FACTORS AFFECTING NATURAL OAK REGENERATION IN BOTTOMLAND HARDWOOD FORESTS IN NORTHERN MISSOURI: LIGHT LEVELS, ACORN LOSSES, OR LACK OF ACORNS?

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ABSTRACT

Successful oak (*Quercus* spp.) regeneration in bottomland forests can be limited by several factors, including number of acorns produced, acorn viability and predation, microsite conditions for germination, and early seedling survival. These factors could influence the development of large oak advance reproduction needed for successful oak regeneration. We designed an experiment to test the importance of some of these factors on oak regeneration in bottomland forests in northern Missouri. We found that low acorn production and high rates of acorn predation were prevalent throughout the stands. Buried acorns showed higher germination rates than acorns placed on the surface of the soil. Our results also indicated that germination of acorns was unaffected by light availability. Thus, our findings suggest that midstory release will not increase germination and therefore should not be expected to increase the initial establishment of new seedlings. However, midstory release could potentially be useful in enhancing development of seedlings following germination.

INTRODUCTION

Natural regeneration is regarded as a more cost-effective option than artificial means of forest establishment (Löf and others 2019). The process of natural regeneration involves several stages that include seed production, seed dispersal, seed germination, seedling survival, and seedling growth or recruitment into the overstory. The success of natural regeneration is contingent on the suitability of species-specific environmental conditions, including site factors and disturbance regimes. Failure at any stage of the regeneration process can result in failure in the regeneration of a species. Understanding species-specific environmental and regeneration needs is important to successfully manage them (Grubb 1977).

Acorn production varies greatly between years and among species, individuals, and locations (Rose and others 2012). The interannual variation in acorn production is usually associated with synchronous acorn production among individuals within a population. However, acorn production levels could also fluctuate depending on the number of fruiting trees or the number of fruits per tree (Greenberg and Parresol 2000). There are contrasting findings regarding the influence of age and size of trees on acorn production. Goodrum and others (1971) found that intrinsic features such as age and size affect acorn production whilst Greenberg (2000) found that measurable tree characteristics such as size do not provide sufficient information to identify individual trees of superior acorn production ability. Other factors, including stand density, genetics, and weather events such as late spring freezes or heavy precipitation that interferes with oak flower survival or pollen dispersal, have been implicated to affect acorn production (Healy 1997, Johnson and others 2002).

Acorns are an important source of food for a wide range of animals including insects, birds, and mammals such as rodents, suids, and cervids due

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to their palatability, nutritiousness, widespread occurrence, and availability during the critical fall and winter seasons (Janzen 1971, Johnson 1994). White-tailed deer (*Odocoileus virginianus*), eastern chipmunks (*Tamias striatus*), and mice (*Mus* spp.) consume a large percentage of fallen acorns on the ground, whereas tree squirrels (*Sciurus* spp.) consume them both on the ground and before they fall (Haas and Heske 2005). Acorn predation by vertebrates or insects could destroy up to 90 percent of acorns, leading to substantial reduction in oak reproduction (Crawley and Long 1995). Masting by oaks is a defensive strategy that allows a higher proportion of acorns to escape predation by satiating acorn predators with excess during mast years and reducing predators during nonmast years (Janzen 1971, Kelly and Sork 2002). This phenomenon, termed as the predator satiation hypothesis, has been demonstrated by studies where relatively lower rates of predation were recorded in high mast production years as opposed to higher rates of predation in low mast production years (Goodrum and others 1971, Kelly and Sork 2002).

Species vary greatly in their requirements for germination, with external factors such as temperature, substrate, moisture, or light as possible germination cues. Plants can be classified into three groups based on their response to light for germination, and these include those that require light to germinate, those that require shade to germinate, and those that have a large percentage of their seeds neutral to light (Flores and others 2016). Acorn germination is not constrained by light availability and can germinate even under a closed canopy (Dey 2002, Moorhead and others 1991). The position of acorns in the soil has also been shown to affect rates of acorn germination. Previous studies have reported higher germination rates for buried acorns compared to acorns placed on top of the soil (Guo and others 2009, Nilsson and others 1996). Acorns require variable times of cold stratification to enhance their germination rates. Pin oak (*Quercus palustris*) acorns, for example, require stratification of 30–45 days at 0–5 °C to break dormancy (Burns and Honkala 1990).

