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Original Article

Red Oak Acorn Yields in Green-Tree Reservoirs and Nonimpounded Forests in Mississippi

JACOB N. STRAUB,[1,2] *Department of Wildlife, Fisheries, and Aquaculture, Box 9690, Mississippi State, MS 39762, USA*
ALAN G. LEACH, *Department of Wildlife, Fisheries, and Aquaculture, Box 9690, Mississippi State, MS 39762, USA*
RICHARD M. KAMINSKI,[3] *Department of Wildlife, Fisheries, and Aquaculture, Box 9690, Mississippi State, MS 39762, USA*
ANDREW W. EZELL, *Department of Forestry, Mississippi State University, Box 9681, Mississippi State, MS 39762, USA*
THEODOR D. LEININGER, *U.S. Forest Service, Center for Bottomland Hardwoods Research, Box 227, Stoneville, MS 38776-0227, USA*

ABSTRACT Although bottomland hardwood forests in southeastern United States are among the most productive ecosystems in North America, indigenous flora, wildlife, and system dynamics have been altered and affected by natural and anthropogenic effects. Historic spatio-temporal dynamic flooding in hardwood bottomlands caused managers to create green-tree reservoirs (GTR; i.e., impounded forested tracts) to enhance predictability of seasonal inundation chiefly for waterfowl habitat and hunting. Bottomland red oaks (*Quercus* spp.) are valuable trees for wildlife that consume acorns they produce. There was inconsistent evidence in the scientific literature, so we tested the null hypotheses of no differences in annual yield, percentage of sound acorns, and proportion of 'high-yielding' red oaks in GTRs and nonimpounded naturally flooded forests (NFF) in western and east-central Mississippi, USA, during autumn–winter, 2008–2012. Mean annual yields of sound acorns from GTRs and NFFs at Noxubee National Wildlife Refuge and Delta National Forest had overlapping confidence intervals in all years of our study; however, percentages of sound acorns were greater in GTRs in 3 of 8 site-year comparisons. We also found conflicting results between study sites regarding which flood regime had the greatest proportion of high-yielding oaks. Our results demonstrate differences in total acorn yield by red oaks may be neither statistically nor biologically different between GTRs and NFFs in Mississippi; however, the proportion of sound acorns may be greater in GTRs relative to NFFs in some years. Future research may determine whether these phenomena are related to surviving trees producing increased seed propagules in response to long-term flooding stress in GTRs or residual trees possessing traits for increased acorn production in some years. Nonetheless, deleterious effects from persistent or prolonged within- and among-year flooding of GTRs are well-documented, suggesting managers should consider these possible consequences in sustaining and regenerating lowland red oak populations.

KEY WORDS acorn, forested wetland, green-tree reservoir, Mississippi, *Quercus* spp, red oak, waterfowl.

Bottomland hardwood forests in southeastern United States are among the most ecologically diverse and productive palustrine wetlands in North America (Mitsch and Gosselink 2007). Primary production in these systems is influenced by fertile alluvial soils, hydrology, nutrient inputs, and a subtropical climate (Reinecke et al. 1989, Faulkner et al. 2011, Barnett et al. 2016). Additionally, intrinsic ecological processes are driven largely by seasonal precipitation and runoff, riverine flooding, decomposition of detritus, subtropical air and water temperatures, and other climate-related events including ice, tropical storms, and hurricanes (Fredrickson 2005*a*).

In the 20th century, availability of mechanical earth- and vegetation-moving equipment facilitated extensive clearing of hardwood bottomlands and associated wetland alterations in the Lower Mississippi Alluvial Valley (MAV), which hastened conversion of forests to croplands (King et al. 2006). Only approximately 2.8 million ha of seasonally flooded bottomland hardwood forests remain in the MAV (Twedt and Loesch 1999). Despite losses of bottomland hardwood forests, remnant and restored tracts are important

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[1]*E-mail: straub.47@gmail.com*
[2]*Current address: 4033 Lake Road North, Brockport, NY, USA*
[3]*Current address: James C. Kennedy Waterfowl and Wetlands Conservation Center, Belle W. Baruch Institute of Coastal Ecology and Forest Science, Clemson University, P.O. Box 596, Georgetown, SC 29442, USA*

for continental wildlife populations, particularly waterfowl and other migratory and resident birds (Heitmeyer et al. 2005).

Efforts to suppress cropland and urban flooding (e.g., levees, reservoirs, dredging, channelizing) have resulted in decreased dynamic seasonal inundation of lowland forests in the MAV (Reinecke et al. 1988). To manage frequency, timing, and duration of inundation in lowland forests, land managers began developing green-tree reservoirs (GTRs) during the 1930s in the MAV to cache water for irrigating rice and other crops and provide consistent flooding of hardwood bottomlands to attract wintering waterfowl for hunting (Fredrickson 2005*b*). A GTR is a forested wetland bounded by a levee(s) and usually equipped with a water control structure(s), enabling flooding of, and retaining water in, impounded areas (Reinecke et al. 1989, Fredrickson 2005*b*). Flooding is accomplished by pumping ground water, gravity flowing water from reservoirs or other sources, or overbank flooding of riverine wetlands. At least 179 GTRs have been developed in the MAV; they are distributed over private, federal, and state lands (Wigley and Filer 1989).

Fredrickson (2005*b*) reported that annual, deep flooding of GTRs (e.g., >60 cm), often to facilitate use of outboard-motor propelled boats to transport hunters, and a frequent inability to drain GTRs as a result of beaver (*Castor canadensis*) damming raised ecological and wildlife management concerns about GTRs. These concerns, pertinent to southern and northern latitude GTRs, focused on basal swelling of trees, crown dieback, loss of tree vigor, tree wind-throw and mortality, changes in tree species composition toward water-tolerant species that do not provide acorn forage for waterfowl (e.g., overcup oaks [*Quercus lyrata*], red maple [*Acer rubrum*], green ash [*Fraxinus pennsylvanica*]), reduced regeneration and seedling survival, decreased density of desirable understory species, increased siltation, increased beaver herbivory, decreased waterfowl use, and decreased production of red oak (*Quercus* spp. [Section Lobatae]) acorns (Wigley and Filer 1989, King 1995, Deller and Baldassarre 1998, Fredrickson 2005*b*).

