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Disentangling factors affecting establishment and growth of white oak (*Quercus alba*) regeneration in Missouri, USA

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ABSTRACT

Due to lower site productivity and lack of aggressive competitors, oak regeneration in Missouri is often considered less problematic than in the rest of the Central Hardwoods Region. However, oak advance reproduction is scarce on more productive sites in the Missouri Outer Ozark Border Subsection where sugar maple has accumulated in the midstory. The purpose of our study was to identify barriers to accumulating competitive white oak advance reproduction in the Outer Ozark Border Subsection at different stages of the regeneration process, including seed germination, seedling establishment, and development as advance reproduction in a mature upland oak-hickory forest. We manipulated light availability through thinning of the overstory and removal of the midstory, and we controlled deer herbivory by installing fenced exclosures. We tracked the performance of sown acorns, naturally regenerated seedlings of known germination year, and underplanted bareroot seedlings. Our results demonstrate the importance of a mast year, as many sown acorns were removed by small mammals or infested with weevils. The underplanted seedlings had a low survival rate (<35%) after five years, during which time a new cohort of seedlings was established following a bumper acorn crop. Neither heavy shade nor deer herbivory limited germination of natural reproduction. Heavy shade limited the growth and persistence of white oak advance reproduction in the understory. Deer herbivory did not impact the survival of white oak but negatively impacted its size. Active management will be necessary to create adequate light for regeneration, which we achieved through either midstory removal or commercial thinning.

1. Introduction

Oak (*Quercus* spp.) has been classified as a foundation genus in eastern United States (U.S.) forests due to its historical abundance and ecological importance (Hanberry and Nowacki, 2016). White oak (*Quercus alba* L.) is often considered emblematic of upland oak forests of the region, with a broad distribution and widespread abundance (Monk et al., 1990; Abrams, 2003). Over the past few decades, white oak sawtimber volume has increased as mature stands throughout its range have continued to grow larger in average stand diameter (Vickers et al., 2025). However, declines in importance value and underrepresentation in small size classes within aging forests have raised concerns for the long-term sustainability of white oak forests (Fei et al., 2011; McEwan et al., 2011; Vickers and Goff, 2025).

Reports of deficiencies in oak seedling populations are concerning because successful oak regeneration relies on the development of competitive advance reproduction in mature stands prior to overstory disturbance (Sander, 1972; Larsen and Johnson, 1998). Advance reproduction accumulates through time from the establishment of new seedlings from acorns, persistence of oak seedlings through resprouting, and eventual growth to large, competitive sizes with adequate light (Johnson et al., 2019). Acorns are highly desirable as food for a multitude of fauna, making new seedling germination inconsistent and serendipitous, except in mast years when enough acorns are produced to satiate insect, bird, and mammal populations (Burns and Honkala, 1990; Greenberg and Zarnoch, 2018; Szymkowiak et al., 2024). White oak acorns germinate shortly after reaching the forest floor and dedicate most of their resources to developing a strong taproot (Burns and Honkala, 1990; Brose, 2011; Rebbeck et al., 2011). Consequently, oaks maintain slow early aboveground growth in favor of developing a high root to shoot ratio that confers a competitive advantage in high disturbance/stress (e.g., drought, fire, herbivory) environments. With adequate light, oak regeneration can persist in the forest understory and develop a large root system through the process of shoot dieback and

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resprouting. Disturbances (e.g., fire) that cause shoot dieback in oak may also help to control competing vegetation. Large oak advance reproduction is highly competitive following canopy disturbance that releases regeneration (Johnson et al., 2019).

Oak regeneration challenges have been attributed, in part, to shifts in disturbance regimes of eastern U.S. forests. The broad distribution of oak in pre-settlement forests was maintained by frequent, low-intensity fire regimes and oaks' ability to tolerate dry or nutrient-poor sites compared to competing species, and white oak was particularly favored because it is more stress-tolerant than many red oak species (Abrams, 1992, 2003). Oak dominance expanded during a period of accelerated disturbance as land was cleared for agriculture before fire suppression and exclusion of the mid-1900s (Abrams, 1992). In the absence of fire and with less frequent and severe disturbances, mesophytic, shade-tolerant species such as maples (*Acer* spp.) and American beech (*Fagus grandifolia* Ehrh.) accumulated in lower size classes of eastern U.S. forests, forming dense understory and midstory canopies and inhibiting oaks from developing into large advance reproduction in the low light environment (Hodges and Gardiner, 1993; Nowacki and Abrams, 2008). Following larger scale canopy disturbances, fast growing species such as yellow-poplar (*Liriodendron tulipifera* L.) and birches (*Betula* spp.) outcompeted and suppressed small oak reproduction.

Increased stand density and the development of a midstory create shade on the forest floor that can inhibit the establishment and growth of oak advance reproduction (Lorimer et al., 1994). Generally, 30% full sunlight is considered optimal for the growth of oak (Phares, 1971). Oak seedlings have been found to grow at light levels of 11–15%, with poor growth or mortality reported for light levels below 5% (Lhotka, Loewenstein, 2009; Motsinger et al., 2010; Brose, 2011). White oak's response to increasing light is modest because they grow more slowly and preferentially dedicate more resources to their roots than many other oak species (Dillaway et al., 2007; Rebbeck et al., 2011). Consequently, silvicultural practices used to favor oak regeneration often include removals of midstory or moderate reductions in overstory density by thinning from below to increase light to the forest floor without releasing fast-growing, shade-intolerant competitors. For example, a modified shelterwood system was developed to reduce stand basal area by first cutting midstory trees to allow development of large oak advance reproduction prior to overstory disturbance (Loftis, 1990). Midstory removal has been found to increase the survival, growth, and root carbohydrates of oak seedlings (Lockhart et al., 2000; Dillaway et al., 2007; Lhotka, Loewenstein, 2009).

Deer populations throughout the eastern U.S. have increased substantially since the early 1900s, resulting in browse impacts that contribute to oak regeneration failures (Rooney, 2001; McEwan et al., 2011; McWilliams et al., 2018). The selective foraging of deer affects the composition of forest understory communities by directly reducing growth through consumption and by altering the competitive dynamics among species (Côté et al., 2004). Previous studies have found overabundant deer populations (> 5.8 deer/km^2) to be negatively correlated with tree seedling abundance in northern U.S. forests and that areas of high browse impact may limit recruitment (Russell et al., 2017a, 2017b). White oak is preferentially browsed by deer in the Central Hardwoods Region (Sample et al., 2023), and deer herbivory has been shown to impact the abundance and size of oak advance reproduction (Rossell et al., 2005; Long et al., 2012; Parker et al., 2020). Deer herbivory has been recognized as an important challenge to forest regeneration, although the magnitude of its impact varies across the white oak range (McWilliams et al., 2018).

White oak regeneration is considered less problematic in Missouri, on the western border of the Central Hardwoods Region, because site productivity is relatively low (Vickers et al., 2019; 2025). However, examples of oak regeneration problems are common in central Missouri, where sugar maple (*Acer saccharum* Marshall) abundance has been increasing and large advance reproduction of white oak is sparce (Rochow, 1972; Nigh et al., 1985; Belden and Pallardy, 2009; Knapp and Pallardy, 2018). Determining the specific factors that limit oak advance reproduction can be difficult, because barriers to success could occur at different stages of the regeneration process, including acorn production and dispersal, germination, initial survival, and subsequent growth and persistence (Dey et al., 2019). When oak advance reproduction is lacking, underplanting may be used to bypass challenges with acorn production and initial seedling establishment and to accelerate the accumulation of oak advance reproduction in preparation for overstory regeneration harvest (Paquette et al., 2006; Dey et al., 2012;).

The goal of this study was to identify factors limiting white oak regeneration in central Missouri on more productive sites in the Outer Ozark Border Subsection. We designed a manipulative field study to affect light availability via thinning of the overstory and removal of the midstory, and we controlled deer herbivory by establishing exclosures. We artificially regenerated white oak using sown acorns and underplanted seedlings. The region experienced a mast year during our study period, which provided opportunity to evaluate treatment effects on natural regeneration of known germination year. The objectives of this study were to: 1) analyze the effects of midstory removal and deer exclosures on the growing conditions (stand density, light availability, and biomass of competitors) for white oak regeneration; 2) analyze the effects of midstory removal and deer exclosures on the performance of three different sources white oak regeneration; and 3) determine relationships between growing conditions and responses of white oak regeneration. The inclusion of different sources of regeneration permits the evaluation of factors that limit the success of oak at three different stages early in the regeneration process: seed, germinant, and seedling.

