



Original Article

Modelling Annual Southern Appalachian Acorn Production Using Visual Surveys

CATHRYN H. GREENBERG,¹ *U.S. Department of Agriculture Forest Service, Southern Research Station, Bent Creek Experimental Forest, 1577 Brevard Road, Asheville, NC 28806, USA*

ABSTRACT Acorn production varies considerably among species, locations, and years with potential effects on populations of acorn-consuming wildlife, oak (*Quercus* spp.) regeneration, and forest ecology. Methods to estimate annual acorn crop size include acorn-trapping (quantitative) or visual surveys (indices or ranks). Forest managers need a tool for converting visual survey data to quantitative estimates of acorn yield within specific years and areas. I used 7 years (2006–2010, 2012, 2016) of visual acorn survey data with acorn trap data from the same individual trees of 5 common eastern oak species in the Pisgah National Forest, North Carolina, USA, to determine whether a known within-year relationship between the proportion of oaks bearing acorns (PBA) and acorn density using trap data (PBA-trap) could be used to predict quantitative (no. of acorns per oak), within-year acorn crops using visual survey data (PBA-visual). At the individual tree level, visually determined percent crown with acorns (PCA-visual) and number of acorns/m² trap or per crown were correlated for all oak subgroups (species, subgenera, and all oaks combined). At the population level, mean PCA-visual was correlated with the mean number of acorns/m² trap or per crown for black oak (*Q. velutina*). Both PBA-visual and mean PCA-visual, and PBA-visual and PBA-trap were correlated for all oak subgroups. At the population level, PBA-visual was a strong predictor of the mean number of acorns/m² trap or per crown for most oak subgroups. Model results can be used as an index of crop size by comparing number of acorns/m² trap or per crown among years or applied to oak inventory data to quantitatively estimate annual acorn crop sizes at the stand level or landscape level. This method enables users to estimate and compare the number of acorns produced within specific years and landscapes, rather than rely on qualitative hard-mast indices. Published 2020. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS acorn crop, acorn crop prediction, hard-mast index, oak, *Quercus* spp., southern Appalachians, visual survey.

Acorns are considered a keystone forest resource because of their influence on wildlife populations and forest ecology, yet acorn production is highly variable among individual trees, species, locations, and years (Greenberg and Paresol 2002). Acorn crop size affects the survival and reproductive success of small mammals that, in turn, influence populations of their predators (Wolff 1996). Populations of many game species, including black bear (*Ursus americanus*; Clark et al. 2005), wild turkey (*Meleagris gallopavo*; Steffen et al. 2002), and white-tailed deer (*Odocoileus virginianus*; Feldhamer 2002) are also influenced by acorn availability. Heavy, selective browsing of seedlings, herbaceous plants, and woody vegetation by high-density white-tailed deer populations can, in turn, affect forest composition and structure (Feldhamer 2002). Acorn production also directly

affects oak (*Quercus* spp.) regeneration (Loftis and McGee 1993). For these reasons, annual hard-mast surveys have been conducted for decades by many state wildlife agencies.

Methods to estimate annual acorn crop size include trapping to estimate number of acorns/m² trap or per crown (e.g., Rose et al. 2012), or visual methods to index crop size on a relative scale. Acorn-trapping is time-consuming and labor-intensive because traps must be constructed and placed under trees, and acorns collected throughout the autumn and counted for multiple individuals and species to obtain accurate estimates of crop size. In contrast, visual surveys are rapid, and conducted once annually just prior to acorn fall, enabling inclusion of large sample sizes required for accurate crop size estimation (Koenig et al. 1994). Visual methods include qualitative surveys to rank acorn crops into categories from none to bumper (Sharp 1958, Graves 1980, Christisen and Kearby 1984), or scored estimates of the percentage of crown with acorns, percentage of twigs with acorns, and number of twigs with acorns on a subsample of oak limbs (Whitehead 1969). Time-constrained acorn

Received: 19 August 2019; Accepted: 20 February 2020
Published:

¹E-mail: katie.greenberg@usda.gov

counts provide ratio-level data of acorn production (e.g., the no. that can be counted in 30 sec), but are not intended to estimate total acorn yield (Koenig et al. 1994). Acorn trapping provides a quantitative estimate of acorn production—the number of acorns produced per oak tree—whereas, hard-mast indices provide a relative ranking and basis for comparison of within- and between-year acorn crop size at a broad scale.

