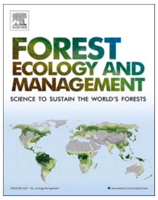
Forest Ecology and Management 481 (2021) 118691

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Oak growth and acorn production in southern Appalachian mature forests and shelterwood with reserves regeneration harvests

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ARTICLE INFO

Keywords:
Acorn production
Crown expansion
Crown release
Oak diameter growth
Shelterwood harvest

ABSTRACT

Oaks (*Quercus*) are economically important, and their seed (acorns) are a valuable food for many animals. Thus, forest managers must consider potential tradeoffs between oak growth and acorn production. I used 13 years of dbh growth and 17 years of acorn trapping data on 195 trees of five common eastern oak species to compare stand-level growth and acorn production between closed canopy mature forest (M) and recent shelterwood with reserves regeneration harvests (SW) (BA 27.3 ± 1.7 m^2/ha in M; $5.1 + 0.8$ m^2/ha in SW at study establishment). I also examined treatment differences in dbh growth, crown expansion, and acorns/m^2 crown at the individual tree level, using a subset of paired (by species and dbh) trees. Despite five times more oak trees and oak BA in M, average annual total acorn production/ha was only double (58,199/ha in M) that in SW (27,298/ha), and was statistically greater in M than SW for total oaks and white oak. Stand- and paired individual tree-level analyses indicated that average acorns/m^2 crown and dbh growth was approximately 70% greater in SW than M for total oaks. Crown area increases were greater in SW than M for total oak (66%) and northern red oak (74%), and crown areas in SW expanded disproportionately to increases in dbh alone. In mixed-oak southern Appalachian forests, silvicultural treatments retaining 20–40 mature oaks/ha with fully released crowns will likely yield 50–100% of acorns produced/ha in mature closed canopy stands, as acorn production by residual trees increases. Retention of multiple oak species will reduce the likelihood of stand-level crop failure, as acorn production differs among species and years.

1. Introduction

Oak (*Quercus*) may be the most important tree genus in the Central Hardwood Region due to their commercial value for timber, and food value of their seed – acorns – to wildlife (Brooke et al., 2019). Acorns are considered a keystone forest resource because of their far-reaching influence on wildlife populations throughout the food chain. Rodent (Wolff et al., 1996), game bird (Steffen et al., 2002), and deer (Feldhamer, 2002) populations are directly linked to acorn abundance and, in turn are prey for carnivorous birds or mammals. Additionally, heavy selective browsing of seedlings, herbaceous plants, and woody vegetation by white-tailed deer (*Odocoileus virginianus*) can affect forest composition and structure when populations are high (Feldhamer, 2002). Acorn production also directly affects oak regeneration (Loftis and McGee, 1993). Because of this, forest managers and wildlife biologists are keenly interested in silvicultural practices that promote oak growth and acorn production.

Acorn crop sizes vary considerably among oak species, individual trees, years, and locations (Greenberg, 2000), highlighting the need for long-term data and large sample sizes when examining how silvicultural treatments or other factors affect acorn production. Several studies indicate that acorn production is positively correlated with tree diameter (Greenberg, 2000), suggesting that silvicultural treatments to promote oak diameter growth could increase acorn yield per tree. In mature forests, the weak, positive relationship between oak diameter at breast height (dbh) and acorn production is largely because crowns (where acorns are produced) expand with dbh (Greenberg 2000; Bechtold, 2003), rather than a greater density of acorns per unit crown area of larger trees (Greenberg, 2000). However, several studies indicate that crown "release" by thinning or other methods can increase acorn yield per tree by increasing acorn density (acorns/m^2 crown), in addition to promoting diameter and crown area growth (Healy, 1997; Healy et al., 1999; Devine and Harrington, 2013). In addition to tree size, acorn production per ha will clearly vary according to the number and species of oak trees in any given forest area (Rose et al., 2012; Greenberg et al., 2014). Thus, potential tradeoffs between increased growth and acorn

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https://doi.org/10.1016/j.foreco.2020.118691
Received 26 August 2020; Received in revised form 7 October 2020; Accepted 8 October 2020

0378-1127/Published by Elsevier B.V.

production per tree by fewer oak trees after crown-releasing silvicultural treatments, versus less acorn production per tree by more trees in mature forest, must be considered when managing for both oak timber volume and mast.

In this paper, I used 17 years (2002–2018) of acorn trapping data on all oak trees (>12.7 cm dbh; total 195 trees) within 31 randomly selected 0.1 ha plots to compare stand-level acorn production between closed canopy mature forest (M) and recent (ca. 1999) shelterwood with reserves regeneration harvests (SW). Stand-level dbh growth over a 13-year period (2003–2016) was also compared between M and SW. I also compared oak dbh growth, crown expansion, and acorns/m^2 crown at the individual tree level, using a subset of paired (by species and 2003 dbh) oak trees over 16 growing seasons (2003–2019). Specifically, I asked (1) does stand-level change (2003–2016) in oak density, dbh, and BA differ between M and SW?; (2) does stand-level average acorn production (acorns/ha) and acorns/m^2 crown differ between M and SW?; (3) does acorns/m^2 crown, or the change (2003–2019) in dbh, crown diameter, and crown area differ between paired (by species and 2003 dbh), individual oaks in M and SW?, and; (4) do measured crown areas of oaks in M or in SW differ from modelled crown areas (based on dbh, developed for oaks in closed canopy, mature forest; Bechtold, 2003) after 16 growing seasons?