2. Methods

2.1. Study area

This study was conducted in upland oak forests at the University of Missouri's Baskett Forest in Ashland, MO (38°45'48.52" N, 92°11'49.26" W). The Baskett Forest is approximately 900 ha and is located in the Missouri Outer Ozark Border Subsection, which is characterized by dissected forested hills and bluffs (Nigh and Schroeder, 2002). Soils in the study area are made up of loess over limestone residuum and are classified as moderately- to well-drained (Nigh and Schroeder, 2002). The most common soil series is Rocheport-Bonnefemme complex, which has a site index of 19.8 m at a base age of 50 for white oak (Soil Survey Staff, n.d.). The mean annual precipitation during the study period (2021–2025) was 1037 mm (Menne et al., 2012). The mean maximum monthly temperature (July) and mean minimum monthly temperature (January) was 31.6°C and −5.2°C, respectively (Menne et al., 2012).

Prior to its public acquisition in the 1930s, portions of the Baskett Forest were cleared for agriculture, primarily on the ridge tops, and the areas that remained forested were grazed by livestock, resulting in a mosaic of pasture and second-growth forests. Witness tree surveys indicate that white oak had the greatest importance values in pre-settlement forests of the central region of Missouri (Wuenscher and Valiunas, 1967). Since 1939, the Baskett Forest has been managed by the University of Missouri. White oak remains a dominant overstory species in the study area while sugar maple has accumulated in smaller diameter classes (Knapp and Pallardy, 2018). The most common overstory species by basal area found in the study area were white oak, black oak (*Quercus velutina* Lam.), sugar maple, and hickories (*Carya* spp.), and sugar maple, ironwood (*Ostrya virginiana* (Mill.) K. Koch), and flowering dogwood (*Cornus florida* L.) were the most common midstory species by basal area.

We compared oak regeneration response at two different locations of the Baskett Forest to examine silvicultural treatment impacts under different initial overstory conditions: 1) reduced overstory density following commercial thinning and 2) intact overstory with no recent management. In 2019, an area of approximately 16 ha was commercially thinned to a target basal area of 16.1 m^2/ha. The prescription used thinning from below, with only merchantable trees (diameter at breast height (DBH) $\geq$ 25 cm) considered for removal, and was applied uniformly throughout the stand. Marking retained healthy, vigorous trees with good form, favoring white oak over all other species, although other species were retained to maintain diversity.

Stand structure was estimated from study plot data collected in 2021, at the time of project initiation. In the commercially thinned stand, the average basal area of overstory trees across all study plots was 22.2 m^2/ha and the average basal area of midstory trees was 1.6 m^2/ha (23.8 m^2/ha total basal area). The total stem density for the commercially thinned stand was 732 trees/ha, of which 433 trees/ha were midstory trees. The mean diameter of all trees in the commercially thinned stand was 15.1 cm (ranging from 1.5 to 111.0 cm).

We used an unmanaged area of similar size (18 ha) to represent intact overstory conditions. At the time of project initiation, the average basal area of overstory trees across all study plots was 26.5 m^2/ha, and the average basal area of midstory trees was 2.7 m^2/ha (29.2 m^2/ha total basal area). The midstory stem density was 902 trees/ha and the total stem density was 1184 trees/ha. The mean diameter of all trees in the unmanaged stand was 11.6 cm (ranging from 1.0 to 89.0 cm). The most common overstory species in the unmanaged stand were also white oak, sugar maple, and hickory species while sugar maple, flowering dogwood, and ironwood were the most common midstory trees. The same experimental design was used in both the commercially thinned stand and the unmanaged stand.

2.2. Experimental design

We used a completely randomized, two by two factorial design to create four different treatment combinations. The factorial design consisted of a midstory removal treatment and an herbivory exclusion treatment, each of which had two levels (either yes or no). In the midstory removal treatment, all midstory trees (DBH $\leq$ 11.5 cm) were cut with a chainsaw in March 2021. Stumps received a one-time application of undiluted Garlon 3 A herbicide (0.36 triclopyr acid equivalent per liter) to prevent resprouting. The midstory removal treatment was uniformly applied within a 30 × 30 m area at each plot. The herbivory exclusion treatment used fences to exclude deer and other animals from the measurement plot. The fences were 1.8 m tall and made of a polypropylene plastic mesh (4.45 × 5.08 cm) with reinforced bottoms. Fences were installed around the perimeter of each 6 × 6 m measurement plot using t-posts at each corner. The fencing was secured with cable ties, which were checked regularly throughout the year for damage, and the bottom of the fence was secured flush with the ground.

The four treatment combinations were replicated four times at each stand (n = 16 plots per stand; n = 32 total), and all plots were randomly located. We used ArcGIS to generate a grid of points of potential plot locations spaced 63 m apart to prevent treatment overlap. The points were numbered sequentially and visited in the field to assess the viability of each. If the location was obstructed by the surrounding microtopography (skid trails, downed trees), then its location was shifted 5 m away in the least obstructed cardinal direction. If potential locations were significantly obstructed, the point was deemed unacceptable and not used. We randomly selected 16 points from those remaining to be measurement plots, for a total of 32 points across the entire study. At each point, we established a 6 × 6 m fixed-area, square measurement plot (to which fencing treatments were applied) centered within a 30 × 30 m area (to which midstory removal treatments were applied), together referred to as the experimental unit. Treatment combinations were randomly assigned to experimental units, resulting in four replicates at each research site, and all treatments were implemented in the spring of 2021.

2.3. Sources of regeneration

This study analyzed the response of three sources of white oak regeneration. Two sources of artificial regeneration were measured, including underplanted seedlings and sown acorns. A white oak mast event occurred during the study period, which provided an abundance of acorns that germinated throughout the study area.

2.3.1. Underplanted oak seedlings

In April 2021, we planted 25 white oak seedlings within each measurement plot. Seedlings were 1–0 bareroot stock provided by the George O. White State Forest Nursery, operated by the Missouri Department of Conservation. Seedlings were planted 1 m apart in a 5 × 5 m grid centered within the measurement plot of every experimental unit. Each seedling was visually inspected for consistency in initial size and damage to the root system, and then seedlings were planted to the root collar using a dibble bar. The average starting height of underplanted seedlings was 31.6 cm and the average starting groundline diameter was 8.45 mm.

2.3.2. Natural oak regeneration

A white oak mast event occurred at the Baskett Forest in the fall of 2022, providing the opportunity to track how our treatments would affect the development of natural white oak regeneration. Although data on acorn production are not available for the area, a long-term monitoring study located at the Baskett Forest has tracked tree regeneration since 2017. Across upland forest monitoring plots for the years 2018–2022, the average annual establishment of new white oak seedlings was 783 per ha. In 2023, an average of 8650 new white oak seedlings per ha established, a 1006% increase from the annual average (unpublished data). This increase in new white oak seedlings supports field observations of bumper acorn production in 2022.

2.3.3. Sown acorns

Building onto our experimental design, we added a split-plot factor to additionally test the effects of acorn predation by small mammals or birds. The whole-plot treatment was the original factorial combination of midstory removal and herbivory exclusion. Within each whole-plot, the split-plot factor was acorn predation control, with two levels (yes or no). Split-plots were 60 × 60 cm and installed equidistant from the measurement plot edges. One split-plot was randomly assigned the acorn predation control treatment and was covered with 0.635 cm hardware cloth to protect sown acorns. Due to the limited number of acorns available, we installed the split-plot treatments in three of the four whole plot treatment replications at each site (n = 12 at each site).

White oak acorns were provided by the George O. White State Forest Nursery. Acorns were float tested to ensure they were not damaged and then were sown in late October 2021 to align with the local phenology of white oak. Within each split-plot, 16 acorns were sown approximately 2.5 cm deep and 10 cm apart in a four by four grid. Each acorn was painted with a dot of paint to be easily identifiable in the field during resampling.