Several studies have established a relationship between hard-mast indices based on visual survey data and acorn density on individual trees. Koenig et al. (1994) and Garrison et al. (1998) reported correlations between time-constrained acorn counts and acorn densities in traps for several California, USA, oak species. Perry and Thill (1999) reported a correlation between 5 visual survey methods and number of acorns/m² trap for white oaks (*Q. alba*). Koenig et al. (1994) also found a linear relationship between time-constrained acorn counts and acorn density in traps for 3 species of western oaks, indicating that this was an effective method of predicting acorn density.

Greenberg and Parresol (2000) determined that the proportion of oak trees bearing acorns (PBA) was correlated with the density of acorns on fruiting trees based on trap data (PBA-trap). Thus, they demonstrated that poor crop years were a function of fewer oak trees producing, and fewer acorns on those trees; conversely, good crop years were characterized by more productive oak trees and more acorns on those trees (Greenberg and Parresol 2000). Subsequently, Greenberg and Warburton (2007) used 21 years of visual survey data, gathered for the North Carolina Wildlife Resource Commission's annual hard-mast index, to verify the synchronous relationship between PBA (based on acorn presence or absence) and acorn density on crowns using visual estimates of the percentage of crown with acorns (PCA-visual). Further, they demonstrated that visual determination of PBA (PBA-visual) based on acorn presence or absence on oaks was, alone, a strong predictor of Whitehead's (1969) hard-mast index values. Consequently, several eastern state wildlife agencies have adopted this, or a modified version, of this fast, simple visual method to index annual acorn crop size, allowing standardized relative crop size comparisons among states or regions. Although PBA-visual provides a simple, rapid method for indexing acorn crop size on a relative scale, it does not provide a mechanism for translating that index (PBA-visual) into the actual number of acorns produced within specific years and areas, when applied to forest inventory data. Direct, rather than relative estimates of acorn availability each year would help wildlife and forest managers predict wildlife population trends, set game harvest limits, and plan silvicultural activities to better promote oak regeneration.

The within-year relationship between PBA, based on presence or absence of acorns in traps (PBA-trap), and acorn density (Greenberg and Parresol 2000) shows promise as a method for determining annual crop size, but requires annual acorn-trapping at hundreds of trees for accurate estimates (Greenberg and Parresol 2000). Visual determination of PBA, based on presence or absence of acorns in

tree crowns (PBA-visual), is less time-consuming than trapping. However, the relationship between trap-based PBA-trap and visual survey-based PBA-visual has not been established, and use of either PCA-visual or PBA-visual in estimating quantitative acorn yield has not been tested.

I used 7 years of visual acorn survey data with acorn trap data from the same individual trees of 5 common eastern oak species to assess whether PCA-visual or PBA-visual can be used to quantitatively estimate acorn production at the tree level or landscape level. Specifically, I asked 1) are PCA-visual estimates correlated with the number of acorns/m² trap or per crown at the individual tree or population (averaged across trees) level; 2) are PBA-visual estimates (proportion of trees with acorns based on acorn presence or absence determined by visual surveys) comparable to PBA-trap (proportion of trees with acorns based on presence-absence in acorn traps); and 3) can visual data (PCA-visual or PBA-visual) be used to predict quantities of acorns based on acorn trap data, at the individual tree level or population level?

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, USA. Average annual rainfall in the region ranges from about 1,000 to 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*), black oak (*Q. velutina*); blackgum (*Nyssa sylvatica*) and sourwood (*Oxydendrum arboreum*) were common midstory 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).

