from browse damage where the dense midstory layer was left intact. Another perspective on this interaction between treatments is that higher light availability may have reduced browse pressure on individual oak seedlings in the midstory removal and shelterwood treatments by increasing the abundance of alternative browse, thereby making deer fencing less beneficial [3,24,48,49]. Precise estimates of white-tailed deer populations across Indiana are not currently available, but our results show that while deer may impact seedling growth more strongly in some areas than others, browse pressure on unprotected seedlings was evident throughout the region encompassed by this study. We observed the weakest effect of deer fencing on seedling height growth at the Nelson-Stokes tract. Nelson-Stokes is located further north than other sites, but also had apparent damage to fencing that was not repaired between years five and ten of the study, preventing us from drawing conclusions about the effects of geography on browse pressure.

The presence of deer also mediated the effects of fertilization, which increased the odds that a seedling would be in a competitive position after 10 years, but only for seedlings not protected by fencing. In some cases, fertilizing seedlings at planting can protect against herbivory by allowing seedlings to grow above the browse line more rapidly, providing nutrients for the production of secondary defense compounds, and aiding in recovery from browse damage, but can make them more palatable to ungulates by increasing foliar nutrient content [50]. However, seedling responses to fertilization can also vary according to site-specific soil chemistry conditions [29], and red oak often shows no evidence of elevated tissue N or positive growth response to fertilization [27,28,51]. Consistent with these studies, we found no effect of fertilization on seedling growth. Therefore, higher nutrient supply did not help seedlings to more rapidly attain escape heights in this study, nor does existing evidence indicate that fertilization affects foliar tannin concentrations or browsing incidence for red oak [28]. Fertilization may have helped seedlings recover from minor or sporadic browse damage, but is unlikely to be a worthwhile investment if browsing is chronic or severe. Fencing is a better, and likely only option on high browse-pressure sites.

Though the shelterwood approach to oak regeneration is designed to reduce understory competition, relative to clearcutting, direct control of understory competition may have further improved outcomes for planted seedlings in some treatment combinations [43,52]. Competition control may be a more palatable approach for private landowners wary of the costs associated with deer fencing, but may have the unintended consequence of increasing browse pressure on planted seedlings [53], and may only be warranted where combined with fencing or reduced deer populations. The results of our study underscore the potential for variable effects of different treatments when applied in combination, and the interactions between deer browse and competition control warrant further investigation.

Increasing adoption of oak regeneration practices may be an even greater barrier than the silvicultural challenges to oak regeneration, in large part due to the economic costs and resulting risk associated with approaches such as fencing [38]. Continuing to develop geographically-specific prescriptions by testing a multitude of treatment combinations can reduce the risk associated with managing for oak regeneration. However, a rigorous economic analysis weighing the risks associated with each approach against their potential benefits is currently lacking in the Midwest and is the next necessary step in advancing the implementation of oak regeneration practices.

5. Conclusions

Regenerating oak forests in the eastern U.S. is a challenge with broad ecological implications and economic consequences. The many impediments to oak regeneration will accordingly require multifaceted solutions. Underplanted oak seedlings require careful management to ensure their success on many sites, but our results emphasize their usefulness for augmenting existing oak reproduction and potentially reducing instances of oak regeneration failure, even without re-entries to reduce understory competition via prescribed fire or herbicides. While natural regeneration will remain the primary means of regenerating oak forests in much of the eastern U.S. [19], artificial regeneration may be particularly suited to privately owned forest tracts, which tend to be relatively small and are more likely to be under-managed [54]. Interactive effects between treatments in our study show that the utility of various management actions to promote oak regeneration can depend particularly on the installation of deer fencing, or potentially on deer population densities. Fencing was far more effective than fertilization, and fertilization had little effect on seedlings protected by fencing. Following a selective crown thinning typical of private timber sales in the eastern U.S. [55], subsequent midstory removal to emulate a shelterwood establishment cut, coupled with deer fencing, can maximize growth and survival of underplanted oak seedlings.

Supplementary Materials: R code used in statistical analyses and the associated input data is available online at http://www.mdpi.com/1999-4907/9/9/571/s1.

Author Contributions: Conceptualization, R.A.R.; Methodology, G.S.F., R.A.R., and M.R.S.; Validation, G.S.F., R.A.R., and M.R.S.; Formal Analysis, G.S.F.; Investigation, G.S.F. and R.A.R.; Resources, R.A.R. and M.R.S.; Data Curation, G.S.F. and R.A.R.; Writing—Original Draft Preparation, G.S.F.; Writing—Review & Editing, R.A.R. and M.R.S.; Visualization, G.S.F.; Supervision, M.R.S.; Project Administration, G.S.F., R.A.R., and M.R.S.; Funding Acquisition, R.A.R.