2.4. Data collection

2.4.1. Growing environment

We described the effects of the study treatments on the growing environment by measuring stand density, light availability, and understory biomass. We measured stand density by tagging and recording the DBH of all trees (height $\geq$ 1.37 m) in each 30 × 30 m experimental unit prior to treatment application. The ID number of trees cut during the midstory removal were recorded to calculate pre- and post- treatment basal area.

In August 2021, we measured light transmittance to the understory using hemispherical photographs captured with a Canon EOS 70D camera fitted with a Sigma 4.5 mm circular fisheye lens. Images were captured either at dawn or during uniformly overcast days (cloud cover of 90% or greater) in the center of each experimental unit using a tripod that held the camera 1.5 m off the ground. The camera lens was oriented north and leveled prior to capturing each photograph. Photographs were later uploaded and analyzed in HemiView version 2.1 (Delta-T Services, 2012) to determine direct and indirect solar radiation reaching the understory of each plot. We then used measurements of direct solar radiation (DSF) and diffuse solar radiation (ISF) to calculate gap light index (GLI) using the following equation (Canham, 1988; Battaglia et al., 2003):

$$GLI = [(ISF * 0.5) + (DSF * 0.5)] * 100$$

The calculation of GLI through hemispherical photography incorporates the path and angle of the sun based on the site location to provide an integrated measure of light availability that has been found to correlate well with canopy light transmittance (Canham, 1988; Battaglia et al., 2003).

We conducted a biomass survey during the growing season of 2024 to compare how study treatments affected vegetation abundance. Two biomass subplots, each 1 m^2, were established at the center of the northern and southern boundary of each measurement plot. All biomass rooted within each subplot was cut down to the soil and separated into three categories: graminoids, forbs, and woody biomass. Biomass was later dried for 48 h and weighed to the nearest 0.01 g to obtain estimates of total biomass (g/m^2).

2.4.2. Underplanted oak seedlings

We recorded the initial height and groundline diameter (GLD) for all seedlings within 2 weeks of planting. Height was measured to the top of the tallest stem by using a meter stick placed perpendicular to the ground and was recorded to the nearest 0.1 cm. Two perpendicular GLD measurements were collected at the root collar of each seedling using digital calipers placed parallel to the ground and recorded to the nearest 0.01 mm. The GLD measurements were later averaged to obtain a single estimate of seedling diameter. We measured height, GLD, and survival status for all planted seedlings at the end of each growing season thereafter for a total of five growing seasons (2021 through 2025). We obtained annual growth values for height and GLD by calculating the difference between the measurement at the end of one growing season and the measurement taken the year prior. The reported growth values are not a true measure of growth as seedlings may dieback and resprout or regrow tissue after experiencing browse. Instead, “growth” represents a measure of the annual net change in height or GLD.

2.4.3. Natural oak regeneration

After the mast year in fall 2022, we flagged each new germinant located within each measurement plot in spring 2023. Each new seedling was assigned a unique identifier. Survival of each seedling was assessed at the end of each growing season through 2025 to determine establishment and early survival of natural reproduction following a mast event. New regeneration was counted at the plot level and later expanded to evaluate establishment and abundance on a per ha basis.

2.4.4. Sown acorns

Acorns were sampled in March 2022 after overwintering. In each split-plot, the total number of acorns remaining, the number of acorns that had germinated, and the number of acorns that had been visibly damaged by rodents or weevils were recorded. Germination was determined by the emergence of the radicle, and damage was determined by partial to completely missing acorn cotyledon. We sampled the sown acorns only once due to the high number removed or consumed by weevils after one winter.

2.5. Data analysis

We used generalized linear mixed modeling to determine effects of midstory removal and deer and small mammal exclosures on growing conditions and oak regeneration. The overstory starting conditions (commercial thinning vs unmanaged) were not included in the models due to a lack of replication. Instead, we considered them to be case studies representing each condition and created separate models for each stand.

Models for growing conditions following treatment application (basal area in 2021, GLI in 2021, and understory biomass in 2024) included fixed effects for midstory removal, herbivory exclusion, and the factorial interaction of midstory and herbivory treatments. Plot was included as a random effect for the biomass model because two measurements were collected from each plot, but no random effects were included for the basal area or GLI models because each of these variables was measured once during the study period.

Response variables for planted oak seedlings included measures of size (height and GLD), growth (annual height and GLD growth increment), and survival. Size and growth responses were modeled using linear mixed models with midstory removal, herbivory exclusion, year, and all interactions as fixed effects. Plot was included as a random effect to account for subsampling of seedlings within experimental units, and year nested within plot was included as a random effect to specify the repeated measures structure. The establishment of natural reproduction (number of new seedlings following the 2022 mast year) and abundance (number of those persisting after three growing seasons (2025)) were analyzed using generalized linear models using a negative binomial distribution and log link function. No random effects were included for the natural regeneration abundance models because count data were summarized at the plot level. We analyzed survival of each regeneration source (planted oak seedlings, natural regeneration established after the 2022 mast year, and sown acorns) using generalized linear mixed models with a binomial distribution and a logit link function. Survival of planted oak seedlings and natural regeneration was modeled following each growing season with a repeated measures structure. Acorn survival was for only the dormant season after sowing. All models were inspected for normality and heteroscedasticity. When a model was in violation of assumptions, the dependent variable was log transformed or log transformed with the addition of a constant when dependent variables contained negative values or zero. We determined statistical significance of fixed effects ($\alpha = 0.05$) by using type III ANOVA for all linear models and a type III chi square for all generalized linear models. Tukey-adjusted pairwise comparisons were used to find significant differences among treatments and growing seasons.

We determined bivariate relationships between oak regeneration responses (planted seedling size, growth, and survival and natural regeneration survival) and the growing conditions (GLI and understory biomass) using linear mixed modeling. Plot was included as a random effect in all models. Bivariate relationships between natural regeneration abundances (establishment and abundance) and growing conditions were determined using generalized linear modeling with a negative binomial distribution. In the case of model significance, the strength of the independent variable was described by the marginal R^2 values for mixed models and Nagelkerke's R^2 for negative binomial models.

All analyses were done using R version 4.4.2 (R Core Team, 2026). Generalized linear models were fit using the R base package functions lm and glm. Mixed models were fit using the lmer and glmer function and in the lme4 package (Bates et al., 2015). The Anova function in the car package was used for running ANOVA and chi square tests on all models (Fox and Weisberg, 2019). Negative binomial error distributions were specified using the glm.nb function from the MASS package (Venables and Ripley, 2002). Tukey-adjusted pairwise comparisons were completed using the emmeans function from the emmeans package (Lenth, Piaskowski, 2026). Marginal R^2 values for mixed models were found using the performance package (Lüdecke et al., 2021).

3. Results

3.1. Growing environment

Averaged across all experimental units, GLI was lower in the unmanaged stand (14%) compared to commercially thinned stand (20%). GLI values ranged from 12% to 37% in the commercially thinned stand, and averaged 16% GLI in experimental units with an intact midstory. The midstory removal treatment increased GLI to 24% on average in the commercially thinned stand, but this increase was not found to be statistically significant ($p = 0.261$). Midstory removal did not significantly affect BA in the commercially thinned stand either ($p = 0.429$). On average, the midstory removal reduced BA by 1.5 m^2/ha resulting in an average residual BA of 21.1 m^2/ha in experimental units that received midstory removal while experimental units with an intact midstory had an average BA of 25.2 m^2/ha.

In the unmanaged stand, GLI values ranged from 8% to 23% across all experimental units, and the midstory removal treatment significantly increased GLI ($p = 0.049$). Average GLI in experimental units that received midstory removal was 17%, and GLI in experimental units with an intact midstory was 12%. However, this trend was not reflected in the residual basal area for the unmanaged stand ($p = 0.944$). On average, the midstory removal treatment in the unmanaged stand reduced BA by 2.9 m^2/ha. The average residual basal area for experimental units that received a midstory removal was 28.7 m^2/ha, which is slightly higher than experimental units with an intact midstory (26.9 m^2/ha). This is because the pretreatment BA for the subset of experimental units assigned to the midstory removal treatment (31.6 m^2/ha) was higher than the subset of experimental units not assigned to midstory removal (26.9 m^2/ha).