2. Methods

2.1. Study area

This study was conducted in the Grandfather and Pisgah Districts of the Pisgah National Forest, within the mountainous Blue Ridge Physiographic Province of western North Carolina. Average annual rainfall in the region ranges from about 1,000–1,500 mm and exceeds 2,500 mm along parts of the southern Blue Ridge escarpment in western North Carolina (McNab, 2011). Soils were predominantly Dystrochrepts and Hapludults (Pittillo et al., 1998). Mature forest ranged from 80 to 120 years old. Cove hardwood forests were dominated by yellow-poplar (*Liriodendron tulipifera*) and northern red oak (*Quercus rubra*), and include magnolia (*Magnolia* spp.), white ash (*Fraxinus americana*), beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), and silverbell (*Halesia carolina*). Upland hardwood forests were dominated by scarlet oak (*Q. coccinea*), chestnut oak (*Q. montana*), and black oak (*Q. velutina*); blackgum (*Nyssa sylvatica*) and sourwood (*Oxydendrum arboreum*) were common mid-story trees. Red maple (*Acer rubrum*), hickories (*Carya* spp.), flowering dogwood (*Cornus florida*), and white oak (*Q. alba*) occurred throughout cove and upland hardwood forests (Pittillo et al., 1998).

2.2. Study design

Study trees (oaks) were from a long-term study (established in 1999) comparing stand dynamics and fruit and nut production between mature, closed-canopy forest (M), and shelterwood with reserves regeneration harvests (SW; harvested 1998–1999) in southern Appalachian hardwood forests. Sample trees were located in 0.1 ha plots (16 M; 15 SW) at elevations ranging from 510 − 1,260 m above sea level and across a wide range of topographic features, such as aspect, slope position, and percent slope. SW stand sizes ranged from 3.2 to 10.5 ha (average = 7.0 ha) and were the same age as mature study stands when they were harvested (80–100 years old). The SW with reserves regeneration harvest (also known as clearcut with reserves regeneration harvest; Miller et al., 2006) method entails retention of about 3.4–4.5 m^2/ha basal area (BA) of mature trees, typically scattered oaks and hickories, to help ensure initiation and development of tree regeneration while retaining a heterogeneous stand structure and hard mast production (acorns and hickory nuts) for wildlife. At study establishment, total average (±SE) stand-level (all species) tree (≥12.7 cm) BA was 27.3 ± 1.7 m^2/ha in M and 5.1 + 0.8 m^2/ha in SW.

2.3. Stand-level oak growth and acorn production

Diameter at breast height (dbh) of all, individually tagged dominant, codominant, and intermediate trees (≥12.7 cm dbh) was measured in 16 M and 15 SW randomly established 20 × 50-m (0.1-ha) plots (31 total plots), during early spring 2003, and again in early spring 2016. All tree species were measured, but the focus of this study was on oaks. Study species included black oak (15 trees), northern red oak (27 trees), and scarlet oak (22 trees) in the red oak group (subgenus *Quercus* section Lobatae), and chestnut oak (90 trees) and white oak (41 trees) in the white oak group (subgenus *Quercus* section Quercus) (total 195 oak trees with acorn traps). Two sample t-tests (SAS 9.4) were used to examine treatment differences in oak (total, and by species) density, dbh, and BA at initial measurement (2003), and determine if stand-level changes (2016 minus 2003 measurements) in those metrics differed between M and SW over the 13-year study period.

Acorns were collected monthly, August – December 2002–2018, from three circular, 0.46-m^2 traps placed randomly beneath each oak tree crown. Well-developed (e.g., not including aborted acorns consisting of primarily cap material) acorns from all collections per tree each year were counted in the lab. Acorns/m^2 crown for each tree was based on the average number of acorns per m^2 trap area. For stand-level (per ha) acorn production analyses, the number of acorns per m^2 crown were multiplied by the total crown area (m^2) per tree, and summed across trees in each plot. Crown area, (a two-dimensional measurement encompassing only the crown's surface area) provides a more accurate metric for acorn production than crown volume (a three-dimensional measurement encompassing both crown area and length) because acorns are produced on the outer branches of oaks (current year growth for the white oak group; prior-year growth for the red oak group), and potentially large error in subjective estimates of crown length (Rose et al., 2012). Crown area (m^2) for each tree was modelled using species-specific crown-diameter equations (Bechtold, 2003) based on the midpoint between 2003 and 2016 dbh measurements (to account for dbh growth over the 16-year study period); predicted crown diameters (Bechtold, 2003) were then used with the formula for circle area (Area = $\pi(r^2)$). Crown-diameter equations (Bechtold, 2003) were developed for mature trees in fully stocked stands; therefore crown diameter and crown area estimates, as well as acorn production estimates based on modelled crown areas, were likely conservative for SW trees where dbh and crowns expanded faster than in M (see Results section). Repeated measures ANOVAs (Proc Mixed; SAS 9.44), in a completely randomized design with compound symmetry covariance structure, were performed to examine effects of treatment, year, and treatment × year interactions on acorn production. Treatment, year, and their interaction were considered fixed effects, and plot within treatment a random effect and the repeated subject factor. Where significant treatment × year interactions were present, years warranting further examination (e.g, were there between treatment differences within years?) were identified, and least square means for partitioned F-tests (SLICE option) were used in PROC MIXED (SAS 9.4) to examine the significance of treatment differences within identified years. Within-treatment differences among years were not examined because between-treatment differences were the main interest, and highly variable acorn production among years is well known. Two-sample t-tests (SAS 9.4) were performed to determine if average (2002–2018) stand-level acorn production (acorns/ha) and acorns/m^2 crown differed between M and SW treatments, for total oaks and each species. In t-tests on acorns/m^2 crown, plots where a given species (for species analyses) or oaks (for total oaks analysis) did not occur were excluded. Stand-level acorn production data were natural logtransformed (+0.1) as needed for ANOVA and two-sample t-tests to reduce heteroscedasticity.