Acknowledgments: The authors wish to acknowledge the support and cooperation of The Nature Conservancy, access to sites provided by participants in The Forest Bank program, and the time and resources of numerous individuals, including Brian Beheler, Chad Bladow, Don Carlson, Emily Frazier, Cassie Hauswald, Doug Jacobs, John McKim, Andy Meier, Chris Neggers, Charlotte Owings, Allen Pursell, and Dan Shaver.

Conflicts of Interest: Several employees of The Nature Conservancy, which provided funding for this project, assisted in data collection and implementation of the study. However, The Nature Conservancy agreed prior to the outset of the study that the results be published, and had no role in study design, data analysis and interpretation, or writing of the manuscript.

References

1. Hanberry, B.B.; Nowacki, G.J. Oaks were the historical foundation genus of the east-central United States. *Quat. Sci. Rev.* **2016**, *145*, 94–103. [CrossRef]
2. Clark, F.B. An historical perspective of oak regeneration. In *Oak Regeneration: Serious Problems Practical Recommendations*; Loftis, D.L., McGee, C.E., Eds.; USDA Forest Service Gen. Tech. Rep. SE-84; U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: Asheville, NC, USA, 1993.
3. Lashley, M.A.; Harper, C.A.; Bates, G.E.; Keyser, P.D. Forage availability for white-tailed deer following silvicultural treatments in hardwood forests. *J. Wildl. Manag.* **2011**, *75*, 1467–1476. [CrossRef]
4. Lorimer, C.G. Causes of the oak regeneration problem. In *Oak Regeneration: Serious Problems, Practical Recommendations*; Loftis, D.L., McGee, C.E., Eds.; USDA Forest Service Gen. Tech. Rep. SE-84; U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: Asheville, NC, USA, 1993; pp. 14–39.
5. Russell, F.L.; Zippin, D.B.; Fowler, N.L. Effects of White-Tailed Deer (Odocoileus Virginianus) on Plants, Plant Populations and Communities: A Review. *Am. Midl. Nat.* **2001**, *146*, 1–26. [CrossRef]
6. Fei, S.; Kong, N.; Steiner, K.C.; Moser, W.K.; Steiner, E.B. Change in oak abundance in the eastern United States from 1980 to 2008. *For. Ecol. Manag.* **2011**, *262*, 1370–1377. [CrossRef]
7. Nowacki, G.J.; Abrams, M.D. The Demise of Fire and "Mesophication" of Forests in the Eastern United States. *Bioscience* **2008**, *58*, 123–138. [CrossRef]
8. Lhotka, J.M.; Loewenstein, E.F. Influence of canopy structure on the survival and growth of underplanted seedlings. *New For.* **2008**, *35*, 89–104. [CrossRef]
9. Jenkins, M.A.; Parker, G.R. Composition and diversity of woody vegetation in silvicultural openings of southern Indiana forests. *For. Ecol. Manag.* **1998**, *109*, 57–74. [CrossRef]
10. Keyser, T.L.; Loftis, D.L. Long-term effects of single-tree selection cutting on structure and composition in upland mixed-hardwood forests of the southern Appalachian Mountains. *Forestry* **2013**, *86*, 255–265. [CrossRef]
11. Raymond, P.; Munson, A.D.; Ruel, J.C.; Nolet, P. Group and single-tree selection cutting in mixed tolerant hardwood-white pine stands: Early establishment dynamics of white pine and associated species. *For. Chron.* **2003**, *79*, 1093–1106. [CrossRef]
12. Morrissey, R.C.; Jacobs, D.F.; Seifert, J.R.; Kershaw, J.A. Overstory species composition of naturally regenerated clearcuts in an ecological classification framework. *Plant Ecol.* **2010**, *208*, 21–34. [CrossRef]
13. Schweitzer, C.J.; Dey, D.C. Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-Cumberland Plateau escarpment region, USA. *For. Ecol. Manag.* **2011**, *262*, 1729–1741. [CrossRef]