On average, biomass of understory vegetation was 43.2–53.0 g/m^2 in the unmanaged stand and the commercially thinned stand, respectively. There were no significant effects of study treatments on biomass for midstory removal (commercially thinned $p = 0.060$; unmanaged $p = 0.060$), herbivory exclusion (commercially thinned $p = 0.560$; unmanaged $p = 0.422$), or their interaction (commercially thinned $p = 0.579$; unmanaged $p = 0.676$) in either stand.

3.2. Oak regeneration

3.2.1. Acorns

Acorn predation was pervasive and observed even in split-plots that received protective treatments. Overall, 59% of acorns were still present in the commercially thinned stand after overwintering, and there were no effects of midstory removal or herbivore exclosure whole-plot treatments on acorn removal ($p \geq 0.147$). The acorn protection treatment resulted in a lower removal rate of acorns than the unprotected split-plot treatment ($p = 0.049$). However, field observations indicate that acorns remaining in split-plots were often those that had been infested by weevils prior to planting, and therefore their presence did not guarantee a new germinant would develop (Table 1). Of the acorns that were not removed from the subplots, 54% germinated in the covered split-plot treatment and 77% germinated in the uncovered split-plot treatment.

Table 1
Summary of all sown acorn outcomes after overwintering.

	Commercial Thinning		Unmanaged	
	Covered	Uncovered	Covered	Uncovered
Total Sown	192 (100%)	192 (100%)	192 (100%)	192 (100%)
Removed (% of total sown)	25 (13%)	132 (69%)	53 (28%)	131 (68%)
Remained (% of total sown)	167 (87%)	60 (31%)	139 (72%)	61 (32%)
Damaged (% of remained)	50 (30%)	10 (17%)	18 (13%)	13 (21%)
Germinated (% of remained)	90 (54%)	46 (77%)	116 (83%)	41 (67%)
Unknown (% of remained)	27 (16%)	4 (7%)	5 (4%)	7 (11%)

In the unmanaged stand, 52% of acorns were still present after overwintering. The same trend was observed in the unmanaged stand in which the acorn protection treatment had lower levels of removal than unprotected split-plots ($p = 0.026$; Table 1). Again, some of the acorns remaining in split-plots showed evidence of weevil damage and therefore did not germinate. When acorns were not removed from the subplots, 83% germinated in the covered split-plots and 67% germinated in the uncovered split-plots (Table 1). There was a significant interaction between the midstory removal treatment and herbivory exclusion treatment in the unmanaged stand ($p = 0.026$), but post-hoc comparisons did not reveal any significant differences among treatment combinations ($p > 0.203$). Plots that received both a midstory removal and fencing had the highest proportion of acorns removed at 74%, followed by control plots with 57% of acorns removed, then plots that received a midstory removal only with 31% of acorns removed, and plots that received fencing only had 17% removed. Field notes indicate that 6 subplots were impacted by burrows underneath the subplots that impacted the removal rate of acorns.

3.2.2. Natural oak regeneration

The 2022 mast event resulted in abundant white oak seedling establishment in both stands, with an estimated average of 10,955 seedlings per ha established in the commercially thinned stand and 20,712 seedlings per ha established in the unmanaged stand. However, there were no effects of midstory removal ($p = 0.958$ and $p = 0.190$), herbivory exclusion ($p = 0.251$ and $p = 0.535$) or their interactions ($p = 0.376$ and $p = 0.249$) in the commercially thinned stand and the unmanaged stand, respectively (Fig. 1).

After three growing seasons, an average of 3611 white oak seedlings per ha were still alive in the commercially thinned stand. Neither the midstory removal ($p = 0.848$) or deer fence exclosures ($p = 0.458$) affected the abundance of white oak seedlings three years after a bumper crop (Fig. 1A). The only factor significantly affecting their survival was growing season ($p < 0.001$), as seedling survival gradually decreased each measurement period and was lowest at the end of the third growing season at 38% (Fig. 1A).

In the unmanaged stand, an average of 8350 white oak seedlings per ha were still alive at the end of the study period, which is more than twice as many in the commercially thinned stand. Fencing did not affect the abundance of white oak seedlings ($p = 0.206$), but the midstory removal treatment did (Fig. 1B; $p = 0.048$). White oak natural reproduction was five times more abundant three years after a bumper crop in plots that received a midstory removal. However, this trend was not reflected in the survival rate of seedlings in the unmanaged stand ($p = 0.732$). Seedling survival decreased each growing season ($p < 0.001$), ending at 43% survival. We also found that deer fencing negatively impacted seedling survival in this stand ($p = 0.002$). Fenced seedlings had a 37% likelihood of survival while those left unprotected had a 73% likelihood of survival (Fig. 1B).

3.2.3. Underplanted oak seedlings

The overall survival of the underplanted white oak seedlings was low after five growing seasons in both stands (Fig. 2). We planted 396 seedlings in the commercially thinned stand, of which 32% survived to the end of our study period. Planted seedling survival was not impacted by midstory removal ($p = 0.980$), herbivory exclusion ($p = 0.152$), or their interaction ($p = 0.773$) in the commercially thinned stand. There were no interactions of growing season with midstory removal ($p = 0.936$) or herbivory exclusion ($p = 0.562$). Survival steadily decreased each growing season ($p = 0.002$) with the greatest decline occurring in the first and second growing seasons (Fig. 2A).