2.4. Paired tree-level oak growth and acorn production

For this portion of the study, dbh and tree crowns were measured in early spring 2003, and again in early spring 2019 on most SW oaks, and a paired M tree of the same species, similar (mean ± SE 1.8 ± 0.4 cm) dbh at study establishment, and forest type (cove [type 56] or upland hardwood [type 53]) classified by the US Forest Service (USFS; Southern Region Silvicultural Examination and Prescription Field Book, for Continuous Inventory of Stand Conditions version 4.02, unpublished report) based on tree species composition at the stand level. Sample size was limited to the number of mature SW oak trees still living (two SW plots contained no living, trapped oaks by 2019) and accessible (three SW plots became inaccessible by 2018 due to deteriorating road conditions) in 2019. In three instances two SW trees were paired with the same M tree, due to an insufficient number of suitable M matches (same species and similar size at study establishment). A total of 21 total oak pairs (10 white oak, 6 chestnut oak, 5 northern red oak) were sampled that included 21 SW trees in 10 plots, and 18 M trees in 9 plots. All sample trees were in dominant or codominant (a few were intermediate) crown positions. Crown radii were measured from bole to dripline using a GRS densitometer at four cardinal directions (N, S, E, and W) and corrected for slope. Two crown diameters were calculated for each tree by summing the N-S, and the E-W radii (+dbh), respectively. Measured (as opposed to modelled) crown areas were calculated using the formula for a circle ($A = \pi r^2$) based on the average both crown diameter measurements for each tree. Paired sample t-tests were used to determine if the change (2019 minus 2003 measurements) in dbh, crown diameter, and crown area, or average (2002–2018) acorns/m^2 crown differed between paired oak trees in M and SW. Paired t-tests were also used to determine whether measured crown areas of oaks in M (pairs: $n = 9$ white, 5 chestnut, and 4 northern red oak) or SW (pairs: $n = 10$ white, 6 chestnut, and 5 northern red oak) differed from modelled crown areas based on dbh, developed for oaks in closed canopy mature forest (Bechtold, 2003) for the same individual trees, after 16 growing seasons. Significance for all analyses was determined at $\alpha < 0.05$.

3. Results

3.1. Stand-level oak growth and acorn production

Average total oak density was nearly five times greater ($p < 0.0004$) in M than SW at study establishment (2003) (Table 1). Black oak, chestnut oak, and northern red oak density was greater in M than SW ($p \leq 0.0476$); white oak density did not differ between treatments (scarlet oak did not occur in SW; therefore no species-level statistical analyses were conducted) (Table 1). Total oak BA was also approximately five times greater ($p < 0.0001$) in M than SW at study establishment; chestnut oak, and northern red oak BA was greater in M than SW ($p \leq 0.0411$), but black and white oak BA did not differ between treatments (Table 1). Mean dbh of total oaks and all tested species except black oak (greater in SW; $p = 0.0034$) did not differ between treatments at study establishment (Table 1). Between 2003 and 2016 average total oak density decreased more in M than SW, but changes in density of individual oak species did not differ between the treatments. Change in BA (2003 to 2016) did not differ between M and SW for total oaks or any oak species. On average, dbh increased more in SW than M for all oaks ($p < 0.0001$) and all tested species during the 13-year study period (Table 1).

Acorns were not collected in two plots in 2004 (one SW; one M), and four plots in 2018 (three SW; one M) for logistical reasons; 21 trees died over the 17-year acorn collection period and were omitted from analyses after death or steep decline. The average number of total acorns/ha/year ranged from 4,989 ± 1,767/ha (2003) to 208,305 ± 67,955/ha (2014) in M, and from 1,237 ± 429/ha (2003) to 105,383 ± 32.077/ha (2014) in SW (Fig. 1). White oak and scarlet oak (which occurred only in M) each contributed about 33% to total crop size in M; chestnut oak and white oak each contributed > 33% to total crop size in SW (Figs. 1, 2). Average total annual acorns/ha in M was twice that in SW, but variability among individual trees and plots was high (Figs. 1, 2). Repeated measures ANOVAs indicated that stand-level acorn production (total acorns/ha) was greater in M than SW for total oaks ($p = 0.0486$) and white oak ($p < 0.0001$) but did not differ between treatments for black oak, chestnut oak, or northern red oak ($p \geq 0.2010$) (Fig. 1). Acorn production differed among years for total oaks and all tested species ($p \leq 0.0002$); no treatment × year interaction effects were detected (Fig. 1). Two-sample t-tests also indicated that acorns/ha (averaged across all years) was greater in M than SW for total oaks ($p = 0.0489$), but not for any tested species ($p = 0.1439 – 0.9559$) (Fig. 2a). Acorns/m^2 crown (averaged across all years) was greater in SW than M for total oaks ($p = 0.0414$) and northern red oak ($p = 0.0112$) but did not differ for black oak, chestnut oak, or white oak ($p \geq 0.1885$) (Fig. 2b).

