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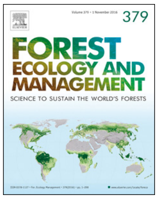

Effects of fertilization and crown release on white oak (*Quercus alba*) masting and acorn quality

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ABSTRACT

Forest management practices that influence mast production in oaks (*Quercus* spp.) are ecologically and economically important for regeneration of future oak forests, timber products, and wildlife that consume acorns. We conducted a 10-year experiment in upland oak-hickory forests of eastern Tennessee to determine the influence of canopy release, fertilization (addition of nitrogen, phosphorus, and potassium), and their combined influence on white oak (*Quercus alba*) acorn production, acorn size and quality, and acorn depredation. We used a robust before-after-control-impact design where we collected pre-treatment acorn production (acorns/m^2 of crown) data from 120 white oaks for 5 years, applied canopy release and fertilizer treatments and then monitored post-treatment acorn production on the same trees for an additional 5 years. Acorn production was temporally variable with 6 of 10 years being near complete mast failures ($\leq 3.67 \pm 8.52$ acorns/m^2 of crown). Also, production varied greatly among individual trees with 11% of trees classified as excellent producers accounting for 31% of all acorns produced, and 41% of trees classified as poor producers accounting for only 17% of all acorns produced. Canopy-released and canopy-released-and-fertilized trees increased acorn production 65% and 47%, respectively, following treatment relative to control trees, with effects greatest in trees classified as poor producers. Fertilization did not influence acorn production or size and did not consistently influence acorn quality. Furthermore, acorn depredation rates did not differ among treatments. Our results indicate crown release is an important management practice when management objectives include increasing white oak acorn production in closed-canopy conditions, whereas fertilization does not influence acorn production.

1. Introduction

Oak (*Quercus* spp.) is considered a keystone genus in eastern deciduous forests (Ellison et al., 2005), and oak-hickory (*Carya* spp.) represents the most common forest type in the eastern US, accounting for more than 30% of all forested land (Oswalt et al., 2014). Acorn production is critically important with regard to regenerating future oak forests, and acorns represent a vital food source for many wildlife species. In fact, more than 100 wildlife species consume acorns, and many wildlife species' populations or nutritional status are directly (e.g., small mammals, American black bear [*Ursus americanus*], and ruffed grouse [*Bonasa umbellus*]) or indirectly (e.g., timber rattlesnake [*Crotalus horridus*]) linked to acorn production (McShea, 2000; Devers et al., 2007; Olson et al., 2015a, 2015b; Fearer, 2016; Azad et al., 2017).

Concerns over the failure to regenerate oaks are well documented, and have far-reaching implications for future forests and associated wildlife (McShea et al., 2007, Dey, 2014). Acorn production represents the first step in the oak recruitment process (Loftis and McGee, 1993; Dey, 2014), and seedling density often is correlated with the previous year's acorn crop. In years of sufficient acorn production, oak seedling recruitment is enhanced, whereas in years of low to moderate production, seedling recruitment may be poor (Johnson et al., 2009). Acorn production in good years (i.e., years with particularly large acorn

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abundance) inundate acorn predators, leading to an abundance of viable acorns, whereas in years of low to moderate acorn production, acorn predators may consume a majority of acorns leading to failed seedling recruitment (Lombardo and McCarthy, 2008; Kellner et al., 2014).

Acorn production is cyclical and intrinsically variable. Masting cycles are influenced by environmental factors, composition of oak species, and the inherent variability between individuals (Wolgast and Trout, 1979; Greenberg, 2000; Johnson et al., 2009). Genetic variability is often implicated for inconsistencies in acorn production between individuals (Wolgast, 1978, Greenberg, 2000, Johnson et al., 2009). However, certain tree and stand characteristics can influence acorn production. Tree age, diameter at breast height, and crown area all can be linked to acorn production potential (Greenberg, 2000), but these factors may not predict acorn production capacity of an individual (Lashley et al., 2009). Stand density and light availability to the crown, a function of stand density, also influence acorn production potential of individuals (Johnson et al., 2009). Therefore, management practices that increase the amount of sunlight reaching the crown of individual oaks may improve acorn production.

Forest management practices and regeneration methods that decrease the stocking level of oak stands and promote increased sunlight penetrating the canopy (e.g., stand thinning and shelterwood harvests, respectively) have proven beneficial to acorn production in red oaks (*Quercus rubra*) (Healy, 1997, Lombardo and McCarthy, 2008). However, the response of white oaks to similar practices is less clear. Olson et al. (2015a) documented increased white oak (*Quercus alba*) acorn production, at the stand level, following partial overstory removal. Acorn production in Oregon white oak (*Quercus garryana*) increased following both partial and full canopy release (Devine and Harrington, 2006). Contrastingly, Kellner et al. (2014) failed to realize differences in acorn production for white oaks with partially released crowns.