Because successful oak regeneration is dependent upon an adequate number of large oak advance reproduction, poor seed crops, high rates of acorn predation, and poor germination can have substantial impacts on the ability of oaks to compete with other species. Most mature oak stands usually have several hundred to thousands of oak seedlings per hectare present on the forest floor (Hayford and others 2023). The absence of adequate oak seedlings on the forest floor in our study sites was particularly worrying in the quest of maintaining or increasing the abundance of oaks. The main goal of this study was to investigate the cause of natural regeneration failures of bottomland oaks in our study sites. Was it due to inadequate acorn production, acorn losses through acorn predation, the effect of light regime, or the effect of the position of acorns in the soil on acorn germination? The specific objectives were to determine 1) the effect of oak density on acorn production; 2) the effects of the position of the acorn in the soil (buried versus not buried), acorn predator exclosures, and acorn production level (low, medium, high) on acorn removal; and 3) the effects of the position of the acorn in the soil (buried versus not buried) and light levels on acorn germination.

We hypothesized that acorn predation would be higher in the open plots than in plots that restricted access to small mammals like squirrels and mice, and in complete exclosure plots that excluded all mammals. It was expected that the complete exclosure plots would restrict access to all known acorn predators and hence retain all or most acorns placed in these plots to ensure higher germination rates compared to the other experimental plots. We also hypothesized that buried acorns would have higher germination rates than acorns that were not buried. We were not expecting acorn germination to be different among the light levels.

METHODS

Study Site

The study was conducted on a 220-ha mixed bottomland hardwood forest at Deer Ridge Conservation Area (DRCA) (40°10’30’’N, 91°48’0’’W) in Lewis County of northeastern Missouri. DRCA has one of the largest tracts of remnant bottomland forest in northeastern Missouri and is adjacent to a channelized segment of the North Fabius River. This site contained contiguous bottomland forest blocks >20 ha, and State ownership facilitated long-term access and control of management activities. The soils of the study area were dominated by Blackoar silt loam (fine-silty, mixed, superactive, mesic Fluvaquentic Hapludolls), Fatima silt loam (fine-silty, mixed, superactive, mesic Fluvaquentic Hapludolls), and Kickapoo fine sandy loam (coarse-loamy, mixed, superactive, nonacid, mesic Typic Udifluvents); each were formed in alluvium but varied in drainage class. All soil series were associated with slopes between 0 and 2 degrees. The site was prone to annual flooding events, with patches of low-lying areas permanently inundated with water. The mean annual temperature and precipitation for the area over a 30-year period (1991–2020) were 11.7 °C and 1,007 mm, respectively (PRISM Climate Group, www.prism.oregonstate.edu). The tree species in the area were predominantly silver maple (*Acer saccharinum*), American elm (*Ulmus americana*), American sycamore (*Platanus occidentalis*), green ash (*Fraxinus pennsylvanica*), boxelder (*Acer negundo*), eastern cottonwood (*Populus deltoides*), pin oak, bur oak (*Quercus macrocarpa*), and swamp white oak (*Quercus bicolor*) (Rives and others 2020).

Experimental Design

All treatments were established in stands with homogenous hydrology. This study used a factorial split-split-plot design. The whole plot treatments included three levels of light availability, and the split-plot treatments were a factorial combination of three levels of acorn predator exclosures and three levels of acorn production. The position of acorns in the soil (buried versus not buried) was the split-split-plot factor.

The three light levels were:

- High light—a uniform, area-based approach was used to reduce basal area of midstory trees in a previously unharvested stand by 65 percent, leaving an understory light level of 18 percent of full sunlight.
- Medium light—a uniform, area-based approach was used to reduce basal area of midstory trees in a previously unharvested stand by 30 percent, leaving an understory light level of 15 percent of full sunlight.
- Low light—no treatment was applied and light level was approximately 5 percent of full sunlight.

The three levels of acorn predator exclosures were installed in August 2020. Each of the acorn predator exclosure experimental plots was 1.52 m by 0.61 m. Exclosures were situated 1 m from each other.