Underplanted seedling survival in the unmanaged stand was

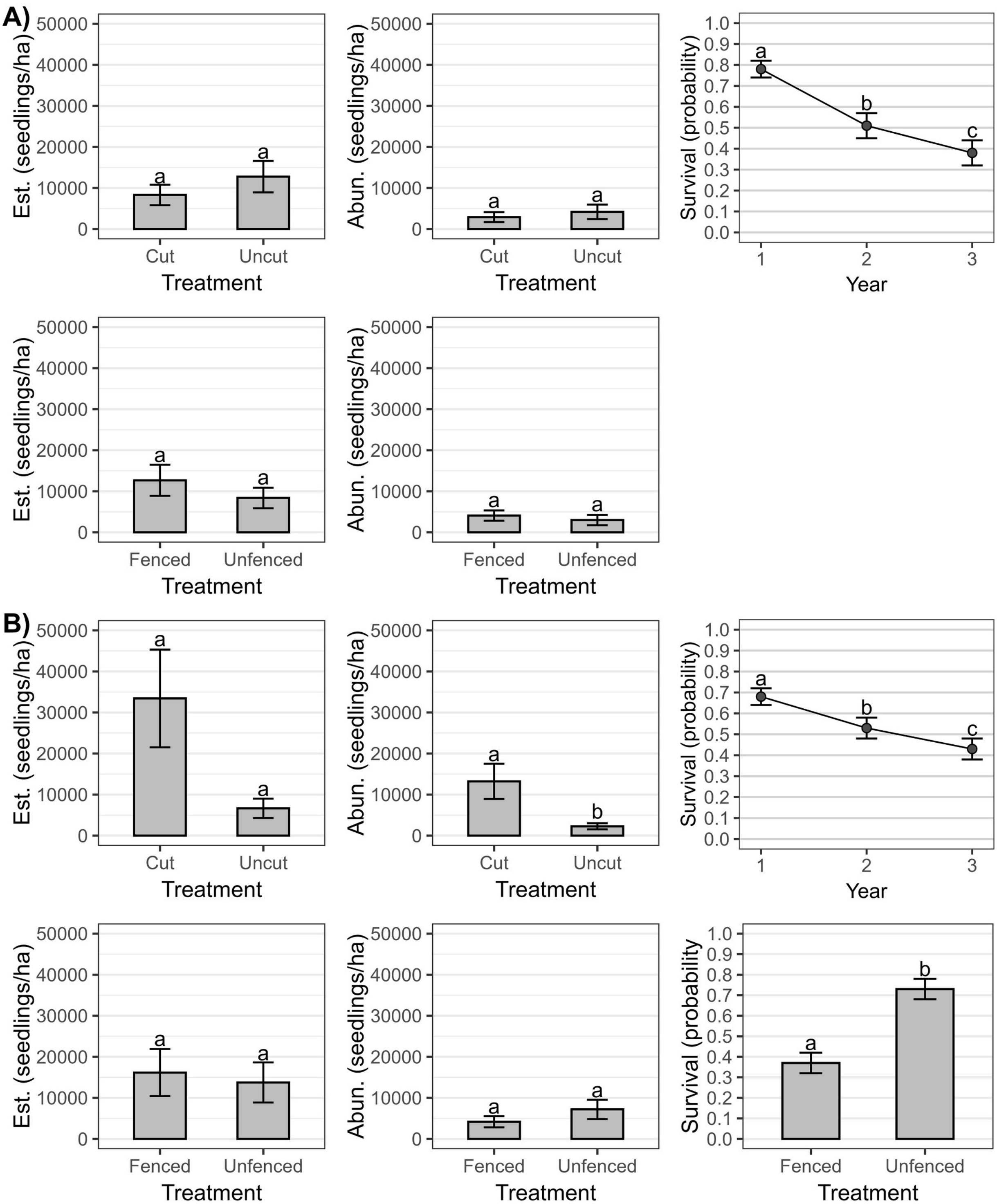

Fig. 1. Establishment (est.), abundance after three growing seasons (abun.), and survival rate of naturally regenerated white oak seedlings resulting from a mast event for the (A) commercially thinned research stand and (B) the unmanaged research stand. Error bars represent ± SE. Different letters indicate significant difference between treatments.

similarly low, with 38% of the 399 planted seedlings still alive after 5 growing seasons (Fig. 2B). The midstory removal treatment ($p = 0.082$), herbivory exclusion ($p = 0.887$), and their interactions ($p = 0.930$) did not affect survival in this stand, and growing season did not interact with midstory removal ($p = 0.648$) or herbivory exclusion ($p = 0.680$). Survival of planted seedlings in the unmanaged stand decreased through time ($p < 0.001$). The steepest decline in survival occurred between the first and second growing season (Fig. 2B).

The herbivory exclusion treatment improved both the annual growth and the size of planted white oak seedlings in the commercially thinned stand, with significant interactions between herbivory exclusion and growing season for height growth ($p < 0.001$), height ($p < 0.001$), and GLD ($p < 0.001$) (Fig. 3). Seedlings protected by fencing had greater height growth than unfenced seedlings in growing seasons 4 ($p < 0.001$) and 5 ($p = 0.010$). Fenced seedlings maintain a positive growth rate throughout the study while unfenced seedlings displayed a negative

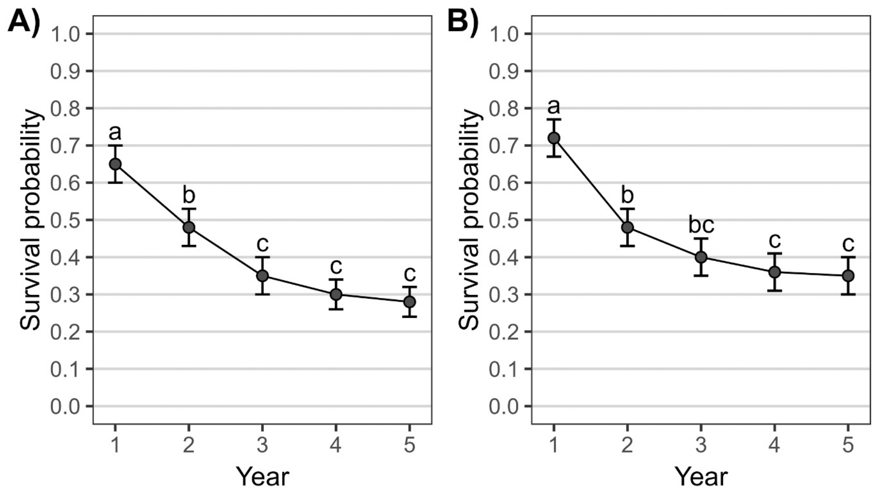

Fig. 2. Mean probability of survival (± SE) for planted white oak seedlings in the commercially thinned stand (A) and the unmanaged stand (B). Different letters indicate a significant difference between years.

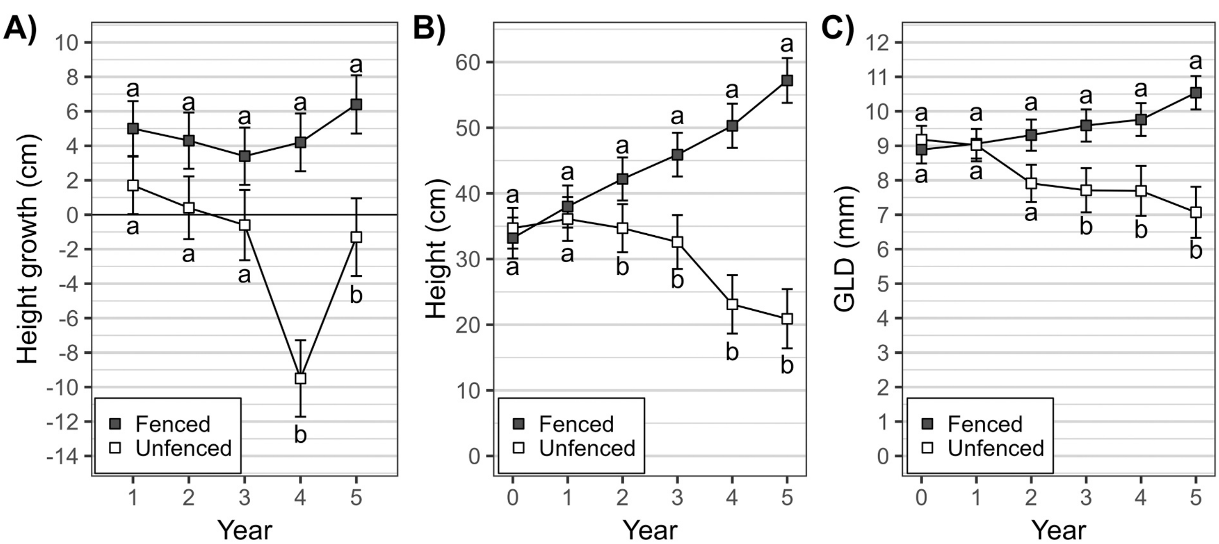

Fig. 3. Mean height growth (A), height (B), and GLD (C) of planted white oak seedlings in the commercially thinned stand. Error bars represent ± SE. Different letters indicate significant difference between treatments within each growing season.

growth rate by the third growing season (Fig. 3A). This pattern is reflected in the average seedling height, with fenced seedlings taller than unfenced seedlings by the end of the second growing season ($p < 0.001$; Fig. 3B). By the end of the study period, fenced seedlings were over twice as tall as unfenced seedlings, and unfenced seedlings were shorter than they were at planting (Fig. 3B). While the herbivory treatment did not affect GLD growth ($p = 0.128$), differences in average GLD between fenced and unfenced seedlings through time generally followed those of seedling height ($p < 0.001$; Fig. 3C). The midstory removal treatment had no effects ($p > 0.115$ for all seedling variables).

Unlike the commercially thinned stand, impacts of both the midstory removal treatment and herbivory exclusion treatment were observed in the unmanaged stand (Fig. 4). There was a significant interaction between midstory removal treatment and herbivory exclusion for height growth ($p = 0.049$). The midstory removal and herbivory exclusion combination resulted in greater annual growth than any other treatment combination ($p = 0.049$) and was the only treatment combination that yielded a positive growth rate (Fig. 4A). For seedling height, there was a three-way interaction for midstory removal, herbivory exclusion, and growing season ($p = 0.049$). Seedlings that were underplanted in midstory removals and protected by fencing were consistently taller than all other treatment combinations, and this trend became statistically significant in the fourth growing season (Fig. 4B). This was the only treatment in which seedlings were taller after five growing seasons than they were at planting. Additionally, we found significant main effects of growing season for height growth ($p < 0.001$) and average GLD ($p = 0.002$). Averaged across all treatments, annual height growth was greatest during the first growing season and then decreased through time, with the lowest growth rate occurring in the fourth growing season (Fig. 4C). Average GLD of planted seedlings fluctuates between 6 and 8 mm throughout the study period and was lowest in the third and fourth growing season (Fig. 4D).