Fertilization is not a common practice in the management of oak forests, and the effects of fertilization on acorn production and quality are unknown. However, fertilization is often recommended by various consultants or private companies to private landowners and hunters as a means to increase acorn production and increase acorn quality (e.g., sweetness) and size for wildlife, primarily game species, such as white-tailed deer (*Odocoileus virginianus*) and wild turkey (*Meleagris gallopavo*; Bassett and Whatley, 2002). Graney and Pope (1978) reported diameter growth rates of white and red oaks fertilized with nitrogen were greater than unfertilized tress, but acorn production was not monitored. Wolgast and Stout (1977) reported an increase in bear oak (*Quercus ilicifolia)* acorn production following fertilization of young stands in New Jersey. Callahan et al. (2008) and Bogdziewicz et al. (2017) reported increased acorn production in small plots that contained red oaks following 15 and 25 years of nitrogen additions, respectively. However, no published study that we could find has investigated the effect of fertilization on white oak acorn production, and none of the studies on other oak species considered the influence of individual variation in production capacity.

In an effort to understand how tree-level forest management practices influence acorn production, size, and quality, we monitored acorn production on 120 white oaks (*Q. alba*) at 3 locations in the southern Appalachian Mountains before and after implementation of 4 treatments (control, crown released, fertilized, and crown released and fertilized). We utilized a robust before-after-control-impact study design with 10 years of acorn production data, 5 years before treatment and 5 years after treatment. We also monitored acorn depredation during the same period. Based on inconsistencies in previous related literature, we hypothesized white oak acorn production, acorn depredation, acorn size, and acorn quality would not be influenced by canopy release or fertilization treatments.

2. Material and methods

2.1. Location

We conducted our study on Chuck Swan State Forest and Wildlife Management Area (Chuck Swan) in eastern Tennessee. Chuck Swan is in the Southern Appalachian Ridge and Valley physiographic region of eastern Tennessee, USA, and comprised 9825 ha. Typical soils on Chuck Swan include acidic silt loam Ultisols on ≥6 percent slopes (Soil Survey Staff, 2017). Chuck Swan receives > 130 cm of precipitation per year and a mean temperature of 13.25 degrees Celsius. Chuck Swan is 92% forested and dominated by mixed-hardwood and oak-hickory forest types. Common overstory trees include white oak, chestnut oak (*Q. montana*), northern red oak (*Q. rubra*), black oak (*Q. veluntina*), mockernut hickory (*C. tomentosa*), pignut hickory (*C. glabra*), yellow-poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), and shortleaf pine (*Pinus echinata*).

2.2. Experimental design

We selected 3 similar oak-hickory forest stands in different watersheds across Chuck Swan that contained white oak trees in the overstory. We randomly selected 40 dominant or co-dominant white oaks in each stand ($n = 120$) to monitor acorn production. We defined dominant or co-dominant trees as trees that received full sunlight to the top of the crown (Smith, 1986, Lashley et al., 2009). We used the same sites and trees for our study as described in Lashley et al. (2009), which contains a detailed description of the site and stands. We collected baseline (pretreatment) acorn production data from all 120 trees from 2006 to 2010. We placed each tree in production classes based on mean acorn production of all trees from 2006 to 2010 following guidelines outlined in Lashley et al. (2009). Production classes included excellent, good, moderate, and poor. Excellent producers produced at least twice the 5-year mean acorns/m^2, good producers produced more than the 5-year mean, but less than twice the mean. Moderate producers produced equal to or less than the 5-year mean but at least 60% of the 5-year mean, and poor trees produced less than 60% of the 5-year mean. Production classes after treatment were based on the mean acorn production of control trees from 2011 to 2015 because these trees had not been influenced by any treatment.

Following 5 years of pretreatment data collection, we stratified trees by production class and randomly placed them into treatment groups. Treatment groups included crown released (CR), fertilized (F), crown released and fertilized (CRF), and control (C; trees with no silvicultural manipulation). In total, treatment groups consisted of 36 C trees, 25 CR trees, 33 F trees, and 26 CRF trees (Table 1). There were more trees in the control group than the treatment groups because in certain cases we could not treat an individual tree without influencing the growing conditions of a neighboring tree in the study.

We conducted a 4-sided crown release through mechanical felling or girdling by removing all trees competing with the crown of each CR or CRF white oak. Crown-release treatments were conducted in February 2011. We collected soil subsamples at 0–15 cm in depth around each tree in the F and CRF treatment groups in February 2011 and combined the subsamples in each stand to obtain 3 stand-level soil samples for analysis. Additional soil samples were taken each year of the study (2011–2015). We fertilized each tree in the fertilization treatments (F and CRF treatments) with 168 kg/ha of actual nitrogen by applying ammonium sulfate ($(NH_4)_2SO_4$) around each tree. Application rates of actual phosphorus (monocalcium phosphate; $CaH_4P_2O_8$) and potassium (potassium chloride; KCl) differed between sites and years based on soil test results. We added enough phosphorus and potassium each year to maintain 101 kg/ha of phosphorus and 269 kg/ha of potassium in the soil (Savoy and Joines, 2009). We calculated the amount of fertilizer needed for each tree by measuring the crown area (i.e., surface area from the trunk of the tree to the edge of the crown) of each tree. We

Table 1
The number of trees within each production class for each treatment before and after treatment. Production classes were determined based on methods outlined in Lashley et al. (2009). Excellent represents trees producing greater than 2 times the average acorn production from 2006 to 2010, good represents trees producing more than the mean acorn production from 2006 to 2010, but less than 2 times the mean from 2006 to 2010. Moderate trees represent trees producing between the 2006–2010 mean acorn production and 60% less. Poor represents trees producing less than 60% of the 2006–2010 mean acorn production. After-treatment production classes were based on the 2011–2015 average acorn production for control trees.