- Complete exclosures prohibited all known acorn predators such as mice, squirrels, and deer from access to the plot. The exclosures consisted of 0.01-m mesh galvanized steel hardware cloth. The exclosure walls were 0.61 m tall, covered at the top, and buried 0.15 m under the soil surface to prevent small mammals from burrowing under the walls.
- Squirrel-mouse plot exclosures restricted access by vertebrates larger than squirrels such as deer. They were constructed with the same wire mesh as complete exclosures, but the hardware cloth was raised 0.15 m above ground level to allow access by mice and squirrels.
- Open plot controls were marked by four rebars where small and large predators had unrestricted access to the experimental plot.

In a 14-year study by McQuilkin and Musbach (1977), the highest number of mature acorns produced in a particular year in 32- to 46-year-old pin oak stands in southeastern Missouri was 492,700/ha, and hence we selected 40 acorns to represent high production in a 0.92 m^2 area. Buried acorns were intended to simulate caches of gray squirrels (*Sciurus carolinensis*). Caches were made by depositing acorns horizontally into a 0.02-m-deep depression and covering them with soil and litter. In the fall of 2020, each of the exclosure and control treatments received one of the following acorn production and position treatments:

- High acorn production—20 acorns were buried halfway in simulated caches in a 4 by 5 grid with each acorn spaced 0.15 m apart. An additional 20 acorns were marked with blue paint and deposited on the soil surface underneath the leaf litter.

- Medium acorn production—15 acorns were buried halfway in simulated caches in a 3 by 5 grid with each acorn spaced 0.15 m apart. An additional 15 acorns were marked with blue paint and placed on the soil surface underneath the leaf litter.
- Low acorn production—10 acorns were buried halfway in simulated caches in a 2 by 5 grid with each acorn spaced 0.15 m apart. An additional 10 acorns were marked with blue paint and placed on the soil surface underneath the leaf litter.

The nine treatment combinations were replicated three times in each of the three light levels for a total of 81 experimental units (fig. 1). The pin oak acorns were purchased from the George O. White State Forest Nursery in Licking, MO. The acorns were collected during the preceding autumn and screened for soundness, stratified, and stored in accordance with standard nursery practices. Acorns were refrigerated after receipt from the nursery for about 1 month prior to field deployment to prevent them from heating up or drying out and to break dormancy. Prior to refrigeration, the acorns meant to be placed on the soil surface were marked with blue paint to differentiate them from those to be buried.

Acorn Crop Measurement

Sixteen wire mesh cone traps, 0.42 m^2 in size, were arrayed in a 4 by 4 grid in each of the nine plots where the acorn exclosures were constructed, with traps spaced 10 m apart (144 traps total, 60.48 m^2 total sample area). This approach was chosen rather than collecting acorns from individual trees because of the variability in acorn production among individuals and the difficulty associated with collection from individuals under closed canopy conditions. The traps did not restrict access to predators.

Data Collection

The remaining acorns or seedlings were counted 8, 21, 43, and 307 days after placement in the exclosure plots on November 4, 2020. We found no acorn germination until the 307th day check. Acorn traps were checked at approximately 2-week intervals from late August until the