3.2. Paired tree-level oak growth and acorn production

Average (2003–2019) dbh increase was approximately 70% greater in SW than M for paired total oaks and all tested species (Table 2). Sixteen-year average crown diameter and crown area increases were also greater in SW than M for paired total oak (65% and 66%, respectively) and northern red oak (77% and 74%, respectively), but did not differ for chestnut oak or white oak (Table 2). Crown areas did not differ between M and SW for total oaks or any species in 2003 ($p \geq 0.2892$); in 2019 crown area of total oaks was greater in SW than M ($p = 0.0162$) but did not differ between treatments for chestnut oak, northern red oak, or white oak ($p \geq 0.1270$) (Fig. 3a,b). In 2019 measured and modelled (Bechtold, 2003) crown areas of the same individual trees did not differ

Table 1
Total initial number of study oak trees and 0.1 ha plots (31 total), and mean (±SE) stand-level density (no./ha), diameter at breast height (dbh; cm), and basal area (BA; m^2/ha) of dominant, codominant, and intermediate total oak trees (≥12.6 cm dbh), black oak (BO), northern red oak (NRO), scarlet oak (SCO), chestnut oak (CO), and white oak (WO) at first measurement (2003; first row) and 2016 (second row), in closed canopy mature forest (M) or shelterwood (SW) harvest (ca. 1999) treatments. Results of two-sample t-tests (t; p-value) evaluate changes (2003 to 2016) in density, dbh, and BA between M and SW, Pisgah National Forest, North Carolina, USA.

Species	Year	n trees	Mean (±SE) density		Density	Mean (±SE) dbh		Dbh	Mean (±SE) BA		BA
		(plots)	M	SW	(t; p-val)	M	SW	(t; p-val)	M	SW	(t; p-val)
Total	2003	195(29)	101.9 ± 17.6	21.3 ± 4.2		40.2 ± 1.7	39.8 ± 3.0		12.5 ± 1.7	2.6 ± 0.5	
	2016		91.9 ± 14.7	20.0 ± 4.3	(2.37; 0.0297)	44.2 ± 1.7	48.8 ± 3.8	(-6.31; <0.0001)	13.9 ± 1.9	3.6 ± 0.7	(0.63; 0.5336)
BO	2003	15(8)	8.1 ± 3.1	1.3 ± 0.9		34.5 ± 3.8	53.5 ± 0.9		0.9 ± 0.4	0.3 ± 0.2	
	2016		6.9 ± 2.5	1.3 ± 0.9	(1.46; 0.1639)	39.1 ± 4.3	65.9 ± 0.6	(-4.83; 0.0029)	0.9 ± 0.4	0.5 ± 0.3	(-0.69; 0.4937)
NRO	2003	27(15)	13.1 ± 3.8	4.0 ± 1.3		41.0 ± 2.8	37.5 ± 5.7		1.8 ± 0.6	0.5 ± 0.2	
	2016		11.3 ± 3.1	3.3 ± 1.3	(-0.00; 0.3322)	47.9 ± 3.1	51.1 ± 8.3	(-2.29; 0.0409)	2.2 ± 0.7	0.8 ± 0.3	(0.48; 0.6335)
SCO[a]	2003	22(8)	13.8 ± 5.9	0.0 ± 0.0		45.4 ± 5.3	----------		2.5 ± 1.0	0.0 ± 0.0	
	2016		11.9 ± 5.3	0.0 ± 0.0	(n/a)	48.4 ± 5.7	----------	(n/a)	2.5 ± 1.1	0.0 ± 0.0	(n/a)
CO	2003	90(17)	48.1 ± 14.9	8.7 ± 3.2		38.9 ± 2.8	34.4 ± 4.6		5.0 ± 1.3	1.0 ± 0.4	
	2016		43.8 ± 12.4	8.7 ± 3.2	(-1.39; 0.1862)	42.8 ± 2.9	42.8 ± 5.3	(-5.12; 0.0001)	5.8 ± 1.5	1.5 ± 0.6	(0.94; 0.3527)
WO	2003	41(12)	18.8 ± 7.4	7.3 ± 3.0		33.5 ± 4.4	37.2 ± 6.0		2.3 ± 1.1	0.8 ± 0.3	
	2016		18.1 ± 7.0	6.7 ± 3.0	(0.05; 0.9639)	35.9 ± 4.5	42.1 ± 6.2	(-6.63; <0.0001)	2.5 ± 1.2	0.9 ± 0.4	(0.19; 0.8521)

[a] t-tests were not performed on scarlet oak, as they did not occur in SW.