METHODS

Acorn Sampling

Field technicians concurrently conducted visual surveys (PCA-visual) and acorn-trapping on 477 oak trees of 5 common oak species for 7 years (2006–2010, 2012, and 2016). Study species included black oak ($n = 36$), northern red oak ($n = 79$), and scarlet oak ($n = 69$) in the red oak group (subgenus *Quercus* section *Lobatae*), and chestnut oak ($n = 174$) and white oak ($n = 119$) in the white oak group (subgenus *Quercus* section *Quercus*). Sample trees represented mature oaks in dominant or codominant canopy positions (a few were intermediate) across a wide range of size classes (means ranged from 42.1 to 60.6 cm diameter at breast height [dbh] across species; Table 1). Sample trees

Table 1. Number of visual surveys conducted concurrently with acorn-trapping during all years (2006–2010, 2012, 2016) combined, range of sample sizes each year (*n*), and mean (\pm SE) dbh (cm) and calculated crown area (m²) for 5 oak species, the red oak subgenus, the white oak subgenus, and all oaks combined, Pisgah National Forest, North Carolina, USA.

Group and species	Total ^a	<i>n</i> trees/yr	Dbh (cm)		Crown area (m ²) ^b	
			\bar{x}	\pm SE	\bar{x}	\pm SE
Red oak group	1,065	118–172	51.2	0.6	41.4	2.0
Black oak	210	20–34	48.2	1.0	41.4	2.7
Northern red oak	452	48–76	60.6	0.9	60.7	3.2
Scarlet oak	403	49–62	42.1	0.9	22.1	3.1
White oak group	1,756	142–287	44.0	0.4	46.5	1.2
Chestnut oak	1,020	79–171	43.8	0.5	35.1	0.9
White oak	736	63–117	44.3	0.7	46.5	2.4
All oaks	2,821	260–459	46.7	0.4	83.2	1.1

^a Most, but not all of the same trees were surveyed and trapped each year; statistics reflect the same trees during multiple years.

^b Crown areas calculated using equations based on tree dbh (Bechtold 2003, Rose et al. 2012).

were located across a wide range of elevation (510–1,260 m above sea level), aspect, slope position, and percent slope. Most trees were in closed-canopy forest; a few (3.4% of trees; 5.2% of total samples, all years) were in young (1999) shelterwood with reserves stands. Field technicians measured diameter at breast height of all sample trees during winter 2006–2007.

Field technicians collected acorns at 2–4-week intervals from mid-August through the completion of acorn drop in late November or December, from 3, circular, 0.46-m² traps placed randomly beneath each tree crown. Technicians counted mature (not including aborts) acorns from each tree (all traps and collections per tree, per year) in the lab. One observer visually surveyed each trapped tree with binoculars (8 × 42 power) for approximately 30 seconds (e.g., Koenig et al. 1994), once during mid-August through early September (prior to acorn fall), to determine the presence or absence of acorns and estimate the PCA-visual. After initial training by an experienced field technician, approximately 3 observers conducted surveys each year; individual observers sometimes differed among years. Most often, observers based PCA-visual on a partial (<100%), presumably representative, view of the crown because complete crowns were rarely visible under the closed-canopy conditions. Error introduced by differences among observers, or differences in visible crown area among trees or years likely reflected “real world” hard-mast surveys conducted by state agencies, and contributed to the experimental variability. Crop size estimates based on traps and visual surveys (PCA-visual) are likely conservative on account of possible arboreal acorn predation or predation from traps (Perry and Thill 1999).

Data Analysis

I used average total (all collections) number of acorns across the 3 traps to estimate number of acorns/m² trap per individual tree. I multiplied the mean number of acorns/m² trap by the estimated tree crown area to estimate the total number of acorns per individual tree crown. I used individual tree dbh

values to calculate crown diameter using crown diameter equations developed for each oak species (Bechtold 2003, Rose et al. 2012), and calculated crown areas using the formula for circle area [$\text{Area} = \pi(r^2)$]. To calculate PBA-trap for each year, I divided the number of trees with acorns (>0 acorns) present in traps by the total number of trees trapped and multiplied by 100. To calculate PBA-visual for each year, I divided the number of trees with PCA-visual >0% by the total number of trees surveyed and multiplied by 100.