Treatment	Number of trees per production class before treatment[a]				Number of trees per production class after treatment[a]				Percent of trees that changed production classes after treatment[b]		
	E	G	M	P	E	G	M	P	−	No change	+
Control	5	10	8	13	3	4	10	19	0.39	0.47	0.14
Fertilized	4	9	4	15	3	10	2	17	0.25	0.56	0.19
Crown release	1	6	5	11	1	8	7	7	0.26	0.39	0.35
Crown release + fertilized	3	8	4	10	5	8	2	10	0.20	0.52	0.28

[a] E = excellent, G = good, M = moderate, and P = poor production class. Represents trees that survived until the end of the study.

[b] (−) = proportion of trees with a lower production class following treatment, (no change) = proportion of trees that did not change production class following treatment, (+) = proportion of trees that increased production class following treatment.

spread the fertilizer around each tree from the trunk to 10 m outside the dripline in March each year from 2011 to 2015.

2.3. Acorn production and depredation

We monitored acorn production for 5 years prior to treatment (2006–2010) and 5 years after treatment (2011–2015). We placed three 1-m^2 acorn-collection baskets suspended above ground under the crown of each tree to determine acorn production. This method allowed us to compare production on a per unit canopy area (m^2). We collected acorns from September through December each year to obtain acorn production from each tree. Collection baskets were monitored 2–5 times each year, depending on the size of the acorn crop. We averaged acorn production across the 3 baskets to determine the average number of acorns produced per m^2 of crown from each tree within a given year.

We opportunistically measured acorn depredation when acorns were present by marking up to 30 acorns from trees with acorns and returning them to the baskets. On subsequent visits, we recounted marked acorns to determine acorn depredation rates (proportion of marked acorns removed). We were not able to determine acorn depredation rates in 2006, 2007, or 2015 because of insufficient mast production. Measuring site-specific depredation rates allowed us to test whether fertilizer treatment affected animal selection once the acorns had fallen, which is an important consideration when trying to assess the biological significance of any changes in acorn quality. We were interested in acorn depredation after acorns had fallen because that is when white-tailed deer, wild turkey, and many other species of wildlife have access to acorns.

We measured the influence of each treatment on acorn production (acorns/m^2 of crown) and acorn depredation rates (proportion of marked acorns removed) using generalized linear mixed models with a before-after-control-impact experimental design in program R (R Foundation for Statistical Computing, Vienna, Austria). We were not able to correct acorn production data by acorn depredation because we did not have acorn depredation rates for all years and all trees. The before-after-control-impact framework allowed us to control for variability in mast production across years, sites, and between individuals, a clear improvement on previous study designs. Additionally, we were able to control for differences in mean acorn production and depredation rate between treatment groups prior to implementation of treatments. We used year, site, and tree as random effects in the linear model. Treatment, period (before or after treatment), and the interaction of treatment and period were the fixed effects. We were interested in the interaction between treatment and period because we wanted to identify how acorn production and depredation differed between treatments prior-to and after treatment. Acorn production data were log-transformed to meet assumptions with normality. We created contrast statements based on the results of the linear model to detect differences between treatments and to determine the effect size of any statistical difference (Schwarz, 2015). Effects sizes were based on back-transformed differences in mean acorn production between treatment groups before and after treatment (Schwarz, 2015).

We also were interested in the influence of treatments on acorn production class. We used the average acorn production for the 5 pretreatment years combined across treatments to assign production class prior to treatment. Trees were stratified across treatments based on these data, but we also were interested in whether treatments influenced the production class of individuals and to determine if treatment of poor individuals improved production enough to out-produce untreated excellent trees. To determine if treatments changed the production class of individuals, we ranked oaks against one another within each treatment based on the 5 post-treatment years. We compared the number of trees that changed production classes (negative or positive) or remained in the same production class following treatment using a Chi-square test of independence at an alpha of 0.05.

2.4. Acorn quality

We compared acorn weights between all four treatments in 2014, a masting year following 4 years of continuous fertilization, to determine the influence of treatments on acorn size. We collected sound (i.e., not infested by weevils) acorns from 9 trees in the control and 9 trees in the fertilized treatment during fall 2014 for nutritional analysis. Acorns were dried, hulled, weighed (g), and analyzed for nutritional quality using wet-chemistry analysis. Acorns were analyzed by Dairy One, Ithaca New York, USA. Acorns were analyzed to determine crude protein, acid and neutral detergent fibers, total digestible nutrients, ethanol-soluble carbohydrates (simple sugars), macronutrients (phosphorus, potassium, calcium, magnesium), and micronutrients (iron, manganese, molybdenum, zinc). We used 2-sample t-tests to determine differences in nutritional quality between acorns from control and fertilized trees. We collected acorns from 9 trees of each treatment (C, CR, CRF, C) and used analysis of variance (ANOVA) in program R to determine differences in weight among the 4 treatments.