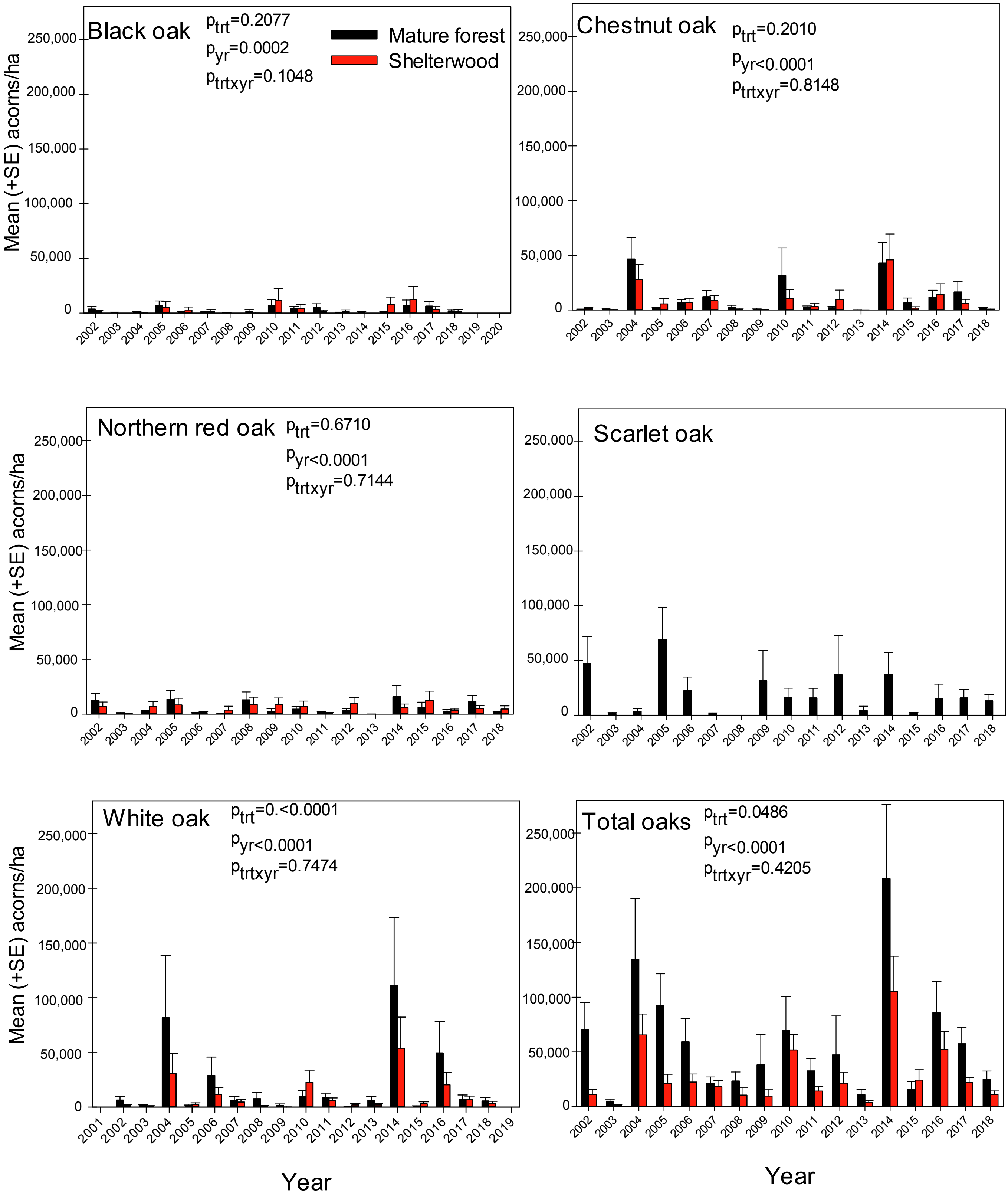

Fig. 1. Mean (±SE) stand-level number of acorns/ha/year (2002–2018) produced by black oak, chestnut oak, northern red oak, scarlet oak, white oak, and total oaks in closed canopy mature forest (M) or shelterwood harvest (SW) (ca. 1999) treatments, Pisgah National Forest, North Carolina, USA. Statistical analyses were not performed on scarlet oak, as they did not occur in SW. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