I used Pearson’s product-moment correlations for each species, subgenus, and all oaks to examine the relationship between visual, relative estimates of acorn production (PCA-visual), and quantitative, trap-based estimates of acorn density (no. of acorns/m² trap, and no. of acorns/crown) at the individual tree level (1 data point/tree/yr), and population level (averages, across all trees; 1 data point/yr; *n* = 7). I natural-log-transformed trap-based estimates of acorn density to reduce heteroscedasticity (Zar 1984). I also performed correlations between within-year PBA-visual and mean PCA-visual to test and confirm the positive relationship between PBA and acorn density already established using trap (Greenberg and Parresol 2000) and visual (Greenberg and Warburton 2007) data. Finally, I performed correlations between PBA-visual and PBA-trap to test the equivalence of trap and visual estimates of PBA.

I used reduced major-axis regression (Sokal and Rohlf 1981) to develop predictive equations of natural-log-transformed number of acorns/m² trap and per crown, with PBA-visual as the predictor variable for each species, subgenera, and for all oaks. Reduced major-axis regression was appropriate because the independent variable (PBA-visual) was a sample-based estimate and, therefore, considered a random variable subject to error. In contrast, ordinary least-squares regression analysis assumes that the independent variable (*X*) is fixed, with no error (see Greenberg and Parresol 2000 for further explanation). For regressions, I report the correlation coefficient, rather than the coefficient of determination because in reduced major-axis regression the slope is different from zero if the correlation coefficient is significant (Ricker 1984). I set significance level at $\alpha = 0.05$.

RESULTS

Field technicians conducted 2,821 visual surveys on oak trees with acorn traps during the 7 years sampled (Table 1). Number of trees sampled each year ranged from 260 to 459; sample sizes were smaller when the sample was split into subgenera or species (Table 1). At the individual tree level (1 data point/tree-yr), PCA-visual and number of acorns/m² trap were moderately correlated ($P < 0.001$; $r = 0.48\text{--}0.61$) for all oak subgroups (species, subgenera, and all oaks combined); correlations between PCA-visual and number of acorns/crown were slightly weaker ($P < 0.001$; $r = 0.40\text{--}0.54$; Table 2). At the population level (averaged across all trees for each year; 1 data point/yr; *n* = 7), mean PCA-visual was correlated with the mean number of acorns/m² trap for black oak ($P = 0.014$; $r = 0.85$), but not for the other oak subgroups ($P = 0.052\text{--}0.169$; $r = 0.64\text{--}0.75$). A similar trend

Table 2. Pearson's product-moment correlations of percent crown with acorns based on visual surveys (PCA-visual) and the mean number of acorns/m² trap or per crown (natural-log-transformed) per individual tree for all years (2006–2010, 2012, 2016) combined for 5 oak species, the red oak subgenus, the white oak subgenus, and all oaks combined, Pisgah National Forest, North Carolina, USA.

Group and species	<i>n</i> (all yr) ^a	PCA-visual (no./m ² trap)		PCA-visual (no./crown)	
		<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>
Red oak group	1,065	<0.001	0.58	<0.001	0.49
Black oak	210	<0.001	0.55	<0.001	0.49
Northern red oak	452	<0.001	0.51	<0.001	0.43
Scarlet oak	403	<0.001	0.61	<0.001	0.54
White oak group	1,756	<0.001	0.52	<0.001	0.45
Chestnut oak	1,020	<0.001	0.48	<0.001	0.40
White oak	736	<0.001	0.53	<0.001	0.46
All oaks	2,821	<0.001	0.55	<0.001	0.47

^a Most of the same trees were surveyed and trapped each year; data points reflect the same trees during multiple years.

was apparent for the correlation between PCA-visual and the number of acorns/crown (Table 3).