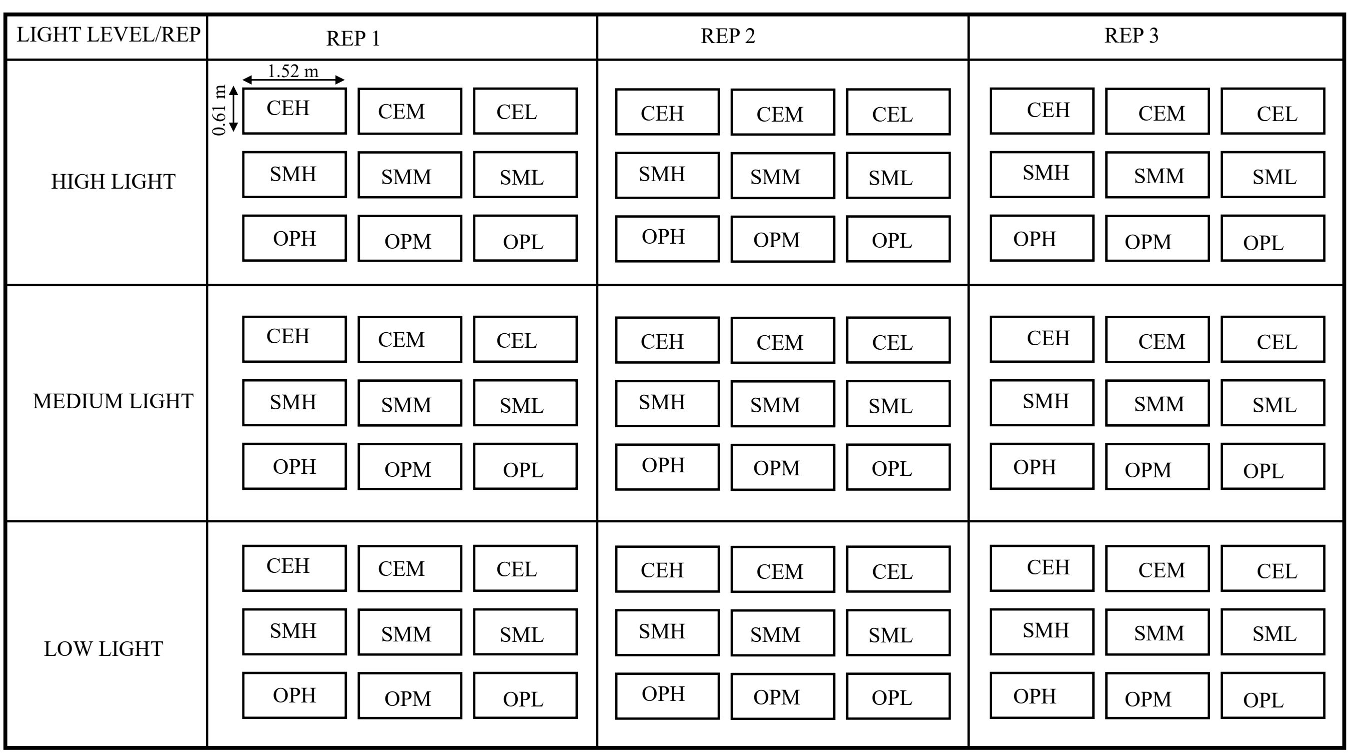

Figure 1—Field layout of nine acorn predator exclosure experimental units replicated three times within each of three light levels. CE = complete exclosure; SM = squirrel-mouse plot; OP = open plot; H = high acorn production; M = medium acorn production; and L = low acorn production.

completion of acorn drop in mid-December in both 2020 and 2021. All mature acorns collected were identified to species, counted, and removed during each visit. We counted all well-developed acorns without distinguishing between insect-damaged and sound acorns or between different acorn sizes.

Data Analysis

We did not have enough data to test the relationship between oak density and acorn production due to low acorn production. All the acorns in the open and squirrel-mouse plots were completely removed within 8 to 21 days after acorn placement in exclosures (table 1). As a result, acorn removal rates could only be tested in the complete exclosure plots. We used logistic regression to test the effects of acorn production level (low, medium, high) and acorn burial status (buried, nonburied) on acorn removal within the complete exclosure plots. We used a generalized linear mixed model with a binomial distribution, a logit link function, and a random intercept that used stand as the subject, using GLIMMIX procedure of SAS (version 9.3, SAS Institute, Inc., Cary, NC). We could not include days of acorn removal in the model because that created convergence issues. Thus, we pooled all data across time periods. The same analysis framework was used to test the effects of light level, acorn burial status, and their interactions on acorn germination at the day 307 sampling. Each acorn that germinated was coded as 1 and nongerminated acorns coded as 0. Germination analysis was conducted on only remnant acorns (i.e., acorns that were not removed by predators) in the complete exclosure plots because all acorns in the open and squirrel-mouse plots were removed by predators. When significant differences were detected among treatments, Tukey's honestly significant difference adjustment was used to evaluate pairwise comparisons.