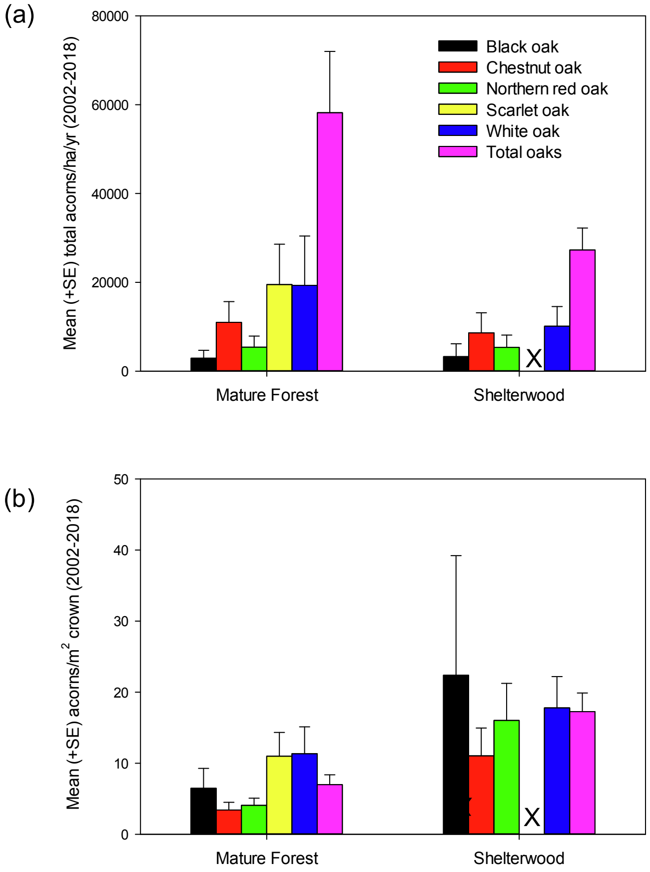

Fig. 2. Mean (±SE) stand-level average (2002–2018) (a) total number of acorns/ha and; (b) acorns/m^2 crown produced by total oaks, black oak, chestnut oak, northern red oak, scarlet oak, and white oak in closed canopy mature forest (M) or shelterwood harvest (SW) (ca. 1999) treatments, Pisgah National Forest, North Carolina, USA. Statistical analyses were not performed on scarlet oak, as they did not occur in SW. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Mean (±SE) 16-year change (2003–2019) in dbh, crown diameter, and crown area by paired (same species and similar (mean ± SE 1.8 ± 0.4 cm) dbh in 2003) chestnut oak (CO; n = 6 pair), northern red oak (NRO; n = 5 pair), white oak (WO; n = 10 pair) and total oaks (n = 21 pair) growing in closed canopy mature forest (M) and shelterwood (SW) harvest (ca. 1999) treatments, and results paired t-tests, Pisgah National Forest, North Carolina, USA.

Species					
	M	SW	Diff	t-val	p-val
Diameter at breast height (cm)					
Total	4.6 + 0.5	10.7 + 0.8	6.1 + 0.7	8.42	<0.0001
CO	4.3 + 0.6	10.4 + 1.2	6.2 + 1.3	4.96	0.0043
NRO	6.8 + 1.2	14.2 + 2.4	7.4 + 2.2	3.33	0.0298
WO	3.7 + 0.5	9.1 + 0.7	5.4 + 0.8	6.52	0.0001
Crown diameter (m)					
Total	2.6 + 0.6	4.9 + 0.5	2.3 + 0.7	3.36	0.0031
CO	3.1 + 0.6	4.9 + 0.5	1.8 + 0.9	2.01	0.1007
NRO	2.0 + 2.2	6.6 + 0.8	4.6 + 1.4	3.16	0.0341
WO	2.6 + 0.6	4.1 + 0.9	1.5 + 1.1	1.41	0.1932
Crown area (m^2)					
Total	30.3 + 8.0	64.8 + 10.8	34.4 + 10.6	3.25	0.0040
CO	33.8 + 6.1	64.6 + 14.4	30.8 + 16.2	1.90	0.1152
NRO	26.7 + 31.0	92.0 + 18.8	65.3 + 19.2	3.39	0.0275
WO	30.1 + 8.7	51.3 + 18.2	21.1 + 16.7	1.27	0.2376