Correlations between annual PBA-visual and mean PCA-visual estimates were relatively strong for all oak subgroups ($P = 0.039$ – <0.001 ; $r = 0.78$ – 0.98 ; Table 4). PBA-visual and PBA-trap were also correlated for all oak subgroups ($P = 0.035$ – 0.004 ; $r = 0.79$ – 0.92 ; Table 5), indicating that both methods of estimating the percentage of trees bearing acorns yielded similar results, and visual determination of the percentage of trees bearing acorns (PBA-visual) is a reliable predictor of acorn yield.

At the population level (acorn density averaged across all trees for each year; 1 data point/yr; $n = 7$), PBA-visual was a strong predictor of the mean number of acorns/m² trap for most oak subgroups, but not for chestnut oak ($P = 0.08$; $r = 0.70$) and all oaks ($P = 0.11$; $r = 0.66$; Table 6). PBA-visual was also a predictor of the mean number of acorns/crown for all oak subgroups except chestnut oak ($P = 0.08$; $r = 0.69$) and all oaks ($P = 0.12$; $r = 0.64$; Table 6; Fig. 1). Equations using PBA-visual were developed to predict the mean number of acorns/m² trap and acorns/crown each year (Table 6; Fig. 2). The visually determined proportion of

Table 3. Pearson's product-moment correlations of mean annual (2006–2010, 2012, 2016) percent crown with acorns based on visual surveys (PCA-visual) and the mean number of acorns/m² trap and per crown (natural-log-transformed) for 5 oak species, the red oak subgenus, the white oak subgenus, and all oaks combined, Pisgah National Forest, North Carolina, USA.

Group and species	<i>n</i> trees/yr	PCA-visual (no./m ² trap)		PCA-visual (no./crown)	
		<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>
Red oak group	118–172	0.052	0.75	0.057	0.74
Black oak	20–34	0.014	0.85	0.028	0.81
Northern red oak	48–76	0.047	0.76	0.054	0.75
Scarlet oak	49–62	0.102	0.67	0.108	0.66
White oak group	142–287	0.104	0.66	0.095	0.68
Chestnut oak	79–171	0.169	0.58	0.185	0.57
White oak	63–117	0.085	0.69	0.077	0.70
All oaks	260–459	0.124	0.64	0.143	0.61

Table 4. Pearson's product-moment correlations of the annual (2006–2010, 2012, 2016) percentage of trees bearing acorns based on visual surveys (PBA-visual), and mean percent crown with acorns based on visual surveys (PCA-visual) for 5 oak species, the red oak subgenus, the white oak subgenus, and all oaks combined, Pisgah National Forest, North Carolina, USA.

Group and species	<i>n</i> trees/yr	<i>P</i>	<i>r</i>
Red oak group	118–172	0.013	0.86
Black oak	20–34	0.039	0.78
Northern red oak	48–76	<0.001	0.98
Scarlet oak	49–62	0.039	0.78
White oak group	142–287	0.007	0.90
Chestnut oak	79–171	0.001	0.95
White oak	63–117	0.016	0.85
All oaks	260–459	0.006	0.89

trees bearing acorns (PBA-visual) ranged from 20% to 78% among years for all oaks combined, and from 6% to 88% among years for other oak subgroups (Table 6). Model results can be used as an index, relative comparison of crop size by comparing number of acorns/m² trap, or number of acorns/crown among years. Alternatively, results can be applied to oak inventory data (e.g., multiplied by the no. of oaks for each subgroup within a given area, assuming dbhs are equivalent to those used in model development; Table 1) to quantitatively estimate annual acorn crop sizes at the stand level or landscape level.