Previous studies of acorn yield in GTRs, nonimpounded naturally flooded forests (NFFs; Wehrle et al. 1995), and unflooded lowland forests have been equivocal. For example, from 2 studies in Missouri, USA, Merz and Brakhage (1964) reported pin oak (*Q. palustris*) acorn production did not differ between NFFs and artificially flooded bottomland areas. McQuilkin and Musbach (1977) reported no difference in production of pin oak acorns in GTRs and adjacent unflooded stands. In contrast, Francis (1983) reported greater Nuttall oak (*Q. texana*) acorn production in nonflooded than in GTR sites in the Mississippi, USA, MAV; whereas, Young (1990), working in the Mississippi Interior Flatwoods region (MIF; Wehrle et al. 1995), reported greater yields of cherrybark oak (*Q. pagoda*) acorns in GTRs than in a nonimpounded control site. Additionally, Guttery (2006), working in the Arkansas, USA, MAV, reported abundant yields of acorns by willow oak (*Q. phellos*) in both years of his study (2004 and 2005) in a GTR constructed in the 1940s, but did not have comparative data from a nonimpounded forested tract. Some studies also reported that the percentage of sound acorns produced in GTRs was greater because autumn–winter inundation kills weevils and other insect predators of acorns (McQuilkin and Musbach 1977). Indeed, these variabilities among studies motivated our study to investigate potential differences in yields of red oak acorns between GTRs and NFFs in the Mississippi MAV and MIF.

Straub et al. (2016) reported acorn yield estimates of red oaks across 5 states and years (2008–2013) in the MAV and MIF. To our knowledge, no previous study has compared several seed production variables and masting characteristics of red oak trees between NFFs and GTRs in the same watershed over successive years in 2 geographical regions of Mississippi or elsewhere. There were inconsistent findings of red oak acorn yields between NFFs and GTRs; therefore, we tested the null hypotheses of no differences in number and percentage of sound acorns produced by red oaks between NFFs and GTRs in the Mississippi MAV and MIF. Additionally, we compared masting propensity, sound-acorn yield distributions, and yield classifications among red oaks in GTRs and adjacent or near NFFs.

STUDY AREA

Our 2 study areas each contained mature bottomland hardwood forests and ≥1 GTR. We split our sampling effort between our 2 sites in western and east-central Mississippi. Within sites, we sampled one GTR and one nearby mature naturally flooded bottomland hardwood stand. Delta National Forest (hereafter, Delta) was managed by the U.S. Department of Agriculture Forest Service in the east-central MAV and located 23 km southeast of Rolling Fork, Mississippi (32° N, 90° W). Delta contained >24,000 ha of bottomland hardwood forests interspersed with palustrine wetlands and was the only national forest consisting exclusively of bottomland hardwoods in the United States (Lowney and Hill 1989). There were approximately 2,000 ha of bottomland hardwood forest managed as GTRs in Delta, which generally were flooded annually from mid-November to early February (Wehrle et al. 1995). We studied in 1 (315 ha) of the 3 units of the Sunflower GTR (540 ha), a bottomland hardwood stand with an estimated age of 80–85 years during our study (2008-2011). The units were flooded by pumping water from the adjacent Little Sunflower River via a pipe. All units of the GTR were flooded annually during winter from 1960 through 1990, after which each unit was flooded on a 3-year rotation. Since 2010, the GTR had not been actively managed because of a faulty water-control structure; however, precipitation and overbank flooding from the Little Sunflower River inundated the GTR during all years of our study. We also studied a NFF tract in Delta located approximately 17 km south of the Sunflower GTR with an estimated age of 90 years. The NFF tract was inundated only in winter 2009–2010 for approximately 8 days from overbank flooding of the Little Sunflower River and associated tributaries.

We obtained temperature and precipitation data for Rolling Fork, Mississippi. The 1981–2010 average annual temperature and annual precipitation for Rolling Fork, Mississippi, was 18.0° C and 139.4 cm, respectively. Fifty-seven percent of annual precipitation historically occurs during December and May. During our study, average annual temperatures were within 1.0° C of long-term averages except in 2008 when the average annual temperature was 3.1° C below long-term average. Annual precipitation totals were above the long-term average in 2008 (196.0 cm) and 2009 (171.8 cm), but below in 2010 (82.7 cm) and 2011 (122.2 cm).

We also sampled GTRs and NFFs in the Sam D. Hamilton Noxubee National Wildlife Refuge (hereafter, Noxubee), located in the MIF in east-central Mississippi, 35 km northwest of of Louisville, Mississippi (33° N, 89° W). Major hydrological features of Noxubee included the Noxubee River, its tributaries, and Bluff and Loakfoma Lakes. Noxubee was approximately 19,400 ha and contained approximately 18,000 ha of bottomland hardwood forest and upland forest with 4 GTRs. The GTRs dated from the 1950s and generally were flooded annually from mid-late November to mid-February. We conducted our study in GTR 1, which was constructed in 1955. This GTR held 162 ha of water and was flooded by gravity-flowing water from Bluff Lake, a 485-ha reservoir contiguous with, and west of, GTR 1. We also studied a NFF tract in Noxubee located approximately 3 km northwest of GTR 1. The NFF tract was never completely inundated during our study; whereas, GTR 1 was flooded all winters of our study. The estimated stand ages of our sites were approximately 90 years, based on red oak age data presented by Young et al. (1995).

We obtained temperature and precipitation data for Louisville, Mississippi. The 1981–2010 average annual temperature and annual precipitation for Louisville, Mississippi was 16.8° C and 146.4 cm, respectively. Most (55% of total) precipitation occurs between during December and May. During our 4 years of study, average annual temperatures were always within 1.0° C of long-term averages. Annual precipitation totals were above the long-term average in 2008 (150.6.0 cm) and 2009 (203.6 cm), but below in 2011 (139.4 cm; annual precipitation data from 2010 were not complete).

METHODS

Survey Design, and Field and Laboratory Methods

We collected data over 4 consecutive years from October 2008–2011 through March 2009–2012. At each study area, we selected a NFF stand to pair with aforementioned GTRs. Within each study area and flood regime (NFF or GTR), we randomly selected sites for 20 (plus 10 alternates) 0.2-ha circular plots using a spatial distance algorithm (GRTS package, https://rdrr.io/rforge/GRTS/; Stevens and Olsen 2004; R Development Core Team version 2.13.2 2016). The GRTS algorithm ensured random distribution of plots within each NFF and GTR (Straub et al. 2016).