3.3. Relationships between growing conditions and white oak regeneration performance

There were no significant relationships between understory biomass and natural reproduction establishment, abundance, or survival in the commercially thinned stand or the unmanaged stand ($p > 0.327$; Table 2). Establishment, abundance, and survival were not correlated with GLI in the commercially thinned stand (where GLI was generally higher; Fig. 5A), but both establishment and abundance were positively

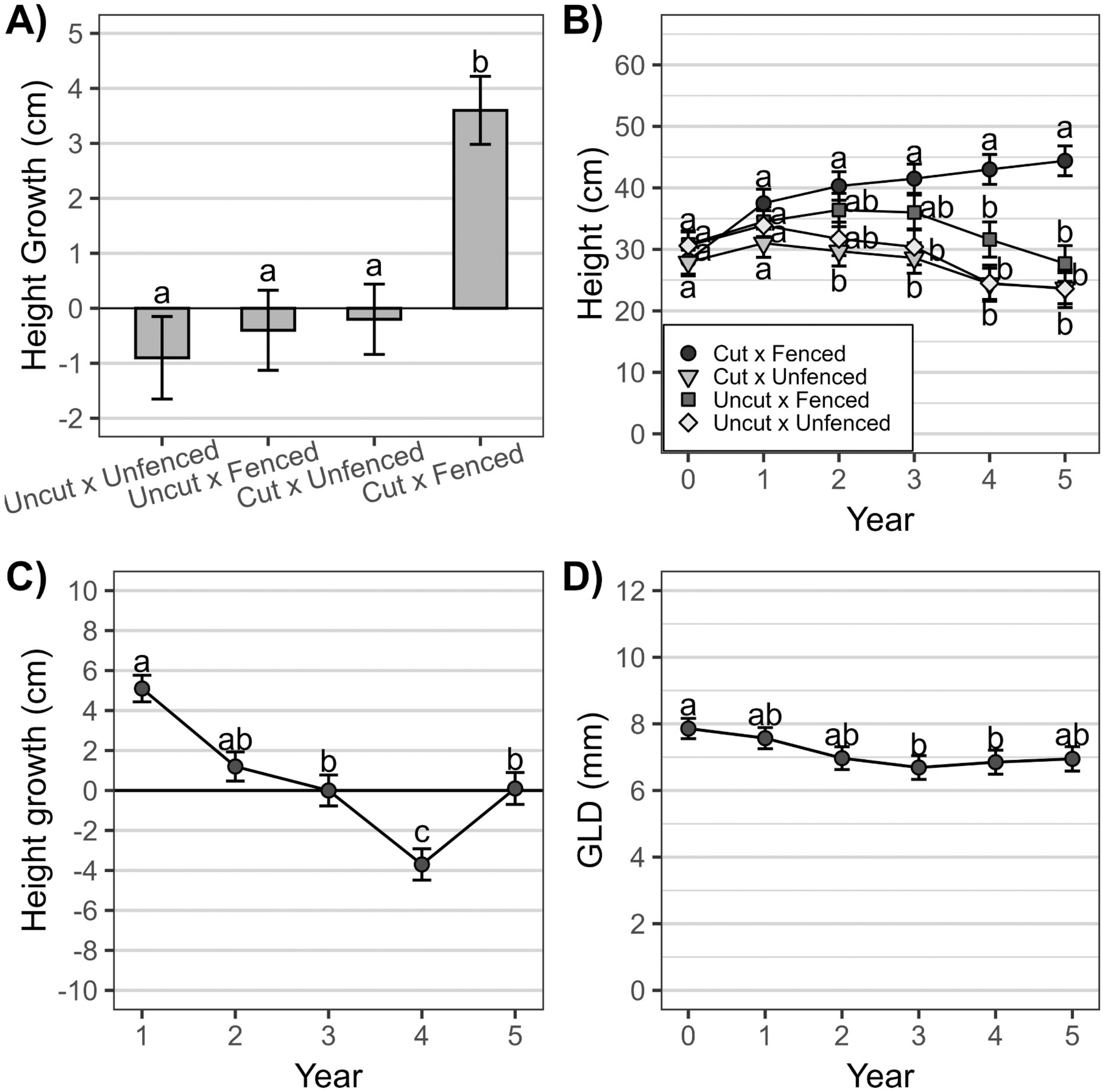

Fig. 4. Mean height growth by year (A), height growth by treatment (B), height (C), and GLD (D) of planted white oak seedlings in the unmanaged stand. Error bars represent ± SE. Different letters indicate significant difference between treatments.

Table 2
Corresponding p-values and r^2 values for bivariate relationships modeled between growing conditions (GLI and understory biomass) and oak regeneration outcomes for each stand.

Variable:	GLI				Biomass			
Research stand:	Commercial Thin p-value	r^2	Unmanaged p-value	r^2	Commercial Thin p-value	r^2	Unmanaged p-value	r^2
Natural Reproduction								
Establishment	0.926	0.001	0.028	0.572	0.327	0.107	0.883	0.003
Abundance	0.767	0.005	0.049	0.529	0.379	0.042	0.725	0.019
Survival	0.841	0.000	0.784	0.001	0.706	0.001	0.607	0.004
Underplanted								
Height growth	0.010	0.183	0.092	0.072	0.001	0.341	0.191	0.049
GLD Growth	0.242	0.044	0.122	0.043	0.008	0.255	0.955	0.000
Height	0.005	0.263	0.085	0.085	0.002	0.429	0.052	0.116
GLD	0.029	0.120	0.122	0.054	0.007	0.238	0.473	0.014
Survival	0.066	0.055	< 0.001	0.148	0.026	0.069	0.120	0.040

correlated with GLI in the unmanaged stand (Fig. 5B). Plots with the highest GLI typically had the greatest establishment of natural reproduction and the greatest abundance of natural reproduction after three years (Fig. 5B). However, GLI did not impact the survival rate of natural reproduction in the unmanaged stand.

Generally, underplanted seedling growth and size were positively related to GLI in the commercially thinned stand but not in the unmanaged stand, although GLI accounted for less than 30% of the

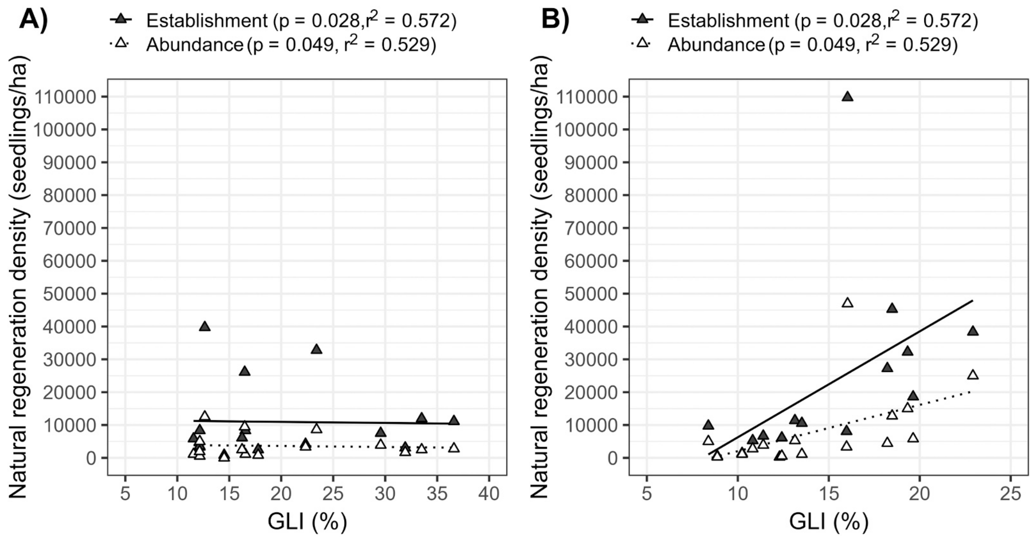

Fig. 5. Establishment of natural white oak seedlings after a bumper crop (solid) and abundance of natural reproduction after 3 growing seasons (dashed) are positively correlated with GLI in the unmanaged stand. Note the difference in x-axis scale as GLI had a more narrow range in the unmanaged stand.

variation in any growth or size variable (Table 2, Fig. 6A). Similarly, understory biomass was positively related to seedling growth and size in the commercially thinned stand but not the unmanaged stand (Table 2), accounting for 42.9% of the variation in seedling height in the commercially thinned stand (Fig. 6B). Underplanted seedling survival was positively related to plot-level GLI in the unmanaged stand, accounting for 14.8% of the variation, but was not significant in the commercially thinned stand (Table 2, Fig. 7).