DISCUSSION

Regression models successfully estimated within-year acorn production for most oak subgroups tested, based on the proportion of trees bearing acorns determined from visual surveys (PBA-visual). Regression results for chestnut oak and all oaks were not informative, suggesting equations for those subgroups may not be valid. Similarly, results for PBA-visual estimates greater than approximately 80% (depending on the oak subgroup) should be interpreted cautiously because these predictions extend beyond the range of data used in modelling. Crop size estimates can be used alone as a quantitative index of annual acorn crop size (relative no. of acorns/m² trap, or per crown each year), or applied to oak inventory data (e.g., no. of mature oak trees) to quantitatively estimate the number of acorns produced within specific forest stands or landscapes each year. Crude estimates of acorn production at the stand level or landscape level can be generated simply by applying equation results

Table 5. Pearson's product-moment correlations of the annual ($n = 7$ yr; 2006–2010, 2012, 2016) percentage of trees bearing acorns based on visual surveys (PBA-visual) and acorn traps (PBA-trap) for 5 oak species, the red oak subgenus, the white oak subgenus, and all oaks combined, Pisgah National Forest, North Carolina, USA.

Group and species	<i>n</i> trees/yr	<i>P</i>	<i>r</i>
Red oak group	118–172	0.005	0.92
Black oak	20–34	0.004	0.91
Northern red oak	48–76	0.016	0.85
Scarlet oak	49–62	0.007	0.89
White oak group	142–287	0.013	0.86
Chestnut oak	79–171	0.035	0.79
White oak	63–117	0.005	0.91
All oaks	260–459	0.011	0.87

Table 6. Range in annual (2006–2010, 2012, 2016) sample size and percentage of trees bearing acorns based on visual surveys (PBA-visual), and reduced major axis regression of annual PBA-visual on the natural-log-transformed mean number of acorns/m² trap and per crown for 5 oak species, the red oak subgenus, the white oak subgenus, and all oaks combined, Pisgah National Forest, North Carolina, USA.

Group and species	<i>n</i> trees	PBA-visual (%)	<i>P</i>	<i>r</i>	Equation ^a [Ln(<i>Y</i>) = <i>b</i> ₀ + <i>b</i> ₁ (PBA-visual)]
Equations for mean no. of acorns/m ² trap					
Red oak subgenus	118–172	4.2–81.4	0.002	0.93	Ln(<i>Y</i>) = -0.67599 + 0.051764(PBA-visual)
Black oak	20–34	0.0–88.2	0.001	0.94	Ln(<i>Y</i>) = -0.46132 + 0.042437(PBA-visual)
Northern red oak	48–76	6.1–79.7	0.038	0.78	Ln(<i>Y</i>) = -0.54933 + 0.048794(PBA-visual)
Scarlet oak	49–62	4.1–87.3	0.003	0.92	Ln(<i>Y</i>) = -0.98462 + 0.054600(PBA-visual)
White oak subgenus	14–287	4.9–76.2	0.041	0.78	Ln(<i>Y</i>) = 0.13684 + 0.047025(PBA-visual)
Chestnut oak	79–171	4.7–74.2	0.078	0.70	Ln(<i>Y</i>) = -0.56496 + 0.050400(PBA-visual)
White oak	63–117	5.2–78.9	0.015	0.85	Ln(<i>Y</i>) = 0.25079 + 0.047071(PBA-visual)
All oaks	260–459	20.0–78.1	0.109	0.66	Ln(<i>Y</i>) = 1.09710 + 0.027852(PBA-visual)
Equations for mean no. of acorns/crown					
Red oak subgenus	118–172	4.2–81.4	0.002	0.94	Ln(<i>Y</i>) = 3.78044 + 0.056018(PBA-visual)
Black oak	20–34	0.0–88.2	0.003	0.93	Ln(<i>Y</i>) = 3.78045 + 0.046504(PBA-visual)
Northern red oak	48–76	6.1–79.7	0.044	0.77	Ln(<i>Y</i>) = 4.00608 + 0.054506(PBA-visual)
Scarlet oak	49–62	4.1–87.3	0.002	0.94	Ln(<i>Y</i>) = 3.39469 + 0.059171(PBA-visual)
White oak subgenus	142–287	4.9–76.2	0.026	0.81	Ln(<i>Y</i>) = 4.08421 + 0.059223(PBA-visual)
Chestnut oak	79–171	4.7–74.2	0.083	0.69	Ln(<i>Y</i>) = 3.65009 + 0.049606(PBA-visual)
White oak	63–117	5.2–78.9	0.006	0.90	Ln(<i>Y</i>) = 4.23700 + 0.058630(PBA-visual)
All oaks	260–459	20.0–78.1	0.122	0.64	Ln(<i>Y</i>) = 5.32369 + 0.036271(PBA-visual)