Within each plot, we identified and inventoried all red oaks ≥25 cm in diameter breast height (DBH; 1.37 m above ground level), because trees of this DBH typically produce acorns (Dey 1995). We used a standard diameter tape to measure DBH to the nearest 0.1 cm. We then randomly selected one red oak tree of the specified DBH within the plot as our sample tree, regardless of species (see statistical analyses for explanation). If a plot did not contain any red oaks ≥25 cm DBH, we moved to the nearest alternate plot and repeated the sampling methodology. We sampled selected trees throughout the study, except if trees died or fell. In these instances, we replaced the lost tree with the nearest red oak of ≥25 cm DBH within that or an alternate plot if a red oak was absent in the former plot.

To collect acorns, we randomly chose a cardinal direction and placed a 1-m^2 sampling frame halfway between the bole and canopy drip line of each selected red oak (Guttery 2006, Straub et al. 2016). We derived crown dimensions by measuring the radii of each sampled tree from the outer edge of bole to the canopy drip line in each cardinal direction. We fabricated frames from 2.5 × 10-cm treated lumber and mounted atop 4 1.5-m lengths of electrical conduit, or we made frames of the same dimensions from 1.3-cm diameter polyvinyl chloride (PVC) pipe. We elevated traps approximately 1.37 m above ground to avoid flooding traps and acorn-pilfering by seed predators. To the wooden or PVC frames, we attached a funnel-shaped piece of fiberglass window screening that extended downward 45 cm. We pushed the legs of the trap 30–40 cm into the ground, giving the trap stability yet keeping it elevated above flood events. We collected acorns from all traps monthly from October through February.

We stored all acorns at −10° C in freezers at Mississippi State University. Subsequently, we thawed and halved acorns using shears and classified them as either sound or unsound based on integrity of the embryo. Sound acorns included those with intact embryos or those with <50% damaged embryo; all others we classified as not sound (Straub et al. 2016). We calculated the proportion of sound acorns as the number of sound acorns divided by total acorns collected. We present estimates as the autumn–winter cumulative mean number of sound acorns produced per m^2 of red oak tree crown in GTRs and NFFs for each site.

Statistical Analyses

The annual proportion of sound acorns was not related to total annual number of acorns ($r^2 = 0.002$. $P = 0.98$); therefore, we treated each as separate dependent variables. We used 2 separate generalized linear mixed-model sets in Program R version 2.13.2 (R Development Core Team version 2.13.2 2016) to model relationships between dependent and explanatory variables. When the number of total sound acorns was the dependent variable, we used a negative binomial model error structure with a log-link function. When the proportion of sound acorns was the dependent variable, we used logistic regression (binomial error structure) with a logit-link function (Zuur et al. 2009).

We used different model structures because of the nature of the response variables (i.e., counts [negative binomial] vs. proportions [binomial]). In both model sets, we accounted for individual variation of trees sampled across years by specifying each tree's unique identification number as a random variable. We calculated average R^2 (i.e., proportion of variance explained by fixed factors) with 95% confidence intervals (CIs) from our mixed-effects models (Nakagawa and Schielzeth 2013).

We included the same covariates in candidate models; these were designated fixed factors, including study area (SITE), flooding regime (REGIME; i.e., NFF or GTR), and year (YR; i.e., 2008, 2009, 2010, or 2011), plus the continuous variables of individual tree DBH and DBH^2. We included the latter quadratic term because acorn yield can be nonlinear relative to tree size (Greenberg and Parresol 2002, Leach 2011). We included a 3-way interaction of SITE × REGIME × YR for all 3 dependent variables to evaluate combined effects of fixed effects. We did not include red oak species as a fixed factor because of the unequal distribution of species between sites and flood regimes (e.g., all data from Delta were from Nuttall oaks except one willow oak [*Q. phellos*] tree); thus, we generalized to red oak acorns. Additionally, treating species as a random offset variable did not improve the fit of our models. Moreover, true metabolizable energy derived by mallards (*Anas platyrhynchos*) and wood ducks (*Aix sponsa*) foraging for red oak acorns is similar among red oak species (2.67–2.76 kcal/g [dry mass]; Kaminski et al. 2003).

In all candidate models, we used a stepwise backward selection procedure, which included starting with the global model and removing the least significant variable until model fit ceased improvement (Juliano 2001). We based assessments of model fit on Akaike's Information Criteria corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). We removed a variable if a model had a lesser AIC_c value than the next higher order model (Zuur et al. 2009). We considered the highest-order interactions initially and then main effects, ensuring main effects were retained if interactions were competitive models. We used the antilog of transformed parameter estimates (β) with 95% confidence intervals to back-transform them to their original scale (Guthery 2008).

Although our analyses combined red oak species, we tested for differences in mean yields of acorns across years of study among cherrybark, willow, and water (*Q. nigra*) oaks in GTR and NFF flood regimes at Noxubee, because these 3 species existed and were sampled there. However, only data from Nuttall oak were used in analyses of data from Delta. We natural-log-transformed acorn yield data and used a factorial analysis of variance to test main effects and interaction of acorn species and flood regime for Noxubee data.

For each tree in year *t*, we calculated a standardized deviate of acorn yield (hereafter, mast parameter) as the mean number of sound acorns in year t – the 4-year mean number of sound acorns from all trees/standard deviation (SD) across all trees and years (Lamontagne and Boutin 2007, 2009). We then identified trees with a mast parameter greater than the absolute value of the least standard deviate, thereby identifying individual 'high-yielding' trees. Mast parameters were calculated separately for each flood regime. To compare relative yields of acorns within study sites, we used criteria modified from Healy et al. (1999), thereby classifying each tree's cumulative seed yield during our study as excellent (≥mean), moderate (<mean but >60% of mean), or poor (≤60% of mean). Specifically, we summed the cumulative number of sound acorns collected from each tree and divided this number by the number of years trees were sampled. We excluded 2 of 41 trees at Noxubee and 4 of 41 trees at Delta, because <3 years of data were available from them. We then calculated a mean number of sound acorns/year for each site separately and used this value to classify trees as excellent, moderate, or poor producers. We used a chi-square goodness-of-fit test for both sites and flooding regime ($n = 4$ tests) to test if observed categorical yield distributions differed from theoretical ones (R Development Core Team version 2.13.2 2016). We assumed theoretical yields by site and flooding regime combinations would be equally distributed among the 3 yield categories. We designated $\alpha = 0.05$.