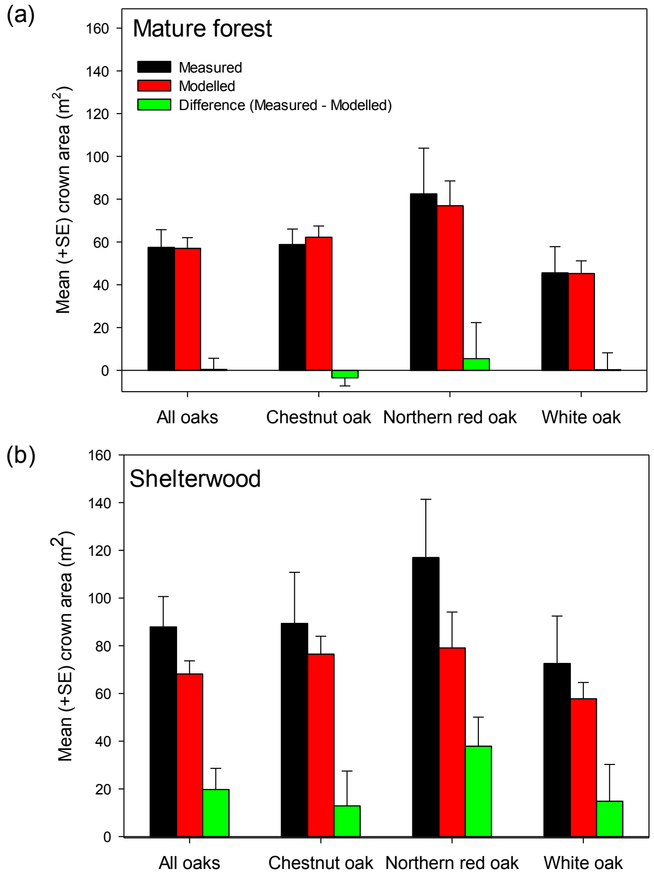

Fig. 3. Mean (±SE) 2019 measured versus modelled crown areas (m^2) of total oaks, chestnut oak, northern red oak, and white oak, and their difference (measured – modelled) for the same individual oak trees growing in closed canopy mature forest (M; total n = 18) and (separately) in shelterwood harvest (SW; total n = 21) (ca. 1999) treatments, Pisgah National Forest, North Carolina, USA. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for total oaks or any tested species in M ($p \geq 0.4117$) (Fig. 3a). In contrast, 2019 measured crown areas were greater than modelled crown areas of the same individual trees in SW, for total oak ($p = 0.0379$) and northern red oak ($p = 0.0360$), but did not differ for white or chestnut oak ($p \geq 0.3642$) (Fig. 3b). Acorns/m^2 crown was greater in SW than M for paired total oaks ($p = 0.0030$) and white oak ($p = 0.0268$), but did not differ between treatments for chestnut or northern red oak ($p \geq 0.1696$) (Fig. 4).

4. Discussion

Overall, study results indicated that on average, oak diameter growth, crown area growth, and acorns/m^2 crown were greater in SW than M. Despite five times more oak trees and oak BA in M, average annual total acorn production/ha was only double (58,199/ha in M) that in SW (27,298/ha). Acorn production was highly variable among species, individuals, and years; this was not surprising, as “masting” behavior is characteristic of oaks, and may be driven by weather, genetics, and resource allocation between growth and acorn production (Koenig and Knops, 2002). High variability and differences in the abundance of oaks and oak species between treatments and among plots likely reduced statistical detection of potential differences in acorns/ha for some species. The disparity between acorns/ha (approximately double in M) and oak density and BA (approximately five times more in M) in M and SW can be attributed to faster crown growth, larger crowns, and more acorns/m^2 crown in SW. At the stand level, average (2002–2018) acorns/m^2 crown was 71% greater for total oaks and 80% greater for northern red oak in SW than M. Results for paired, individual trees corroborated stand-level results, indicating that acorns/m^2 crown averaged 70% greater for total oaks, and 66% greater for white oaks in SW than M. Further, stand-level estimates of acorn production in SW were likely conservative (e.g., less of a difference between M and SW than estimated), as they were based on modelled crown areas developed for trees growing in fully stocked stands (Bechtold, 2003), whereas results of this study clearly indicate that total oak crown areas in SW grew faster and were generally larger than crown areas of similar-sized trees in M. Factors contributing to a greater density of acorns in SW oaks likely include greater light availability to oak crowns, allowing for increased photosynthesis and energy allocated to increased flower production and fruit development (Johnson et al., 2009). Greater crown exposure may also enhance successful wind pollination (Whitehead, 1983).

At the stand level, average 13-year total oak dbh growth was 69% greater in SW than in M; all tested species also showed 67.3% (white oak) to 72.8% (black oak) greater dbh increase in SW than in M between 2003 and 2016. Results for paired, individual trees having similar dbh's at study establishment corroborated stand-level trends; average 16-year (2003–2019) total oak dbh growth was 70% greater in SW than in M; all tested species also showed a 68% (northern red oak) to 71% (chestnut oak and white oak) greater dbh increase in SW than in M. Other studies also show greater dbh growth rates of mature (>70 yrs) sawtimber-sized oaks following heavy thinning, with the greatest growth seen following full (100%) crown release (e.g. Singer and Lorimer, 1997; Ward, 2002). Studies report increases in dbh of 53% (Ward, 2002), 59% (Smith and Miller, 1991), and 89% (Smith et al., 1989) for red oaks (primarily northern red oak) within 5–6 years of full crown release, compared to closed-canopy controls. Smith et al. reported an 80% greater dbh increase of chestnut oak compared to controls after 5 years. For white oak, some studies report dbh increases of 61% (Smith and Miller, 1991) to 117% (Smith et al., 1989) greater within 5 years of full crown release, compared to fully stocked stands. Other studies report much smaller post-release increases in white oak dbh compared to controls. For example, Miller and Stringer (2004) reported 27% greater dbh growth of fully released than unreleased 70–75 year old white oak over a 17-year period. Results of this study generally corroborate others showing that dbh growth of mature oak trees after full crown release is faster than in fully stocked, closed canopy forest stands.