3. Results

3.1. Acorn production

Four trees (1 F, 2 CR, and 1 CRF) died as a result of wind throw or unknown causes during the course of our study and were removed from all analyses. Acorn production was variable across years. Two of five years prior to treatment were masting years (76.55 ± 8.74 (± SE) acorns/m^2 and 70.29 ± 6.91 acorns/m^2; 2008 and 2010, respectively), whereas the remaining 3 years were mast failures (≤3.67 ± 0.79 acorns/m^2). One year post-treatment was a masting year

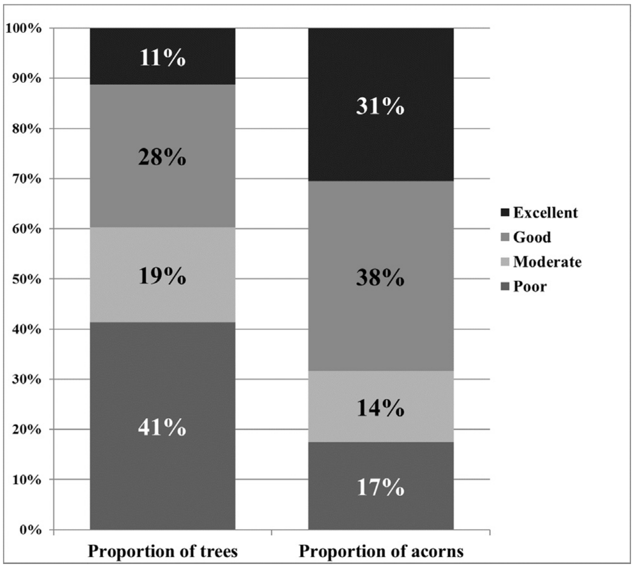

Fig. 1. Proportion of white oak (*Quercus alba*) trees that represent each production class and each classes' contribution to total acorn production at Chuck Swan State Forest, TN, USA. Production classes were determined based on methods outlined in Lashley et al. (2009). Excellent represents trees producing greater than 2 times the average acorn production from 2006 to 2010, good represents trees producing more than the mean acorn production from 2006 to 2010, but less than 2 times the mean from 2006 to 2010. Moderate trees represent trees producing between the 2006–2010 mean acorn production and 60% less. Poor represents trees producing less than 60% of the 2006–2010 mean acorn production.

(99.91 ± 122.7 acorns/m^2; 2014), one year was a moderate production year (18.60 ± 32.09 acorns/m^2; 2012), and the remaining three years were mast failures ($\leq$0.74 ± 4.06 acorns/m^2).

When separated into production classes based on mean acorn production, excellent and good producing trees represented 39% of the trees, but accounted for 69% of acorn production (Fig. 1). Poor-producing trees represented 41% of the trees, but accounted for only 17% of the acorns produced (Fig. 1). The amount of trees in each production class was not equitable for each treatment, with excellent trees being underrepresented in CR and CRF treatments (Table 1). Half of the trees in all treatments maintained their respective production classes after treatment. The production classes improved for 35% and 28% of trees in the CR and CRF treatments, respectively, compared to 14% of C trees and 19% of F trees (Table 1). However, results of the Chi-square test of independence indicated changes in production classes were not significant between treatments (χ^2 = 5.10, *p*-value = 0.53).

Year accounted for the majority of the variability in acorn production followed by individual and site (Table 2). Treatment groups differed in acorn production prior to treatment (Table 2) with trees in the CR group (23.81 ± 4.43 (± SE) acorns/m^2) producing fewer acorns prior to treatment than trees in the C group (34.17 ± 5.14 acorns/m^2) when averaged across years (Fig. 2). There was a significant treatment group and period interaction, indicating treatment influenced acorn production (Table 2). Fertilization did not influence acorn production, whereas CR and CRF increased mean acorn production (Table 2). Crown-release treatments (CR and CRF) tended to impact poor-producing trees more than trees in other production classes (Fig. 3). Crown-released and CRF trees increased acorn production 65 ± 23% and 47 ± 20%, respectively (Fig. 4), following treatment relative to control trees, but were similar to one another (β = −0.11, 95% CI = −0.40, 0.18).

Table 2

Acorn production (acorns per m^2 of crown) results from generalized linear mixed model with a before-after-control-impact experimental design. Model compared differences in acorn production for white oaks (Quercus alba) under different forest management treatments (control, crown release, fertilize, and crown release + fertilize), 2006–2015, Chuck Swan State Forest, TN, USA.

Parameter	Estimate	95% CI	*p*-value[a]
Fixed effects			
(Intercept)	0.21	−1.08 to 1.50	0.757
Fertilize	−0.1	−0.34 to 0.14	0.439
Crown Release	−0.34	−0.60 to −0.08	***0.031***
Crown Release + fertilize	−0.24	−0.50 to 0.02	0.098
Period (after treatment)	−0.84	−2.65 to 0.96	0.383
Fertilize * period (after treatment)[b]	0.16	−0.08 to 0.40	0.226
Crown Release * period (after treatment)[b]	0.5	0.23 to 0.77	***0.005***
Crown Release + fertilize*period (after treatment)[b]	0.39	0.13 to 0.65	***0.017***
Random effects	Variance	Standard deviation	
Tree	0.12	0.35	
Year	2.10	1.45	
Site	0.02	0.14	
Residual	0.65	0.81	

[a] Significance was determined using an alpha-level of 0.05.

[b] Estimates and 95% confidence intervals for treatment * period parameters are estimates compared to control trees and were based on contrast statements.