RESULTS

Sampled red oaks did not differ in DBH between GTRs and NFFs at Delta ($t_{1,36} = 0.84$, $P = 0.41$) and Noxubee ($t_{1,32} = 0.63$, $P = 0.53$; Table 1). We removed the lone willow oak at Delta prior to analysis; therefore, Nuttall oak comprised all sampled trees in Delta NFF ($n = 19$ trees) and GTR ($n = 20$ trees). Willow oaks ($n = 12$ [60%]) dominated in the Noxubee GTR, followed by cherrybark oak ($n = 5$ [25%]) and water oak ($n = 3$ [15%]). In the Noxubee NFF, cherrybark oaks were most common ($n = 9$ [45%]), followed by willow ($n = 8$ [40%]) and water oaks ($n = 3$ [15%]).

The global model best explained variation in numbers of sound acorns; it included the 3-way interaction of REGIME × SITE × YR and additive effects of DBH and DBH^2 (Table 2). This model was 8.1 AIC_c units lower than the next model and 192.5 units lower than the null model (i.e., intercept only). Marginal R^2 ($\bar{x} = 0.52$, 95% CI = 0.46–0.60)

Table 1. Average, minimum and maximum diameter at breast height (DBH; cm) for red oak species in green-tree reservoirs (GTR) and naturally flooded forests (NFF) at Delta National Forest (Delta) and Noxubee National Wildlife Refuge (Noxubee), Mississippi, USA, during 2008–2012.

Site	Species	Flood regime	DBH $\bar{x}$	SE	Min.	Max.	n[a]
Delta	Nuttall	GTR	64	2.7	26	112	79
		NFF	58	2.8	26	111	73
Noxubee	Willow	GTR	69.7	3.5	28	109	47
		NFF	54.2	2.4	36	72	28
	Cherrybark	GTR	89.8	5.6	67	131	19
		NFF	80.1	3.6	59	133	35
	Water	GTR	34.7	1.8	30	43	12
		NFF	47.2	4.5	30	66	12
	All red oaks	GTR	69.1	3.1	28	131	78
		NFF	65.2	2.6	30	133	75

[a] Total trees sampled among all years.

Table 2. Model structure, number of parameters (*K*), Akaike Information Criterion corrected for small sample size (AIC_c) and amount of variation explained by fixed (R^2_{marg}) effects for variation in total sound red oak acorn yield and proportion of sound-acorn yield in bottomland hardwood forests of Noxubee National Wildlife Refuge and Delta National Forest, Mississippi, USA, during autumn–winter 2008–2012.

Response variable	Family	Link	Optimal model structure[a]	*K*	AIC_c	$R^2_{marg.}$
Sound acorns	Negative binomial	log	REGIME × SITE × YR + DBH + DBH^2	20	2,389.5	0.519
Proportion sound	Binomial	logit	REGIME × SITE × YR + DBH[b]	18	2,332.9	0.275

[a] Explanatory variables include flooding regime (REGIME), study site (SITE), year (YR), tree diameter at breast height (DBH), and nonlinear quadratic term for DBH (DBH^2).
[b] Competitive model of REGIME × SITE × YR was 0.7 AIC_c units higher.

indicated fixed variables accounted for approximately half of explained variation in sound-acorn yield.

Mean yields of sound red oak acorns had overlapping 95% CIs between GTRs and NFFs at both sites and among years (Fig. 1). Back-transformed parameter estimates from the top-ranked model indicated sound-acorn yield was greatest in the GTR at Noxubee in 2009–2010 ($\bar{x} = 177.7$ acorns/m^2, 95% CI = 94.7–333.2); this yield was 3.4 times greater than for the NFF in this year ($\bar{x} = 51.9$ acorns/m^2, 95% CI = 27.7–97.2; Fig. 1). Sound-acorn yield was least in the GTR at Delta in 2011–2012 ($\bar{x} = 0.6$ acorns/m^2, 95% CI = 0.2–1.4); yield also was low that year in the paired NFF ($\bar{x} = 12.0$ acorns/m^2, 95% CI = 5.8 – 24.8). Holding all variables constant, yield of sound acorns related positively to DBH ($\hat{\beta} = 0.608$, 95% CI = 0.339–0.877) up to approximately 85 cm, followed by a slight inverse relationship beyond this threshold ($\hat{\beta} = -0.333$, 95% CI = −0.528 to −0.139; Fig. 2).

Species-specific yield of sound acorns varied by flood regime at Noxubee ($F_{2,138} = 3.96$, $P = 0.02$). Across all years, confidence intervals of back-transformed mean yield of sound cherrybark oak ($\bar{x} = 18.4$ acorns/m^2, 95% CI = 12.2–27.6), willow oak ($\bar{x} = 12.7$ acorns/m^2, 95% CI = 8.0–20.0), and water oak ($\bar{x} = 10.3$ acorns/m^2, 95% CI = 5.1–20.7) overlapped for the Noxubee NFF. For the Noxubee GTR, confidence limits for mean yields of cherrybark oak ($\bar{x} = 28.0$ acorns/m^2, 95% CI = 16.0–48.7) and willow oak ($\bar{x} = 40.3$ acorns/m^2, 95% CI = 28.4–57.3) overlapped, but together they were nearly 4 times that of water oak ($\bar{x} = 6.8$ acorns/m^2, 95% CI = 3.4–13.6), which resulted in the significant effect of flood regime.

The most supportive model explaining variation in proportion of sound acorns was the interaction of REGIME × SITE × YR and an additive linear effect of DBH (Table 2). The top-ranked model was competitive with another model (i.e., 0.7 AIC_c of best model), but the top-ranked model was 1,653.6 AIC_c units lower than the null model. The second-most-supportive model lacked the additive linear effect of DBH. The 95% CI of $\hat{\beta}$ for DBH overlapped zero and DBH was absent from a competitive model, so we did not interpret it as having a significant effect on the proportion of sound acorns collected from red oaks. Marginal R^2 (0.275) indicated fixed variables accounted for <30% of the explained variation in proportion of sound acorns. Fixed effects from the best model indicated proportions of sound acorns were greater in GTRs than NFFs in 3 of 8 site–year comparisons (Noxubee 2008–2009, Noxubee 2009–2010, and Delta 2010–2011; Fig. 3); NFFs never had proportions of sound acorns greater than GTRs.