4. Discussion

By including three different sources of oak regeneration, we were able to assess potential limiting factors that impede the accumulation of oak advance reproduction throughout the regeneration process. Barriers to securing advance reproduction begin with seed production, dispersal, and germination, with acorns an important food source for a variety of organisms, including deer (McShea and Healy, 2002; McShea et al., 2007). However, we did not observe any apparent trends in acorn removal from fenced plots during our study, indicating that acorn survival was not limited by larger animals such as deer. Acorn removal was high in plots without protection from hardware cloth. Other studies have similarly observed high rates of acorn consumption in the absence of deer, often by rodents (Russell and Fowler, 2004; Haas and Heske, 2005; Kellner et al., 2014; Greenberg and Zarnoch, 2018). Deer alone seem unlikely to inhibit the establishment of new oak germinants. Instead, acorn survival, and therefore germination, in years of low or moderate acorn production is inhibited by small consumers like rodents or birds.

Our results highlight the importance of mast years for oak regeneration. In a non-mast year, acorns that were not protected from depredation were mostly removed. Despite initially passing the float test, many of the acorns remaining after overwintering showed evidence of weevil infestation, indicated by hollow acorn shells with holes bored into the sides. This may have resulted in the removal rates we report to be slight underestimates if rodents are avoiding acorns with detectable weevil damage. Regardless, less than 25% of the acorns sown in unprotected plots resulted in germination. Although weevil infestation occurred before being sown in our research plots, other studies have found the proportion of acorns damaged by weevils decreases during mast years and that weevil infestation is pervasive in years of poor production (Kellner et al., 2014; Lombardo and McCarthy, 2008). During mast years, enough acorns are produced to overwhelm consumers and establish a new cohort of white oak seedlings. A single mast event for oak can result in 2470–24,700 germinants per hectare (1000–10,000 germinants per acre) depending on the region and species (Johnson et al., 2019). The mast year in this study resulted in 11,000–21,000 germinants per hectare, suggesting that acorn production, dispersal, and germination are not limiting to oak regeneration in these stands, at least periodically with the occurrence of masting events.

There was some evidence that shade limited early establishment of white oak seedlings from acorns in our study. In general, however, the sown acorns that evaded consumption germinated regardless of treatment and associated light levels. Acorns are nutrient dense and early growth is supported by resources stored in the cotyledons until seedlings establish a root system and must rely on photosynthesis for energy (Crow, 1988). It is unlikely that shade levels in our study had meaningful effects on germination. However, light was positively correlated with natural white oak seedling establishment and abundance after three growing seasons following the masting event in the unmanaged stand, where light levels were below 10% in some plots. Because initial establishment was recorded in May, several months after masting, we may have captured a trend in early survival after overwintering rather than abundance of true germinants. We also found that the midstory removal treatment increased the abundance of natural white oak seedlings after three growing seasons following masting in the unmanaged stand. Other studies have found that midstory removal improves the density of natural oak reproduction (Brose, 2011; Hackworth et al., 2020). Although white oak is conventionally thought to be among the most shade-tolerant of the oaks, heavy shade can limit its performance (Brose and Rebbeck, 2017) and contributes to low abundance of natural reproduction in undisturbed forests of central Missouri.

Our results demonstrate the relationship between light availability and the size of white oak reproduction, with shade levels in undisturbed stands limiting the development of large advance reproduction. Generally, the ideal light environment for oak is 30% full sunlight (Phares, 1971), but other studies have found a range of 11–15% full sunlight was sufficient for stimulating the growth of underplanted oak seedlings (Lhotka, Loewenstein, 2009, Parrott et al., 2012; Motsinger et al., 2010). In our study, few plots exceeded 30% light, all of which occurred in the commercially thinned area. These plots also had the largest underplanted white oak seedlings after five growing seasons. The heavier shade in the unmanaged stand muted the relationship between light and seedling growth but also made the midstory removal treatment more important for eliciting a seedling growth response. The growth increases following midstory removal in the unmanaged stand were modest but comparable to other studies (Lockhart, 2000; Parrott et al., 2012; Hayford et al., 2024).

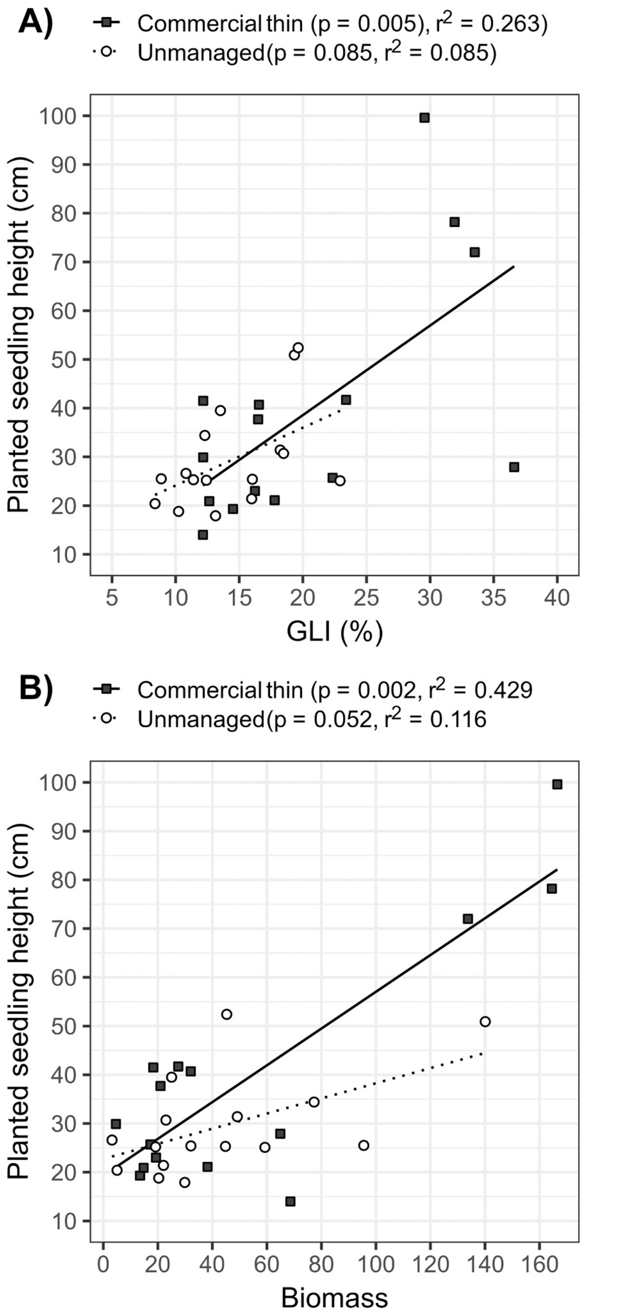

Fig. 6. Bivariate relationships between average planted seedling height after 5 growing seasons with GLI (A) and biomass (B) for both research stands.