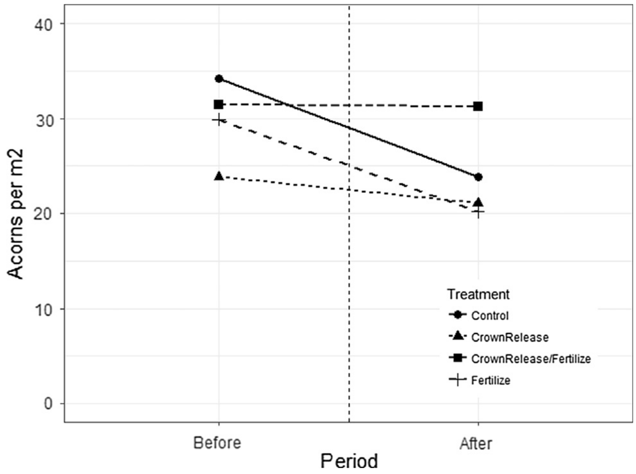

Fig. 2. Average white oak acorn production (acorns/m^2) based on period, before treatment (2006–2010) and after treatment (2011–2015), for the 4 treatment groups at Chuck Swan State Forest, 2006–2015, TN, USA. Error bars were omitted to improve the clarity of the figure.

3.2. Acorn depredation

Acorn depredation rates (proportion of acorns removed) were greatest in 2009 (0.75 ± 0.05), 2013 (0.74 ± 0.14), 2012 (0.54 ± 0.03), and 2011 (0.50 ± 0.29), years of moderate or poor acorn production. Acorn depredation rates were lowest in 2014 (0.08 ± 0.01), 2008 (0.23 ± 0.03), and 2010 (0.27 ± 0.02), years of high acorn production. We were only able to compare depredation rates between treatments in good acorn production years (2008, 2010, 2012, and 2014). Treatments did not influence acorn depredation rate, and rates were similar between all treatments prior to and after treatment (Table 3). Year accounted for the largest variation in acorn depredation rates (Table 3).