Across sites, flooding regimes, and years, 45 (15%) of 307 individual tree–year combinations were categorized as ‘high-yielding’ trees, yielding from 134 to 719 acorns/m^2/year. Most ($n = 40$) ‘high yielding’ tree–year combinations were at Noxubee; of these, 63% percent ($n = 25$) were located in the GTR. At Delta, 4 of 5 ‘high yielding’ trees were in the NFF. Willow, cherrybark, and water oaks comprised 60%, 25%, and 15%, respectively, of ‘high yielding’ trees at Noxubee. Zero-detected acorn yield (either sound or unsound) was more common at Delta ($n = 22$ [14%] trees) than Noxubee ($n = 2$ [1%] trees). At Delta, mast failures by individual red oaks were more common in the GTR ($n = 15$

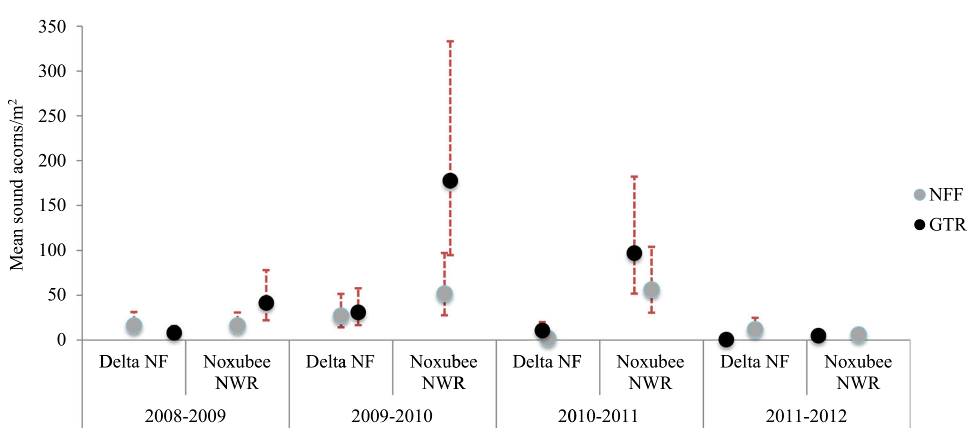

Figure 1. Mean number of sound acorns/m^2 crown with 95% confidence intervals collected from red oak trees in green-tree reservoirs (GTRs) and naturally flooded forests (NFFs) at Delta National Forest and Noxubee National Wildlife Refuge, Mississippi, USA, 2008–2012.

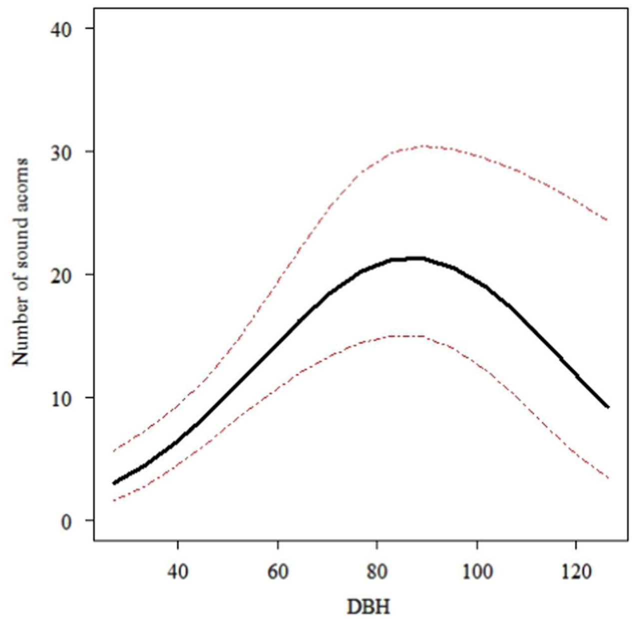

Figure 2. Relationship between diameter at breast height (DBH) and number of sound acorns/m^2 crown collected from red oaks trees at Delta National Forest and Noxubee National Wildlife Refuge, Mississippi, USA, from 2008 to 2012. Black line represents $\hat{\beta}$ from DBH and DBH^2 from best model while red dashed line is 95% confidence interval from these parameters.

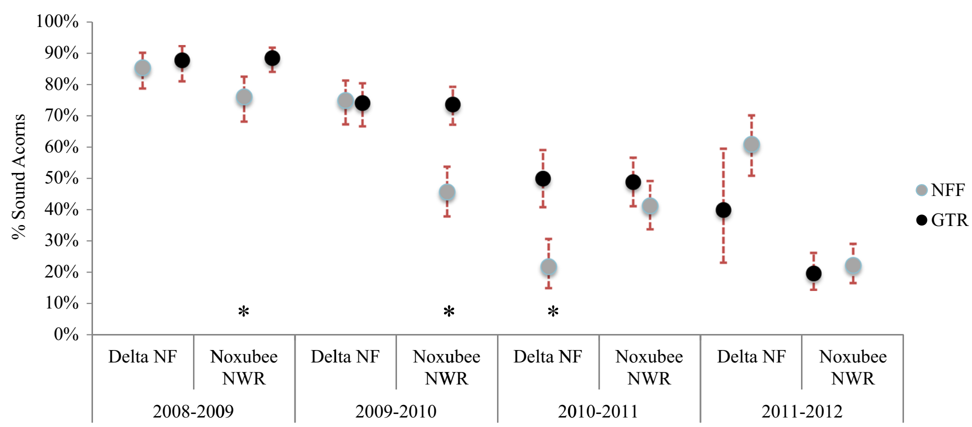

Figure 3. Mean proportion of all acorns collected that were classified as sound with 95% confidence intervals from red oak trees in green-tree reservoirs (GTRs) and naturally flooded forests (NFFs) at Delta National Forest and Noxubee National Wildlife Refuge, Mississippi, USA, from 2008 to 2012. Asterisks indicate where significant differences occurred.

[19%] trees) than the NFF ($n = 7$ [9%] trees). At Noxubee, the only 2 instances (3%) of mast failure were in the NFF.