^a To convert to actual (rather than natural-log-transformed) no. of acorns, take the antilog of equation result; acorns = exp(*Y*; Fig. 2).

for number of acorns/crown to each mature tree (assuming that average dbh values are analogous to those used in this study), and multiplying by the number of mature trees (per species, subgenera, or all oaks) present. Alternatively, more refined estimates of acorn production at a stand level or landscape level can be generated by applying results of equations predicting the number of acorns/m² trap each year to predicted crown areas for individual trees (based on species and dbh; Bechtold 2003, Rose et al. 2012) and summed across all trees. Rose et al. (2012) developed predictive models of average acorn production for eastern oaks that can be applied to oak inventory data (Greenberg et al. 2014), but their models do not provide estimates of within-year acorn crop yields, which fluctuate considerably. My acorn production models provide a method to quantitatively estimate acorn crop sizes each year, rather than rely on indices that rank crops from low to high, with no indication of actual acorn quantities produced at the tree level or landscape level.

Despite the strong correlation between PBA-visual and number of acorns/m² trap or per crown at the population level, results showed only a modest correlation between PCA-visual estimates and the number of acorns/m² trap or per crown at the individual tree level, or between mean PCA-visual and mean number of acorns/m² trap or per crown at the population level for all oak subgroups except black oak. This was likely due to error in PCA-visual estimates, trap-based estimates, or both. PCA-visual estimates are potentially hampered by observer bias, obstructed views of tree crowns in closed-canopy forest, and difficulties in seeing acorns as a result of crown height, tree foliage, wind, cloud cover, or sun angle (Perry and Thill 1999). Acorn size, color, or position on twigs can also influence the accuracy of visual surveys, and differs among species and subgenera (Koenig et al. 1994, Perry and Thill 1999). The number of acorns falling into traps may be affected by acorn predation

from traps or tree crowns (Gysel 1956, Perry and Thill 1999), trap placement beneath crowns, the relatively small proportion of tree crown sampled by traps, or acorns “missing” traps as a consequence of bouncing off limbs as they fall. Despite these same error sources, Perry and Thill (1999) reported a strong correlation ($r = 0.81–0.87$) between indices from 5 visual survey methods and white oak acorn density/m² trap. Results here indicated that PBA-visual derived from PCA-visual (acorns present if PCA-visual >0%) proved to be a strong predictor of acorn crop size for most oak subgroups, indicating that potential error in PCA-visual estimates and acorn-trapping was less important when only acorn presence or absence data were required, and sample size was large.

The predictive power of PBA on annual acorn production results from the strong, positive relationship between PBA and number of acorns per tree; these factors act synchronously, resulting in highly variable acorn crops among years. This relationship, and the predictive power of PBA on annual acorn production, was established previously by Greenberg and Parresol (2000), but their PBA estimates were based on presence or absence of acorns in traps (PBA-trap), rather than visual surveys. Greenberg and Warburton (2007) also illustrated this relationship using visually determined PBA (PBA-visual) to predict hard-mast indices. However, neither method provided a linkage between PBA-visual and actual numbers of acorns produced. My results show that PBA-trap and PBA-visual yield similar estimates of PBA, and PBA-visual can be used successfully to predict annual acorn production.