3.3. Acorn quality

Treatment did not influence acorn weight (F-value = 0.305, p-

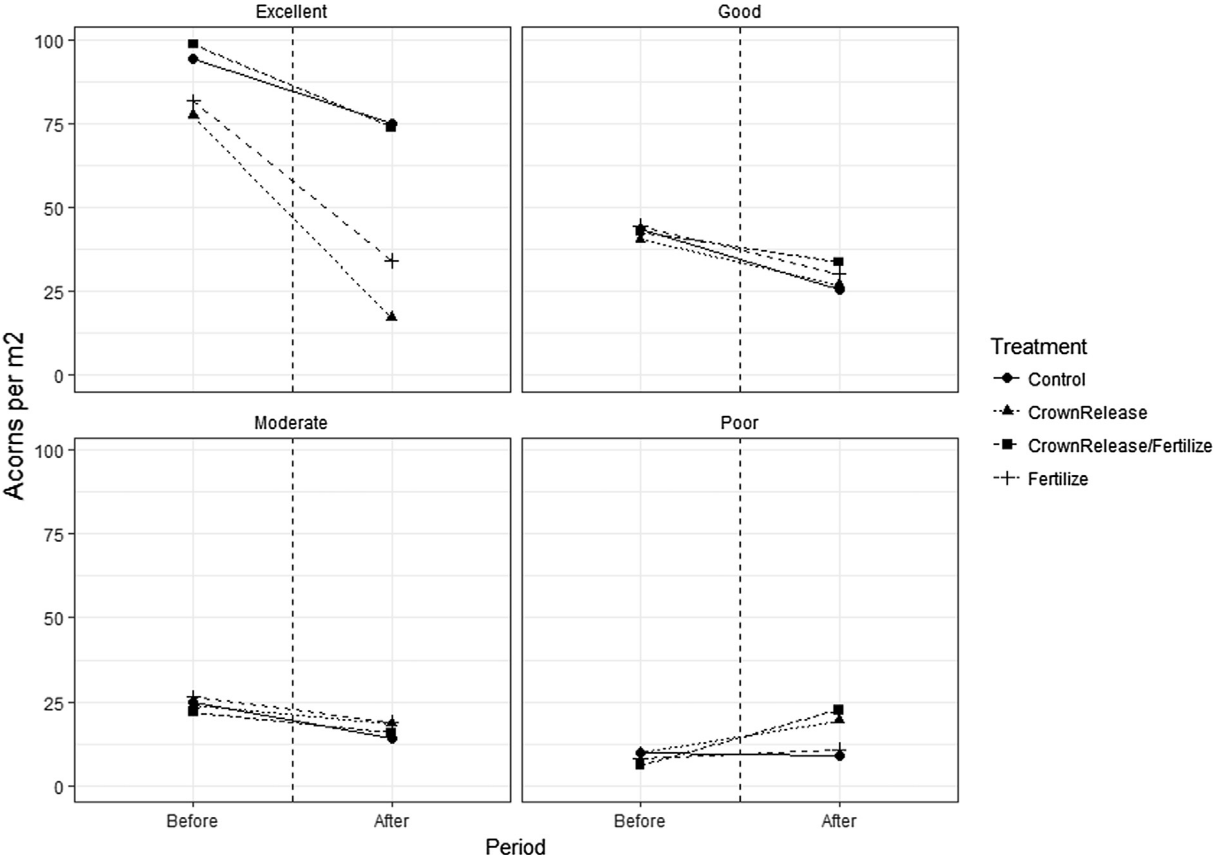

Fig. 3. Average white oak acorn production (acorns/m^2) based on period, before treatment (2006–2010) and after treatment (2011–2015), and production class (excellent, good, moderate, and poor) for the 4 treatment groups at Chuck Swan State Forest, 2006–2015, TN, USA. Production classes were determined based on methods outlined in Lashley et al. (2009). Excellent represents trees producing greater than 2 times the average acorn production from 2006 to 2010, good represents trees producing more than the mean acorn production from 2006 to 2010, but less than 2 times the mean from 2006 to 2010. Moderate trees represent trees producing between the 2006–2010 mean acorn production and 60% less. Poor represents trees producing less than 60% of the 2006–2010 mean acorn production. Error bars were omitted to improve the clarity of the figure.

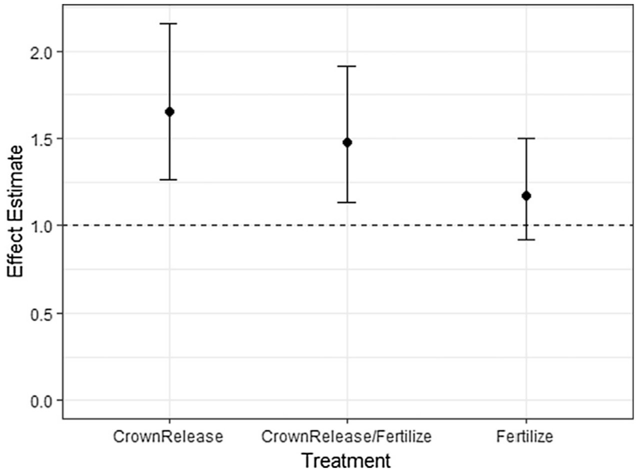

Fig. 4. Effects plot for white oak (*Quercus alba*) acorn production following various forest management treatments from 2006 to 2015, Chuck Swan State Forest, TN, USA. Treatments with error bars overlapping the dashed line are not significantly different from control trees. Effect sizes were based on back-transformed differences in mean acorn production between treatment groups before and after treatment (Schwarz 2015).

value = 0.822) and hulled acorns averaged 1.55 ± 0.02, 1.49 ± 0.03, 1.47 ± 0.03, and 1.61 ± 0.03 g for C, F, CR, CRF trees respectively. Fertilization also did not influence ethanol soluble carbohydrates, total digestible nutrients, acid detergent fiber, or neutral detergent fibers

Table 3
Acorn depredation (percent of acorns removed) results from generalized linear mixed model with a before-after-control-impact experimental design. Model compared differences in acorn depredation for white oaks (Quercus alba) under different forest management treatments (control, crown release, fertilize, and crown release + fertilize), 2008, 2010, 2012, and 2014, Chuck Swan State Forest, TN, USA.

Parameter	Estimate	95% CI	*p*-value[a]
Fixed effects			
(Intercept)	0.27	−0.06 to 0.60	0.24
Fertilize	0.00	−0.10 to 0.10	0.94
CrownRelease	−0.03	−0.14 to 0.08	0.64
CrownRelease/fertilize	−0.01	−0.11 to 0.09	0.87
Period (after treatment)	0.04	−0.42 to 0.50	0.87
Fertilize*period (after treatment)[b]	−0.04	−0.17 to 0.09	0.53
Crown Release*period (after treatment)[b]	0.04	−0.09 to 0.18	0.53
Crown Release/fertilize*period (after treatment)[b]	0.01	−0.11 to 0.14	0.85
Random effects	Variance	Standard deviation	
Tree	0.005	0.069	
Year	0.054	0.231	
Site	0.004	0.064	
Residual	0.052	0.238	

[a] Significance was determined using an alpha-level of 0.05.
[b] Estimates and 95% confidence intervals for treatment*period parameters are estimates compared to control trees and were based on contrast statements.

Table 4
Results from 2-sample t-tests comparing white oak (Quercus alba) acorn quality between fertilized and unfertilized (control) acorns collected in 2014, Chuck Swan State Forest, TN, USA.

	Control		Fertilized		
Quality measurement	Mean	SE	Mean	SE	*p*-value[a]
Crude Protein (%)	4.422	0.137	5.156	0.273	***0.029***
Acid detergent fiber (%)	3.711	0.216	4.133	0.225	0.195
Neutral detergent fiber (%)	6.744	0.278	7.233	0.186	0.163
Ethanol soluble carbohydrates (%)	9.822	0.666	10.100	0.433	0.731
Total digestible nutrients (%)	84.889	0.111	84.889	0.111	0.990
Calcium (%)	0.076	0.004	0.074	0.005	0.857
Phosphorus (%)	0.108	0.003	0.122	0.003	***0.004***
Magnesium (%)	0.061	0.003	0.066	0.002	0.229
Potassium (%)	1.001	0.025	1.000	0.031	0.978
Iron (ppm)	10.778	0.401	10.667	0.441	0.854
Zinc (ppm)	7.000	0.333	8.111	0.512	0.088
Copper (ppm)	5.222	0.324	4.778	0.278	0.313
Manganese (ppm)	127.889	16.421	137.889	13.985	0.649
Molybdenum (ppm)	0.344	0.078	0.144	0.038	***0.035***

[a] Significance was determined at an alpha-level of 0.05.