Average annual sound-acorn yield at Noxubee was >4 times greater than at Delta (Table 3). Yield classifications were distributed evenly among excellent, moderate, and poor producing trees at Delta in the NFF ($P = 0.11$) and at Noxubee in both the GTR ($P = 0.45$) and NFF ($P = 0.08$; Table 3). However, there were more poor producers and less

Table 3. Average annual yield (acorns/m^2 crown) and observed yield categories (expected yield distribution in parentheses) for red oaks in green-tree reservoirs (GTRs) and naturally flooded forests (NFFs) of bottomland hardwood forests in Noxubee National Wildlife Refuge and Delta National Forest, Mississippi, USA, autumn–winter 2008–2012.

			Yield category[a]				
Site	Mean acorn yield (seeds/m^2 crown)	Flood regime	Excellent	Moderate	Poor	χ^2	*P*
Delta	25.1	GTR	7 (6.3)	1 (6.3)	11 (6.3)	8.00	0.02
		NFF	7 (6.0)	2 (6.0)	9 (6.0)	4.33	0.12
Noxubee	104.4	GTR	8 (6.6)	8 (6.6)	4 (6.6)	1.60	0.45
		NFF	7 (6.3)	2 (6.3)	10 (6.3)	5.16	0.08

[a] Each tree's cumulative (i.e., length of study) seed yield classified as excellent (≥mean), moderate (<mean but >60% of mean) or poor (≤60% of mean).

moderate producers than expected in the GTR at Delta ($P = 0.02$; Table 3).

DISCUSSION

We found equivocal evidence regarding differences in yields of sound red oak acorns between GTRs and NFFs at our study sites, and thus could not reject the null hypothesis of no difference in red oak acorn yields between flooding regimes. Specifically, red oak trees in the GTR at Noxubee produced almost 2 times more sound acorns over the years of our study compared with trees in the NFF at Noxubee (5,928 vs. 3,189 acorns); whereas, red oak trees at Delta in the NFF produced 1.3 times more sound acorns than trees in the GTR (1,546 vs. 1,189 acorns). We found some evidence that proportions of sound acorns were greater in GTRs than NFFs, although this only occurred in 2 years at Noxubee and 1 year at Delta. However, the number of trees that failed to mast in any year were more common in GTRs than NFFs at both sites. High-yielding red oak trees were more common in the GTR at Noxubee than the NFF, but the opposite phenomenon occurred at Delta. Thus, we conclude that long-term GTR flood regimes at Noxubee and Delta did not produce consistent detectable and detrimental effects on yields and proportions of sound red oak acorns from trees sampled in our study.

An explanation for failing to find a consistent difference in yield of sound red oak acorns between GTRs and NFFs might pertain to the water-level management by local managers over the past decades. For instance, the Sunflower GTR at DNF has been flooded on a rotational basis from approximately 1990 through 2010, but before this time period it was flooded annually. Since 2010, consistent flooding of this GTR has been irregular because of faulty infrastructure. In contrast, the GTR at Noxubee has apparently been flooded annually for >4 decades leading up to our study; however, the exact timing, depth, and duration of water on the trees were unknown. Given variation in hydrologic regimes and edaphic and other environmental variables linked to hydrology, observed among- and within-year differences in acorn yield are not surprising. Having more information on the true water regimes than merely testing for differences in acorn yield might increase insight into how these bottomland hardwood systems function.

Between sites, red oak trees at Noxubee produced more acorns and did so more consistently than trees at Delta. Our study forests at Noxubee and Delta were similar in that they both supported large contiguous stands of bottomland hardwood trees with red oaks of similar ages and GTR management histories and generally annual flooding regimes. However, these sites have key physical and environmental differences that might explain why we observed differences in masting between sites. Delta is within the MAV, a large floodplain of the Mississippi River, while Noxubee is located within the MIF. Geomorphology, sediment and nutrient transport, soil fertility, and plant species composition differ between a 'major' bottom such as Delta and a 'minor' bottom such as Noxubee (Hodges 1997). Although Hodges (1997) considered major bottoms more productive than minor ones, acorn yield in our study was greater on a yearly basis in the minor Noxubee bottom than Delta, regardless of flooding regime. An obvious difference between sites and potential explanation is the species composition of red oaks. At Noxubee, willow, cherrybark, and water oak were common, whereas we sampled only Nuttall oak at Delta and deleted the single willow oak in our sample. Cherrybark, water, and willow oak in particular are known for shorter masting intervals and producing some of the greatest seed yields among oaks in the red oak genus (Johnson et al. 2009). By contrast, Nuttall oaks have a longer masting interval and produce fewer seeds/tree than willow, water, and cherrybark oaks (Straub et al. 2016). Perhaps differences between sites are less a function of local environmental conditions than species-specific traits, which is consistent with our finding that sound-acorn yields by cherrybark and willow oaks in the Noxubee GTR nearly doubled those for water oak. During the 1980s, Young (1990) also observed greater cherrybark oak acorn production in a GTR than a nonimpounded NFF at Noxubee.

At Noxubee, yearly average yield of red oak acorns was similar between the GTR and NFF; however, there were more excellent and moderate producers of acorns than expected in the GTR, proportionally more sound acorns in the GTR in 2 years (2008–2009 and 2009–2010), and almost 2 times more sound acorns collected in the GTR than the NFF cumulatively over 4 years. Differences between Noxubee sites in acorn yield may not be related to tree species or size because these were similar between NFFs and GTRs.

We suggest hypotheses for the increased yield of red oaks in the Noxubee GTR. First, because the Noxubee GTR has been flooded almost annually since the 1960s, we cannot discount the role of increased soil moisture and nutrient deposition on trees in the GTR (Gray and Kaminski 2005). By contrast, very rarely are red oaks outside of the GTRs at Noxubee inundated for more than a few days during the nongrowing season and soil moisture and sediment deposition are lower than in the GTR (Hatten et al. 2014). However, studies have demonstrated deleterious effects of long-term flooding in GTRs on tree health and mortality (Wigley and Filer 1989, Fredrickson 2005*b*). Thus, a second possible explanation for the superior acorn yield in the Noxubee GTR may be that only the most resilient trees have survived long-term annual flooding in the GTR, and these were the trees that persisted and which we sampled. A third possible explanation is that trees in the GTR are responding to the stress of annual flooding as reflected by basal swelling of boles and trading-off growth with increased seed production (Knops et al. 2007, Sala et al. 2012). Some studies have shown growth of trees in GTRs was less than that outside of impounded areas (North et al. 1996, cf. Francis 1983). Indeed, some plants faced with stressors will opt for propagule production over growth, theoretically as a 'bet-hedging' strategy to promote fitness (Obeso 2002). Regardless of the mechanism, we observed a greater frequency of excellent and moderate acorn producers in the GTR at Noxubee compared with its NFF counterpart.