14. Loftis, D.L. A shelterwood method for regenerating red oak in the Southern Appalachians. *For. Sci.* **1990**, *36*, 917–929.
15. Kellner, K.F.; Swihart, R.K. Timber harvest and drought interact to impact oak seedling growth and survival in the Central Hardwood Forest. *Ecosphere* **2016**, *7*, 1–15. [CrossRef]
16. Brose, P.H.; Van Lear, D.H. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. *Can. J. For. Res.* **1998**, *28*, 331–339. [CrossRef]
17. Brose, P.H.; Gottschalk, K.W.; Horsley, S.B.; Knopp, P.D.; Kochenderfer, J.N.; McGuiness, B.J.; Miller, G.W.; Ristau, T.E.; Stoleson, S.H.; Stout, S.L. *Prescribing Regeneration Treatments for Mixed-Oak Forests in the Mid-Atlantic Region*; USDA Forest Service Gen. Tech. Rep. NRS-33; U.S. Department of Agriculture, Forest Service, Northern Research Station: Newtown Square, PA, USA, 2008.
18. Gordon, A.M.; Simpson, J.A.; Williams, P.A. Six-year response of red oak seedlings planted under a shelterwood in central Ontario. *Can. J. For. Res.* **1995**, *25*, 603–613. [CrossRef]
19. Dey, D.C.; Gardiner, E.S.; Schweitzer, C.J.; Kabrick, J.M.; Jacobs, D.F. Underplanting to sustain future stocking of oak (*Quercus*) in temperate deciduous forests. *New For.* **2012**, *43*, 955–978. [CrossRef]
20. Dey, D.C.; Spetich, M.A.; Weigel, D.R.; Johnson, P.S.; Graney, D.L.; Kabrick, J.M. A suggested approach for design of oak (*Quercus* L.) regeneration research considering regional differences. *New For.* **2009**, *37*, 123–135. [CrossRef]
21. Sander, I.L.; Graney, D.L. Regenerating oaks in the central states. In *Oak Regeneration: Serious Problems, Practical Recommendations.*; Loftis, D.L., McGee, C.E., Eds.; USDA Forest Service Gen. Tech. Rep. SE-84; U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: Asheville, NC, USA, 1993.
22. Jarnemo, A.; Minderman, J.; Bunnefeld, N.; Zidar, J.; Mansson, J. Managing landscapes for multiple objectives: Alternative forage can reduce the conflict between deer and forestry. *Ecosphere* **2014**, *5*. [CrossRef]
23. Murray, B.D.; Webster, C.R.; Jenkins, M.A.; Saunders, M.R.; Haulton, G.S. Ungulate impacts on herbaceous-layer plant communities in even-aged and uneven-aged managed forests. *Ecosphere* **2016**, *7*, 1–20. [CrossRef]
24. Miller, B.F.; Campbell, T.A.; Laseter, B.R.; Ford, W.M.; Miller, K.V. White-tailed deer herbivory and timber harvesting rates: Implications for regeneration success. *For. Ecol. Manag.* **2009**, *258*, 1067–1072. [CrossRef]
25. Royo, A.A.; Kramer, D.W.; Miller, K.V.; Nibbelink, N.P.; Stout, S.L. Spatio-temporal variation in foodscapes modifies deer browsing impact on vegetation. *Landsc. Ecol.* **2017**, *32*, 2281–2295. [CrossRef]
26. Schreffler, A.M.; Sharpe, W.E. Effects of lime, fertilizer, and herbicide on forest soil and soil solution chemistry, hardwood regeneration, and hardwood growth following shelterwood harvest. *For. Ecol. Manag.* **2003**, *177*, 471–484. [CrossRef]
27. Tripler, C.E.; Canham, C.D.; Inouye, R.S.; Schnurr, J.L. Soil nitrogen availability, plant luxury consumption, and herbivory by white-tailed deer. *Oecologia* **2002**, *133*, 517–524. [CrossRef] [PubMed]
28. Burney, O.T.; Jacobs, D.F. Species selection—A fundamental silvicultural tool to promote forest regeneration under high animal browsing pressure. *For. Ecol. Manag.* **2018**, *408*, 67–74. [CrossRef]
29. Cha, D.H.; Appel, H.M.; Frost, C.J.; Schultz, J.C.; Steiner, K.C. Red oak responses to nitrogen addition depend on herbivory type, tree family, and site. *For. Ecol. Manag.* **2010**, *259*, 1930–1937. [CrossRef]
30. Kellner, K.F.; Riegel, J.K.; Swihart, R.K. Effects of silvicultural disturbance on acorn infestation and removal. *New For.* **2014**, *45*, 265–281. [CrossRef]
31. Zaczek, J.J.; Lhotka, J.M. Seedling reproduction established with soil scarification within an oak overwood after overstory removal. *North J. Appl. For.* **2004**, *21*, 5–11.
32. Spetich, M.A.; Dey, D.C.; Johnson, P.S. Shelterwood-planted northern red oaks: Integrated costs and options. *J. Appl. For.* **2009**, *33*, 182–186.
33. Homoya, M.A.; Abrell, D.B.; Aldrich, J.R.; Post, T.W. The natural regions of Indiana. *Proc. Indiana Acad. Sci.* **1984**, *94*, 245–268. [CrossRef]
34. Parrott, D.L.; Lhotka, J.M.; Stringer, J.W.; Dillaway, D.N. Seven-Year Effects of Midstory Removal on Natural and Underplanted Oak Reproduction. *North J. Appl. For.* **2012**, *29*, 182–190. [CrossRef]
35. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2018; Available online: https://www.R-project.org/ (accessed on 15 March 2018).
36. Bates, D.; Maechler, M.; Bolker, B.; Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. [CrossRef]