RESULTS

In total, 2,430 acorns were monitored for removal by predators during the 1-year study period within the exclosure plots. All acorns (buried and not buried) were removed from the open and squirrel-mouse plots by the 21st day following placement in the exclosures. For the complete exclosure plots, the proportion of acorns removed was 0.39 by the last sample date (table 1). In most cases, the predators could not access the acorns in the complete exclosure plots. However, in the few instances where the predators were able to access the complete exclosure plots, probably due to faulty construction, most or all acorns were removed (fig. 2). The simulated acorn production level affected the rate of acorn removal within the complete exclosure plots ($P = 0.02$, fig. 3). The rate of acorn removal was lower within the complete

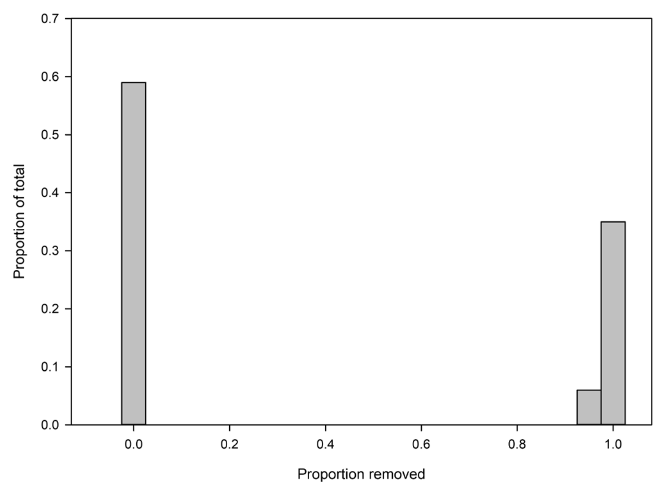

Figure 2—Histogram showing the rate of acorn removal within the complete exclosure plots at final day (day 307) of monitoring at Deer Ridge Conservation Area, Lewis County, MO.

Table 1—Proportion of acorns removed from predator exclosures by number of days

	Not buried acorns			Buried acorns		
Days	Open	Squirrel-mouse	Complete	Open	Squirrel-mouse	Complete
0	0.00	0.00	0.00	0.00	0.00	0.00
8	1.00	0.99	0.14	0.99	0.97	0.10
21	1.00	1.00	0.37	1.00	1.00	0.36
43	1.00	1.00	0.37	1.00	1.00	0.37
307	1.00	1.00	0.39	1.00	1.00	0.39

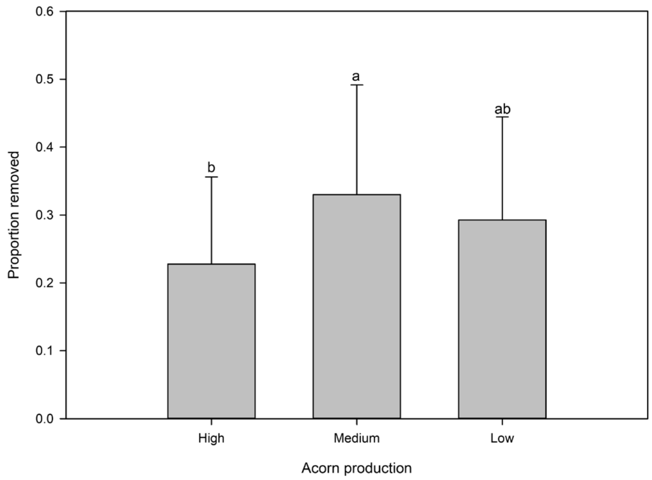

Figure 3—Acorn production level effect on average proportion of acorns removed within the complete exclosure plots at Deer Ridge Conservation Area, Lewis County, MO, 2020–2021. Different letters indicate significant differences among acorn production levels. Error bars represent one standard error from the average.