The duration of our study is at least one alternative explanation for why we encountered a greater GTR effect at Noxubee compared with Delta. During the 4 consecutive years that we sampled red oaks at the 2 sites, trees at Delta never experienced a 'boom' in seed yield. Acorn yield was low overall at Delta, so we failed to detect any meaningful differences in average annual seed yield between GTRs and NFFs. In fact, there were 22 trees from which we never collected an acorn within a year at Delta, whereas this only happened twice at Noxubee. McQuilkin and Musbach (1977) reported pin oaks in a bottomland hardwood forest in Missouri had peak production only in 3 of 14 years. Our study failed to record a peak seed-production year at Delta; perhaps, this phenomena resulted because Nuttall oaks have longer masting intervals than willow, water, and cherrybark oaks, which comprised the dominant species at Noxubee. Additionally, although our 2 study sites were latitudinally similar, they were nearly 200 km apart, and red oak acorn yield patterns were not synchronized among years of study at these 2 sites. Straub et al. (2016) found a similar asymmetry in red oak acorn yield patterns between Delta and Tensas River National Wildlife Refuge in Louisiana, USA, over a 4-year period. Tensas is approximately 50 km southwest of Delta. If there is spatial autocorrelation in acorn yield among populations of red oaks in Mississippi, it did not extend the distance between our study sites.

Although mean sound-acorn yield/m^2/year was similar between GTRs and NFFs at both sites, the cumulative number of sound acorns was greater in GTRs at both Noxubee and Delta even though sampling effort was identical in GTRs and NFFs. At Noxubee, we collected nearly twice (5,206 vs. 3,189) as many sound acorns in the GTR compared with the NFF. Considering our seed sampling traps were only 1 m^2 and composition of red oaks in the GTR was as low as 20%, extrapolation of our results to the entire Noxubee GTR (162 ha) over the 4-year period would equate to approximately 88.8 million sound acorns compared with 54.4 million acorns for a NFF of equivalent size. This finding might have implications for red oak regeneration and wildlife forage carrying capacity between the 2 flooding regimes and sites.

MANAGEMENT IMPLICATIONS

Despite not finding a reduction in red oak acorn yield in GTRs, managers should be concerned with other potential long-term consequences of GTR management on red oaks (Wigley and Filer 1989, Fredrickson 2005*b*). For example, others have found reduced seedling survival, regeneration, and basal area of red oaks associated with excessive winter flooding (North et al. 1996, Gray and Kaminski 2005). In addition to effects on red oaks, lesser aquatic invertebrate biomass and diversity in some GTRs than NFFs suggest that hydrological management of GTRs should be adapted to mimic regimes of NFFs in the same watershed and not flood GTRs to maximum capacity and depth each winter (Foth et al. 2014, Foth et al. 2018). Hagy and Kaminski (2012) observed greatest use and foraging activity by dabbling ducks (*Anas* spp.) in MAV emergent wetlands ranging in depths from 3 to 16 cm, suggesting shallowly flooded forested and other wetlands would facilitate foraging by ducks. Additionally, the Arkansas Game and Fish Commission (AGFC) has recognized and demonstrated negative effects of long-term annual deep flooding GTR forests and implemented management to vary timing, depth, and duration of flooding of GTRs to emulate flood dynamics of NFF (Anonymous 2017). We recommend monitoring and evaluation of this and other hydrological regimes that have been suggested to sustain bottomland hardwood forests in GTRs (Wehrle et al. 1995, Fredrickson 2005*a*; Foth et al. 2014, Foth et al. 2018).

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LITERATURE CITED

Anonymous. 2017. Conserving Arkansas's flooded timber legacy, Arkansas Game and Fish Commission. Little Rock, USA.

Barnett, A., J. Fargione, and M. P. Smith. 2016. Mapping trade-offs in ecosystem services from reforestation in the Mississippi Alluvial Valley. Bioscience 66:223–237.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Deller, A. S., and G. A. Baldassarre. 1998. Effects of flooding on the forest community in a greentree reservoir 18 years after flood cessation. Wetlands 18:90–99.

Dey, D. C. 1995. Acorn production in red oak. Ontario Ministry of Natural Resources, Sault Ste. Marie, Canada.

Faulkner, S., W. Barrow, B. Keeland, S. Walls, and D. Telesco. 2011. Effects of conservation practices on wetland ecosystem services in the Mississippi Alluvial Valley. Ecological Applications 21:S31–S48.

Foth, J., R. M. Kaminski, J. B. Davis, J. N. Straub, and T. D. Leininger. 2018. Aquatic invertebrate community composition, diversity, and biomass in non-impounded bottomland hardwood forests and greentree reservoirs. Journal of the Southeastern Association of Fish and Wildlife Agencies 5:125–135.

Foth, J., J. N. Straub, J. B. Davis, and R. M. Kaminski. 2014. Aquatic invertebrate abundance and biomass in Arkansas, Mississippi, and Missouri bottomland hardwood forests during winter. Journal of Fish and Wildlife Management 5:243–251.

Francis, J. K. 1983. Acorn production and tree growth of Nuttall oak in a green-tree reservoir. U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, USA.