After five growing seasons, our underplanted white oak seedlings remained small; none of our plots averaged 1.0 m tall and few individual seedlings reached 1.5 m tall. White oak dedicates early growth to developing a large root system, with conservative aboveground growth rates. Consequently, early height growth of white oak is less responsive to moderate light increases than other oak species (Dillaway et al., 2007; Rebbeck et al., 2011; Brose and Rebbeck, 2017), which may contribute to the limited effects of midstory removal on seedling height in our study. Treatment effects on root size may be more pronounced (e.g., Brose, 2011), although we did not measure root system size in our study. Measures of stem diameter may reflect root size (Dey and Parker, 1997a), although resprouting affects this relationship and can result in root collar diameter being more indicative of root size than stem diameter (Knapp et al., 2006). While we found that treatment effects on stem diameter (GLD) generally followed those of seedling height, it is

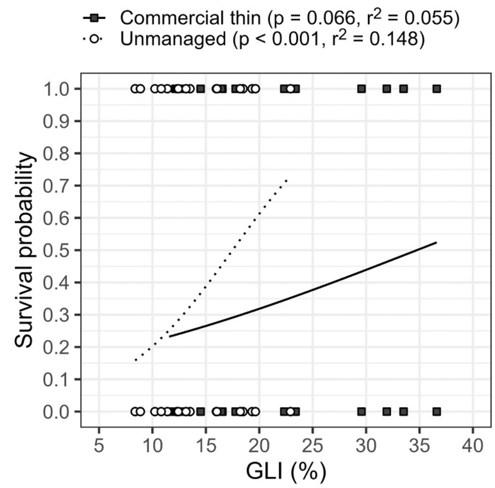

Fig. 7. Bivariate relationships between planted seedling survival after 5 growing seasons with GLI for both research stands.

likely that root growth was impacted by study treatments in ways that we were not able to detect.

Our results suggest that either midstory removal or commercial thinning could be used to relieve shade limitation to white oak seedling growth. Similar light levels were achieved with either treatment, and we did not find additional beneficial effects of midstory removal on underplanted white oak seedling growth in the commercially thinned stand. In general, the goal with either approach is to stimulate oak advance reproduction growth in preparation for subsequent overstory harvests once the advance reproduction reaches a competitive size (Loftis, 1990; Lockhart, 2000; Lhotka, Loewenstein, 2013). However, decisions on cutting intensity or method may depend on factors such as site productivity and the abundance or composition of competing species (Loftis, 1990). On sites of intermediate productivity, midstory removal has been found to improve the growth of shade-tolerant competition, like red maple, ultimately leaving a high proportion of oak advance reproduction overtopped (Parrott et al., 2012; Hackworth et al., 2020). Other studies have shown midstory removal to improve the survival and growth of yellow-poplar, a common shade-intolerant oak competitor, resulting in growth rates surpassing oak in riparian areas (Lhotka, Loewenstein, 2013). The conditions in Missouri, where site productivity is relatively low and there are fewer aggressive oak competitors (i.e., yellow-poplar) in the region, likely allow greater flexibility in the cutting approach and intensity compared to other areas within the white oak range.

Deer populations can have significant impacts on tree regeneration, although the expected browse impacts in Missouri are generally lower than other regions of the eastern U.S. (Albright, 2025). In Virginia, where estimated browsing intensity was high (67 deer/km^2), deer severely reduced the survival of hardwood seedlings, including oak, in oak-hickory forests (Rossell et al., 2005). However, with lower abundance of deer (6.0–14.1 deer/km^2), herbivory impacts are associated with differences in oak reproduction size rather than seedling density (Csigi, Holzmueller, 2015; Parker et al., 2020). We did not find deer exclosures to impact the abundance or survival of white oak reproduction. Although we do not have deer density data for our study, the Baskett Forest does not allow hunting and likely has higher deer populations than surrounding areas in the region. It is likely that deer populations in central Missouri are not a major factor limiting the presence or abundance of white oak seedlings, although our results clearly show impacts of herbivory on white oak seedling size.

Deer herbivory inhibited the development of large advance reproduction in our study, with average seedling height in plots without exclosures lower at the end of the study than at the time of planting.

Deer exclosures resulted in underplanted white oak seedlings that were nearly double the height of seedlings exposed to herbivory. Deer fencing has been found in other studies to increase the height of regenerating hardwoods by similar amounts (Long et al., 2012; Csigi, Holzmueller, 2015). In addition to direct effects of browsing on seedling height through removal of aboveground tissue, herbivory may have indirect effects by reducing photosynthesis and growth potential. Deer fences have been associated with improved root characteristics, such as root collar diameter, root length, and biomass (Long et al., 2012). The larger GLDs observed in fenced plots in the commercially thinned stand may also be indicative of improved root development. Protecting seedlings from browse while they develop a robust root system may be important for accumulating competitive advance reproduction and positioning seedlings to be more responsive to increased light from other management treatments. In the unmanaged stand, the benefits of increasing light through midstory removal was modulated by deer herbivory, such that increased mean seedling height through time was only observed with both midstory removal and deer exclosure. Similarly, Miller et al. (2017) found that a combination of deer fencing with silvicultural treatments that alleviated shade were key to developing sufficient oak advance reproduction ready for release. Taken together, these results suggest that when multiple limiting factors are present, such as both heavy shade and deer herbivory, they may have additive or interacting effects on oak seedlings.

Aside from direct effects of deer browse on oak seedlings, herbivory can have complex interactive effects with the understory plant community that change the competitive environment for regenerating oak seedlings. In the absence of deer browse, palatable species can establish or expand their abundance, potentially increasing competition for oak regeneration (Abrams and Johnson, 2012; Miller et al., 2014). In our study, field observations suggested that understory biomass was greater within deer exclosures, yet we found no statistical difference in understory biomass due to the deer exclosure treatment. We also found underplanted white oak seedling size to be positively correlated to understory biomass, which we speculate is due to local differences in site quality or resource availability that improved growing conditions for both white oak seedlings and surrounding vegetation. While this has not yet been problematic, continued development of competing vegetation could have future impacts on the success of oak regeneration.

We found the overall success of underplanting to be mixed. Underplanting is recommended to quicken the accumulation of advance reproduction by establishing oak where natural regeneration is lacking (Dey et al., 2012). Success of underplanting depends on seedling survival and timely development into large advance reproduction that will be competitive following a regeneration disturbance (Dey et al., 2008). While our study treatments favorably impacted underplanted white oak seedling growth, survival was low (28–35%) and not affected by our study treatments. Some studies have reported early survival of underplanted bareroot oak seedlings ranging from 66% to 99% when shade is reduced (Dey and Parker, 1997b; Parrott et al., 2012; Lhotka, Loewenstein, 2013). Other studies have reported survival rates below 30%, similar to survival rates from our study, for bareroot northern red oak and pin oak seedlings, likely due to competition associated with increased light availability (Hayford et al., 2023; Plaugher and Schuler, 2025).

Several factors, including seedling stock characteristics and growing conditions after planting, are important for the success of planted oak seedlings (Dey et al., 2008). Planting high quality seedlings with a basal diameter of 10–12 mm improves the likelihood of artificial red oak species regeneration developing into competitive advance reproduction (Dey et al., 2012). The average initial GLD of the bareroot seedlings in our study was below this minimum threshold (8.45 mm, ranging from 2.69 to 23.80 mm), but we did not find a relationship between initial seedling size and probability of survival (data not shown), suggesting that seedling quality was not the primary driver of mortality. Alternatively, our study area experienced a period of prolonged drought after planting. Although oak species are classified as drought tolerant (Johnson et al., 2019), a period of water stress after transplanting may have increased mortality in our study. Inconsistent survival reported across studies raises questions about underplanting as an effective and reliable approach for oak regeneration, requiring more research into causes of mortality and management solutions to reduce it.

5. Conclusion

Our experimental design allowed us to track the progress of white oak advance reproduction throughout the initial regeneration stages, allowing us to disentangle potential limitations during the process of accumulating oak advance reproduction. Our results demonstrate the importance of masting events that overcome environmental stressors and acorn predation to establish a new cohort of white oak seedlings from natural regeneration. Neither light availability nor deer herbivory appeared to limit germination, but heavy shade limited the persistence of white oak seedlings in the understory. Once seedlings were established, heavy shade and deer herbivory became barriers to the development of large white oak advance reproduction. We achieved a light environment adequate for promoting oak advance reproduction through midstory removal or commercial thinning. Overall, we found mixed success of underplanted white oak seedlings, as mortality steadily increased through time, and the occurrence of a masting event resulted in the widespread establishment of a new white oak seedling cohort though natural regeneration. Regardless of the source of regeneration, however, active management to increase light availability and patience appear important for increasing white oak seedling populations.

CRediT authorship contribution statement

Benjamin O. Knapp: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Abby L. Huffman:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Daniel C. Dey:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

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

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Data Availability

Data will be made available on request.

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