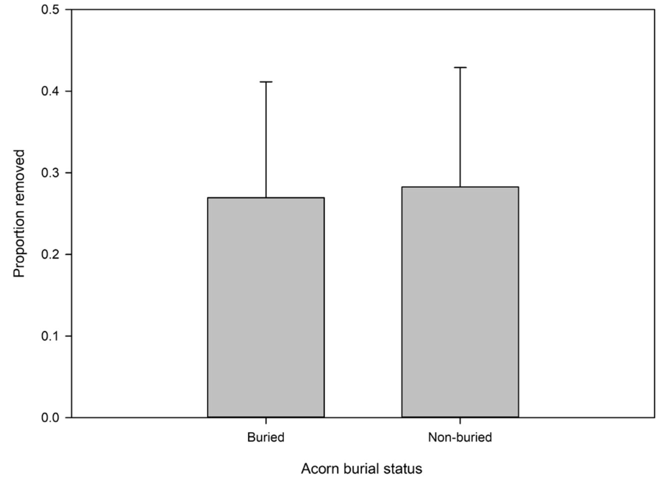

Figure 4—Average proportion of acorns removed by predators from complete exclosure plots by burial status at Deer Ridge Conservation Area, Lewis County, MO, 2020–2021. Error bars represent standard error from the average.

exclosure plots that received high acorn production than those that received medium acorn production. The rate of acorn removal within the low acorn production level treatment, however, was not different from the medium and high acorn production. There was no significant difference in proportion of removal between acorns that were buried and not buried in the complete exclosure plots (*P* = 0.52, fig. 4).

There was a significant effect of acorn burial status on proportion of germination (*P* = 0.03, fig. 5), where greater proportion of buried acorns that remained in the complete exclosure plots germinated than acorns that were not buried. Germination of acorns was not different among the three light levels (*P* = 0.59, fig. 5). The mean proportion of germination across the three light levels was 0.32. We did not have sufficient data to test the relationship between oak density and acorn production due to low acorn production. In total, we found only 54 acorns during the 2-year study period, and these were found in 3 of 144 acorn traps, and in 1 of 9 plots.