(Table 4). Fertilization increased acorn crude protein from 4.4 ± 0.14% to 5.2 ± 0.27% and phosphorus from 0.11 ± 0.003% to 0.12 ± 0.003% and decreased molybdenum from 0.34 ± 0.08 ppm to 0.14 ± 0.04 ppm, but did not affect the other nutrients tested (Table 4).

4. Discussion

4.1. Acorn production

When increasing acorn production is of interest to natural resource managers, releasing the crown of white oak trees should be of utmost importance. Fertilization had no effect on acorn production. Moreover, none of our treatments influenced the consistency of acorn production as indicated by mast failure in all treatments 3 of 5 years after treatment. Even though crown release increased acorn production, the benefits were only realized during good masting years when there was an abundance of acorns.

As with other studies on oak mast production, we observed significant temporal variability in acorn production. Our data suggest moderate to good production years occur only about 4 out of every 10 years in white oaks. This yearly variation is not surprising given the impact of environmental conditions on acorn production, particularly during flowering (Johnson et al., 2009). Given the strong influence of environmental factors and the fact that our treatments did not manipulate environmental conditions, it is no surprise that our treatments had no influence on the periodicity of acorn production. These results provide further evidence that environmental conditions (i.e., weather) are the primary driver in masting cycles, and masting potential may not be primarily controlled by the availability of resources (i.e., light and nutrients). However, when environmental conditions do not constrain acorn production, individual white oak trees may be limited in production capacity by competition for light from surrounding trees.

An interesting result of this study was the variability in acorn production between individual trees. For example, a large proportion of acorns (69%) were produced by a small proportion (39%) of trees (Fig. 1). This is similar to findings in other oak species in the northeast and southeast (Healy et al., 1999; Greenberg, 2000). Our findings combined with findings from previous studies highlight the individual variability in acorn production and the fact that a few individual oaks are responsible for a majority of an acorn crop in a given year.

Although our chi-square test indicated there were no differences in the change of production classes (positive or negative) between the treatments, crown release treatments tended to impact poor-producing trees more than other production classes (Fig. 3). Following treatment, poor-producing trees in the CR and CRF treatments increased acorn production to levels similar to trees in the moderate production class, whereas C and F trees produced similar amounts of acorns before and after treatment (Fig. 3). The increased acorn production by poor-producing trees in the CR and CRF treatments contributed significantly to the difference in acorn production between treatments as poor-producing trees represented almost half of the CR and CRF trees. However, poor-producing trees still were not able to produce as many acorns as good or excellent trees. When comparing excellent trees in the CR treatment before and after treatment, it looks as though crown release reduced acorn production (Fig. 3). However, there was only one excellent tree in the CR treatment, and the decrease in acorn production likely was an anomaly and result of low sample size.

The amount of light reaching the crown has been correlated with acorn production (Johnson et al., 2009). Intuitively, we would expect to see an increase in individual-level acorn production following crown-releasing oaks or thinning in an oak stand because the crowns of residual trees would expand to fill canopy gaps. Jackson et al. (2007) reported an 8% and 25% increase in the crown area of white oaks in one year following partial canopy removals and shelterwood harvests in Tennessee, respectively. However, the response of acorn production to canopy disturbance in previous studies is ambiguous. For example, studies on red oak acorn production in New England reported individual and stand–level acorn production was greater for trees in thinned stands compared to unthinned stands, but only in years of marginal acorn production (Healy 1997). Similarly, Olson et al. (2015a) reported increased acorn production in white oaks after partial overstory removal in an oak stand in Missouri. Bellocq et al. (2005) observed increased production in released trees of red oaks in Ontario, CA. Acorn production for white and black oaks in Indiana was not influenced by partial crown release (Kellner et al., 2014). Similarly, acorn production did not differ for white oak trees following canopy thinning in Tennessee, but acorn production in this study was only tracked 1 year, a poor acorn production year (Jackson et al., 2007). Our results indicate crown release of individual white oak trees is an effective method to increase individual acorn production, and likely was a result of an increase in branch density within the crowns, or increased depth of released crowns, in addition to expanded crown area. In contrast to Healy (1997), we only observed an increase in good acorn production years.

Other studies may have failed to detect a difference in acorn production following canopy disturbance for a multitude of reasons. One of the most plausible reasons is because of the inherent variability in acorn production between individuals. Past studies may have inadvertently removed excellent- or good-producing trees from treated stands and therefore biased results (Greenberg and Parresol, 2002), particularly given that a small proportion of the trees can produce the majority of mast. Unknowingly removing those few best-producing oaks from a stand could reduce acorn availability and have unintended consequences for future oak regeneration or wildlife populations. Similarly, failing to account for inherent differences in acorn production between treated and untreated trees prior to treatment implementation also may bias results and lead to incorrect conclusions. We accounted for this variability by collecting pre-treatment acorn production data and incorporating those data into a before-after-control-impact framework. Ideally, steps should be taken to identify excellent- and good-producing trees prior to management activities, especially forest stand improvement practices intended to increase acorn availability for wildlife (Healy, 2002, Bellocq et al., 2005, Lashley et al., 2009).