Fredrickson, L. H. 2005*a*. Contemporary bottomland hardwood systems: structure, function, and hydrologic condition resulting from two

centuries of anthropogenic activities. Pages 19–35 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri-Columbia, Puxico, USA.
Fredrickson, L. H. 2005*b*. Greentree reservoir management: implications of historic practices and contemporary considerations to maintain habitat values. Pages 479–486 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri-Columbia, Puxico, USA.
Gray, M. J., and R. M. Kaminski. 2005. Effect of continuous versus periodic flooding on survival of oak seedlings in Mississippi greentree reservoirs. Pages 487–494 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri-Columbia, Puxico, USA.
Greenberg, C. H., and B. R. Parresol. 2002. Dynamics of acorn production by five species of southern Appalachian oaks. Pages 149–172 *in* W. J. McShea, and W. M. Healy, editors. Oak forest ecosystems. Johns Hopkins University Press, Baltimore, Maryland, USA.
Guthery, F. S. 2008. Primer on natural resource science. Texas A&M University Press, College Station, USA.
Guttery, M. R. 2006. Evaluation of artificial regeneration of oaks, willow oak acorn production, light conditions following midstory control, and the effects of long-term annual flooding on forest vegetative composition in an Arkansas greentree reservoir. Thesis, Mississippi State University, Mississippi State, USA.
Hagy, H., and R. M. Kaminski. 2012. Apparent seed use by ducks in moist-soil wetlands of the Mississippi Alluvial Valley. Journal of Wildlife Management 76:1053–1061.
Hatten, J., A. Ezell, R. M. Kaminski, B. Frey, J. Sloan, and J. N. Straub. 2014. Influences on soil and sediment carbon and nitrogen in red oak bottomlands in the Mississippi Alluvial Valley and Interior Flatwoods. Soil Science Society of America Journal 78:248–260.
Healy, W. M., A. M. Lewis, and E. F. Boose. 1999. Variation of red oak acorn production. Forest Ecology and Management 116:1–11.
Heitmeyer, M. E., R. J. Cooper, J. G. Dickson, and B. D. Leopold. 2005. Ecological relationships of warmblooded vertebrates in bottomland hardwood ecosystems. Pages 281–307 *in* L. H. Fredrickson, S. L. King, and R. M. Kaminski, editors. Ecology and management of bottomland hardwood systems: the state of our understanding. University of Missouri-Columbia, Puxico, USA.
Hodges, J. 1997. Development and ecology of bottomland hardwood sites. Forest Ecology and Management 90:117–125.
Johnson, P. S., S. R. Shifley, and R. Rogers. 2009. The ecology and silviculture of oaks. CABI International, New York, New York, USA.
Juliano, S. 2001. Nonlinear curve fitting: predation and functional response curves. Design and Analysis of Ecological Experiments 2:178–196.
Kaminski, R. M., J. B. Davis, H. W. Essig, P. D. Gerard, and K. J. Reinecke. 2003. True metabolizable energy for wood ducks from acorns compared to other waterfowl foods. Journal of Wildlife Management 67:542–550.
King, S. 1995. Effects of flooding regimes on two impounded bottomland hardwood stands. Wetlands 15:272–284.
King, S. L., D. J. Twedt, and R. R. Wilson. 2006. The role of the Wetland Reserve Program in conservation efforts in the Mississippi River Alluvial Valley. Wildlife Society Bulletin 34:914–920.
Knops, J. M., W. D. Koenig, and W. J. Carmen. 2007. Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. Proceedings of the National Academy of Sciences 104(43):16982–16985.
Lamontagne, J. M., and S. Boutin. 2007. Local-scale synchrony and variability in mast seed production patterns of *Picea glauca*. Journal of Ecology 95:991–1000.
Lamontagne, J. M., and S. Boutin. 2009. Quantitative methods for defining mast-seeding years across species and studies. Journal of Vegetation Science 20:745–753.
Leach, A. G. 2011. Red oak acorn production, mass, and gross energy dynamics in the Mississippi Alluvial Valley. Thesis, Mississippi State University, Mississippi State, USA.
Lowney, M. S., and E. P. Hill. 1989. Wood duck nest sites in bottomland hardwood forests of Mississippi. Journal of Wildlife Management 53:378–382.
McQuilkin, R. A., and R. A. Musbach. 1977. Pin oak acorn production on green tree reservoirs in southeastern Missouri. Journal of Wildlife Management 41:218–225.
Merz, R. W., and G. K. Brakhage. 1964. The management of pin oak in a duck shooting area. Journal of Wildlife Management 28:233–239.
Mitsch, W. J., and J. G. Gosselink. 2007. Wetlands. Fourth edition. John Wiley & Sons, Hoboken, New Jersey, USA.
Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear-mixed effects models. Methods in Ecology and Evolution 4:133–142.
North, M., J. Chen, G. Smith, L. Krakowlak, and J. F. Franklin. 1996. Initial response to understory plant diversity and overstory tree diameter growth to a green tree retention harvest. Northwest Science 70:24–35.
Obeso, J. R. 2002. The costs of reproduction in plants. New Phytologist 155:321–348.
R Development Core Team (version 2.13.2). 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Reinecke, K. J., R. C. Barkley, and C. K. Baxter. 1988. Potential effects of changing water conditions on mallards wintering in the Mississippi Alluvial Valley. Pages 325–337 *in* M. L. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, USA.
Reinecke, K. J., R. M. Kaminski, D. J. Moorhead, J. D. Hodges, and J. R. Nassar. 1989. Mississippi Alluvial Valley. Pages 203–247 *in* L. M. Smith, R. L. Pederson, and R. M. Kaminski, editors. Habitat management for migrating and wintering waterfowl in North America. Texas Tech University Press, Lubbock, USA.
Sala, A., K. Hopping, E. J. McIntire, S. Delzon, and E. E. Crone. 2012. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. New Phytologist 196:189–199.
Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.
Straub, J. N., R. M. Kaminski, A. G. Leach, A. W. Ezell, and T. D. Leininger. 2016. Acorn yield and masting traits of red oaks in the lower Mississippi River Alluvial Valley. Forest Science 62:18–27.
Twedt, D. J., and C. R. Loesch. 1999. Forest area and distribution in the Mississippi alluvial valley: implications for breeding bird conservation. Journal of Biogeography 26:1215–1224.
Wehrle, B. W., R. M. Kaminski, B. D. Leopold, and W. P. Smith. 1995. Aquatic invertebrate resources in Mississippi forested wetlands during winter. Wildlife Society Bulletin 23:774–783.
Wigley, T. B., and T. H. Filer. 1989. Characteristics of greentree reservoirs: a survey of managers. Wildlife Society Bulletin 17:136–142.
Young, G. L. 1990. Effect of greentree reservoir management on selected ecological characteristics of a bottomland hardwood community on Noxubee National Wildlife Refuge, Mississippi. Thesis, Mississippi State University, Mississippi State, USA.
Young, G. L., B. L. Karr, B. D. Leopold, and J. D. Hodges. 1995. Effect of greentree reservoir management on Mississippi bottomland hardwoods. Wildlife Society Bulletin 23:525–531.
Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

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