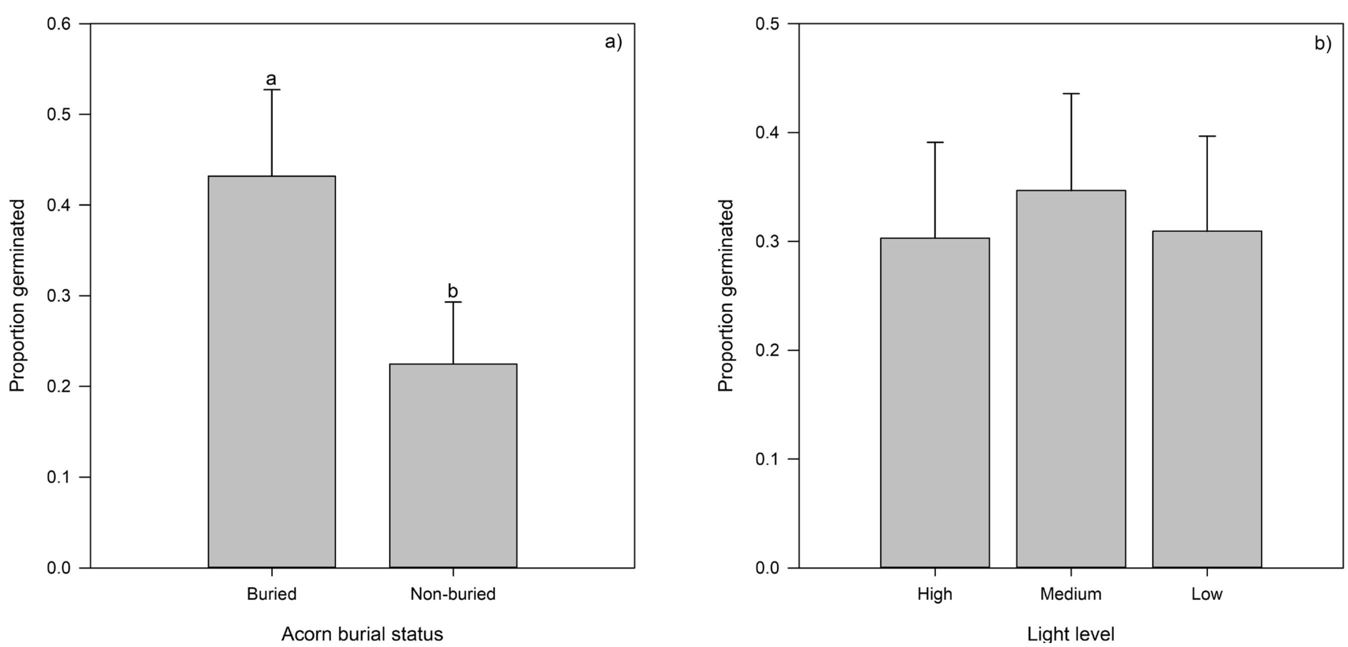

Figure 5—Average proportion of acorns that germinated by (a) burial status and (b) light level at Deer Ridge Conservation Area, Lewis County, MO, 2020–2021. Error bars represent standard error from the average. Different letters indicate significant differences according to pairwise comparisons.

DISCUSSION

Results indicated low acorn production and high acorn predation. Acorn removal was extremely rapid, with complete removals within 8 to 21 days after acorn placement in the open plots that allowed access by all mammals, and squirrel-mouse plots that allowed access by small mammals. Although we did not find any bottomland studies with this finding, some upland studies in China have reported instances where acorns deployed on the ground were rapidly removed within a few hours to a few days (Li and Zhang 2003, Wang and others 1999). In our study, low acorn production might have contributed to rapid removal rates within the open and squirrel-mouse experimental plots. Our results also suggest that small mammals, rather than deer, were probably the most important acorn predators. Other studies have reported that large animals like deer do not substantially contribute to acorn predation because mice, squirrels, and other small-sized animals compensate for their effect when they are excluded (Borchert and others 1989, Greenberg and Zarnoch 2018). Acorns removed by deer are consumed and have no further chance of germination, whereas acorns moved by squirrels and other small animals may be cached for later germination (Kellner and others 2014).

We found that acorn removal did not differ between buried and nonburied acorns. Gómez and others (2003) reported that burial did not increase acorn survival from predation. This probably occurred because acorns were consumed by several predators that could detect buried acorns with very high efficiency. Other studies have reported that burying acorns reduced acorn predation (Haas and Heske 2005, Kollmann and Schill 1996). However, the acorns were buried much deeper in those studies (burial depth ranged from 2 to 8 cm) than in our study, where acorns were buried halfway, suggesting that caching by animals may protect acorns from further predation.

Our results indicated that acorn burial improved germination. Although Barnett (1977) reported that burial of white oak (*Quercus alba*) acorns had no effect on germination, other studies have found that acorn burial increased germination (Guo and others 2009, Haas and Heske 2005, Kollmann and Schill 1996, Nilsson and others 1996). Buried acorns are exposed to a moist soil environment that prevents seed desiccation and may reduce damage from drying, intense sunlight, low temperature, or fungi (Kollmann and Schill 1996, Nilsson and others 1996).

Germination of acorns was unaffected by light availability. Acorn germination is not constrained by light availability because the seed is relatively large and supplies most of the carbohydrates for growth until seed reserves are depleted (Dey 2002). According to Moorhead and others (1991) acorns can germinate under a closed canopy. Since the midstory release treatments used in our study did not increase germination, they should not be expected to increase the establishment of new seedlings. However, after germination, the midstory release could be used to enhance development of the seedlings as reported in other bottomland studies (Lockhart and others 2000).

CONCLUSIONS

Our results suggested that predators have an important influence on the proportion of acorns that eventually have a chance of germination. We found that removal of acorns was extremely rapid if small mammals had access to acorns. The low acorn production in our stands might have contributed to rapid acorn removal rates observed due to a lack of acorn availability in the area. Our results also suggested that burial provided the necessary microclimate that enhanced germination of remnant acorns compared to surface acorns that might be exposed to damage by drying, intense sunlight, low temperature, or fungi. We found that germination occurred irrespective of light availability. Our results suggest the importance of mast years, in which high levels of acorn production may be necessary to satiate small mammal predation, for natural regeneration of pin oak in bottomland forests. While midstory release treatments may not be expected to increase germination rates, the greater light availability provided through well-timed release may improve early seedling survival and growth following germination. Alternatively, due to the low acorn production and high rates of acorn predation in our study sites, artificial regeneration might be useful for establishing seedlings rather than relying on natural regeneration.

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