37. Hothorn, T.; Bretz, F.; Westfall, P. Simultaneous inference in general parametric models. *Biometr. J.* **2008**, *50*, 346–363. [CrossRef] [PubMed]
38. Knoot, T.G.; Schulte, L.A.; Rickenbach, M. Oak conservation and restoration on private forestlands: Negotiating a social-ecological landscape. *Environ. Manag.* **2010**, *45*, 155–164. [CrossRef] [PubMed]
39. Sander, I.L.; Johnson, P.S.; Rogers, R. *Evaluating Oak Advance Reproduction in the Missouri Ozarks*; USDA Forest Service Gen. Tech Rep. NC-251; U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: St. Paul, MN, USA, 1984; 16p.
40. Healy, W.M.; Lewis, A.M.; Boose, E.F. Variation of red oak acorn production. *For. Ecol. Manag.* **1999**, *116*, 1–11. [CrossRef]
41. Lhotka, J.M.; Loewenstein, E.F. Effect of midstory removal on understory light availability and the 2-year response of underplanted cherrybark oak seedlings. *South J. Appl. For.* **2009**, *33*, 171–177.
42. Craig, J.M.; Lhotka, J.M.; Stringer, J.W. Evaluating Initial Responses of Natural and Underplanted Oak Reproduction and a Shade-Tolerant Competitor to Midstory Removal. *For. Sci.* **2014**, *60*, 1164–1171. [CrossRef]
43. Miller, G.W.; Brose, P.H.; Gottschalk, K.W. Advanced Oak Seedling Development as Influenced by Shelterwood Treatments, Competition Control, Deer Fencing, and Prescribed Fire. *J. For.* **2017**, *115*, 179–189. [CrossRef]
44. Stange, E.E.; Shea, K.L. Effects of Deer Browsing, Fabric Mats, and Tree Shelters on Quercus rubra Seedlings. *Restor. Ecol.* **1998**, *6*, 29–34. [CrossRef]
45. Jenkins, L.H.; Jenkins, M.A.; Webster, C.R.; Zollner, P.A.; Shields, J.M. Herbaceous layer response to 17 years of controlled deer hunting in forested natural areas. *Biol. Conserv.* **2014**, *175*, 119–128. [CrossRef]
46. Jenkins, L.H.; Murray, B.D.; Jenkins, M.A.; Webster, C.R. Woody regeneration response to over a decade of deer population reductions in Indiana state parks 1. *J. Torrey Bot. Soc.* **2015**, *142*, 205–219. [CrossRef]
47. Wakeland, B.; Swihart, R.K. Ratings of white-tailed deer preferences for woody browse in Indiana. *Proc. Indiana Acad. Sci.* **2009**, *118*, 96–101.
48. Kellner, K.F.; Swihart, R.K. Simulation of oak early life history and interactions with disturbance via an individual-based model, SOEL. *PLoS ONE* **2017**, *12*, 1–23. [CrossRef] [PubMed]
49. Johnson, A.S.; Hale, P.E.; Ford, W.M.; Wentworth, J.M.; French, J.R.; Anderson, O.F.; Pullen, G.B. White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. *Am. Midl. Nat.* **1995**, *133*, 18–35. [CrossRef]
50. Burney, O.T.; Jacobs, D.F. Ungulate herbivory of boreal and temperate forest regeneration in relation to seedling mineral nutrition and secondary metabolites. *New For.* **2013**, *44*, 753–768. [CrossRef]
51. Schuler, J.L.; Robison, D.J. Performance of northern red oak enrichment plantings in naturally regenerating Southern Appalachian hardwood stands. *New For.* **2010**, *40*, 119–130. [CrossRef]
52. Lorimer, C.G.; Chapman, J.W.; Lambert, W.D. Tall understorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* **1994**, *82*, 227–237. [CrossRef]
53. Dalgleish, H.J.; Lichti, N.I.; Schmedding, N.; Swihart, R.K. Exposure to herbivores increases seedling growth and survival of American chestnut (*Castanea dentata*) through decreased interspecific competition in canopy gaps. *Restor. Ecol.* **2015**, *23*, 655–661. [CrossRef]
54. Ross-Davis, A.; Broussard, S. A typology of family forest owners in North Central Indiana. *North J. Appl.* **2007**, *24*, 282–289.
55. Kittredge, D.B.; Finley, A.O.; Foster, D.R. Timber harvesting as ongoing disturbance in a landscape of diverse ownership. *For. Ecol. Manag.* **2003**, *180*, 425–442. [CrossRef]