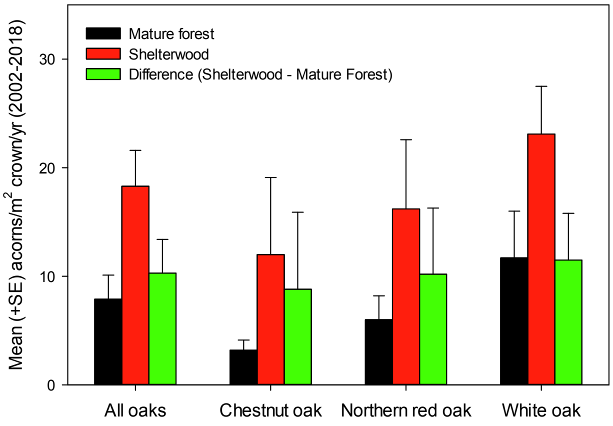

Fig. 4. Mean (±SE) (2002–2018) acorns/m^2 crown produced by paired (same species and similar (mean ± SE 1.8 ± 0.4 cm) dbh in 2003) total oaks (n = 21 pair), chestnut oak (n = 6 pair), northern red oak (n = 5 pair), and white oak (n = 10 pair) growing closed canopy mature forest (M) or shelterwood harvest (SW) (ca. 1999) treatments, Pisgah National Forest, North Carolina, USA. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Crown diameter and crown area grew faster in SW than M, as well. At the individual (paired) tree level, average 16-year crown diameter growth was 65% greater for total oaks, and 77% greater for northern red oak in SW than in M; crown diameter growth of other tested species did not statistically differ between SW and M, but a similar trend was apparent. Crown area increases by paired trees showed similar trends, with a 66% greater increase for total oaks and a 74% greater increase for northern red oak in SW than in M; after 16 years (2019), crown area for paired total oaks was greater in SW than in M. Small sample sizes for paired oaks may have impeded detection of statistically significant differences in crown diameter and crown area for some species. Other studies also report oak crown area expansion following canopy release. Trimble and Tryon (1966) reported that 55 year-old (25–56 cm dbh) northern red oak crown radii extended into group selection openings by 0.28 m for each 2.54 cm increase in dbh. Miller (1997) reported that 80 year-old northern red oak crown diameters increased by 0.2 m/year following crown release, compared to 0.1 m/year in controls. Jackson et al. (2007) reported an 8% crown area expansion by white oak one year after a partial canopy release, and 25% expansion one year following a shelterwood harvest in Tennessee.

Comparisons of 2019 measured to modelled crown areas of the same trees in M and SW (ca. 20 years post-harvest) indicated that crown area growth in M was similar to expected based on dbh alone, but greater than expected in SW. Species-specific crown-diameter equations (used to model crown areas in this study) are based on dbh (Bechtold, 2003), and were developed using mature trees in fully stocked stands. Thus, if crown area was simply a function of dbh, modelled- and measured crown areas should be similar in both M and SW. Measured crown areas that were greater than modelled crown areas in SW – but not in M – indicated that crowns expanded more rapidly in SW, where tree crowns were fully exposed to light, than in M where a high density of trees generally limited full sunlight to reaching only the top of the crown.

This study corroborates results of others showing that increased acorn production by residual trees partially compensates for reduced oak density and BA in two-aged stands where tree crowns are released (e.g., Perry and Thill, 2003; Perry et al., 2004; Bellocq et al., 2005; Olson et al., 2015). Some studies suggest that differences in acorn production between stands with fully released oak crowns and mature, closed-canopy forest are most apparent during some years than others, but results differ. Brooke et al. (2019) reported a 65% increase in white oak acorn production during the 10 years following full crown release, with increased production by "poor producers" during years of greater overall acorn production ("mast years"). Similarly, Healy (1997) reported greater acorn production by individual northern red oak trees, and more acorns/ha in thinned than control stands (density of large oaks was similar between treatments), with treatment differences most pronounced in marginal mast years, when a greater proportion of trees in thinned stands bore acorns. In contrast, Devine and Harrington (2006) reported greater acorn production by released Oregon white oak during years of overall higher mast crops. In this study, despite large differences in total stand-level acorn production among years, treatment differences were not detected within any given year, regardless of total crop size.

5. Conclusions

Oak crowns of residual trees expanded faster, grew larger, and produced up to 80% (total oaks) more acorns/m^2 crown in shelterwood harvests than trees in mature, closed canopy stands, substantially closing the gap between total acorn production (acorns/ha) in M and SW despite far fewer oaks and much less oak BA in SW. Oak dbh also increased faster in SW than M, but crown areas in SW expanded to a greater area than predicted by dbh alone. Forest managers must weigh multiple objectives, including timber growth and yield, regeneration, habitats for multiple wildlife species, and availability of acorns and other wildlife foods, when developing forest management plans and prescriptions (Perry and Thill, 2003). Results of this study indicate that full crown release by shelterwood with reserves regeneration harvests promotes acorn production by mature residual oak trees due to rapid crown expansion and more acorn/m^2 crown. In mixed-oak southern Appalachian forests, silvicultural treatments retaining 20–40 mature oaks/ha with fully released crowns will likely yield 50–100% of acorn production/ha in mature closed canopy stands, as acorn production by residual trees increases. Identifying and retaining “good” acorn producing oaks (Healy, 1999) prior to harvest could potentially further increase post-harvest acorn yields. Retention of multiple oak species will reduce the likelihood of stand-level crop failure, as acorn production differs among species and years (Greenberg, 2000; Rose et al., 2012).

Declaration of Competing Interest

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

Acknowledgments

This study was funded by the USDA Forest Service, Southern Research Station, Bent Creek Experimental Forest. Special thanks to J. Adams, K. Frick, B. Benz, M. Wind, T. Roof, E. Watson, and D. Stone for fieldwork, and many other forestry technicians and volunteers for assisting with collecting and processing acorns. I thank the staff at the Pisgah National Forest, especially T. Oprean and J. Blanton for their assistance in finding study sites. Frank Roesch and an anonymous reviewer helped to improve this manuscript. The author has no conflict of interest.

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