Five consecutive years of continued fertilization adding 168 kg of N per ha and maintaining P and K at 101 and 269 kg per ha, respectively, did not influence acorn production. It is not surprising that fertilization without canopy disturbance did not influence acorn production because the crowns could not expand. Fertilization therefore, could not lead to increased density of flowering sites that would enable increased acorn production. Additionally, fertilization combined with crown release did not increase acorn production over crown release alone, further indicating fertilization has no influence on acorn production of mature white oaks. White oaks are adapted to thrive in areas with shallow or nutrient-deficient soils, indicating acorn production in naturally occurring oak stands is more limited by light than soil nutrients.

Fertilization has been reported to increase stem diameter growth in oak trees (Ward and Bowersox, 1970; McQuilkin, 1982; Graney and Pope, 1987). However, few studies have investigated the impact of fertilization on acorn production. Wolgast and Stout (1977) did report an increase in acorn production following fertilization of bear oaks, but fertilized stands were relatively young (< 13 years old), compared to our stands that represented mature white oaks, therefore light may not have been the most limiting factor in their study. Similarly, increased acorn production was reported following fertilization of mature red oak trees in Massachusetts (Callahan et al., 2008; Bogdziewicz et al., 2017). However, individual acorn production was not measured prior to treatment, therefore inherent variability between individual trees was not accounted for in these 2 studies. If acorn production differed between treatment groups prior to treatment, the results of fertilization would be confounding. Had we not accounted for variability in acorn production between individuals and treatment groups in our analysis, we would have failed to detect a treatment effect and came to an incorrect conclusion. Given the results of our study, fertilization of naturally-occurring mature white oaks, with or without crown release, is unlikely to elicit an increase in acorn production.

4.2. Acorn depredation

Unsurprisingly, acorn depredation rates were greater in years of poor acorn production (≥ 50% of acorns were removed) than in years of good acorn production (< 30% of acorns removed). The treatments in our study did not impact acorn depredation rates. These findings are consistent with Kellner et al. (2014) who did not report a change in acorn depredation rates following partial canopy removal of white oaks and black oaks in Indiana. A possible limitation of our sampling method for acorn depredation was that we were only able to determine differences in depredation rate between treatments in good acorn production years. In years, of poor acorn production, we were not able to track the depredation rate of trees with few to no acorns present in the baskets. Another possible limitation is that we were not able to account for depredation of acorns prior to acorn fall. Tree squirrels, birds, weevils, and other insects remove, consume, or degrade acorns prior to acorn fall (Johnson et al., 2009). However, popular press articles recommend fertilization of oaks to benefit game species, such as white-tailed deer and wild turkey. Therefore, we were most interested in differences in depredation rates after acorns had fallen and become available to these animals.

4.3. Acorn quality

Fertilizing oak trees for increased acorn size and quality is often promoted to landowners, land managers, and hunters through popular press and product advertisements (Bassett and Whatley, 2002). These articles and advertisements claim (without supporting data) fertilization increases acorn nutritional quality, palatability, or “sweetness,” with no reference to what nutritional characteristics contribute to quality, palatability, or sweetness (Bartylla, 2010). We used measures of ethanol soluble carbohydrates (simple sugars), acid detergent fiber, neutral detergent fiber, and total digestible nutrients as approximations of acorn sweetness, palatability, and overall quality, respectively. Fertilization did not influence any of these metrics or acorn size, but did influence crude protein, phosphorus, and molybdenum. However, based on the lack of influence fertilization had on acorn depredation, the relatively slight change in crude protein, phosphorus, and molybdenum is unlikely biologically relevant to species such as white-tailed deer or wild turkey. A small increase in crude protein at this time of year is not meaningful because protein requirements among vertebrate wildlife consuming acorns is relatively low, with a lack of active tissue and bone growth during this time (Hellgren et al., 1989, Hewitt, 2011). Acorns are a high-energy food (i.e., high in carbohydrates; Kirkpatrick and Pekins, 2002), which is more valuable during this time of year for consumers. An increase in total digestible nutrients or ethanol soluble carbohydrates would be more important to meet energetic demands of species such as white-tailed deer, but these metrics were not influenced by fertilization. We believe our results warrant the discontinuation of recommendations to fertilize white oaks for increased acorn production or quality and size in mature white oak stands.

4.4. Management implications

Releasing the crowns of white oak trees can be an effective method to increase acorn production as well as increase forage and cover for various wildlife species (Lashley et al., 2011, McCord et al., 2014). Removing competing undesirable tree species should be an initial objective of managers. However, inherently poor-producing oak trees also may be removed when competing with good or excellent producing individuals given crown-released poor producers did not produce as many acorns as un-manipulated good or excellent producers. Mast surveys must be conducted during good mast years in order to identify good- or excellent-producing individuals. Fertilization was an ineffective and impractical technique to increase acorn production or size, and did not impact acorn quality in a biologically meaningful manner for most wildlife species. Therefore, we do not recommend fertilizing mature white oaks to increase acorn production or acorn quality. Oak represent an ecologically important tree genus and our results can help positively influence practices that increase acorn production to aid in the regeneration of future oak forests and manage wildlife that benefit from oak mast.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.11.020.

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