Precise estimates of PBA-visual must be obtained for acorn production models to be accurate. Greenberg and Warburton (2007) found that the number of sample trees (by species, subgenera, or all oaks) required to obtain precise (within 5% of the true proportion) PBA estimates ranged from 60–165 at an 80% confidence level, increasing to 139–385 at a 95%

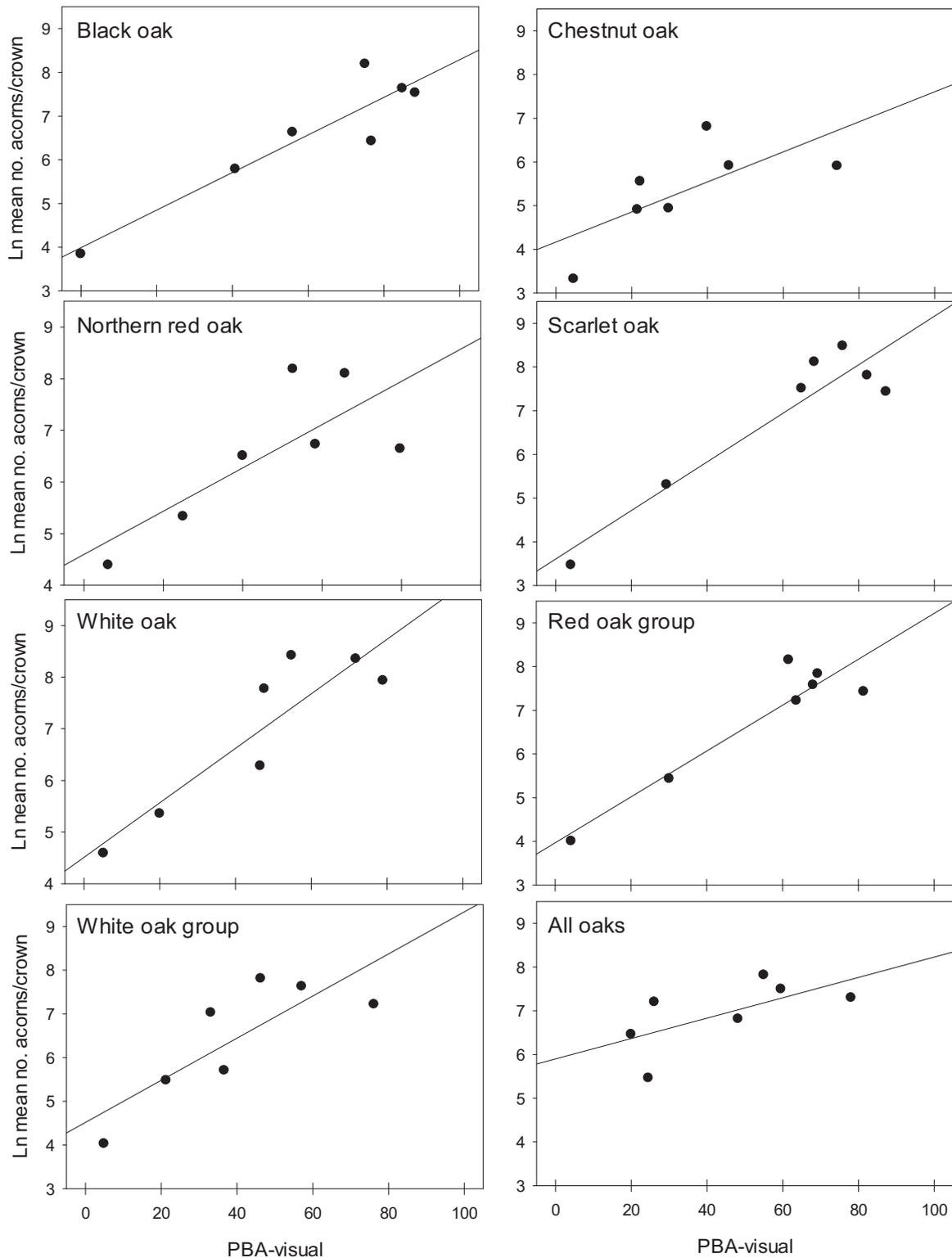


Figure 1. Regression of natural-log-transformed mean number of acorns/crown with visually determined proportion of oaks bearing acorns (PBA-visual; 2006–2010, 2012, 2016) for 5 oak species, the red and white oak subgenera, and all oaks combined, Pisgah National Forest, North Carolina, USA.

confidence level, with fewer samples required during poor (low PBA) and good (high PBA) crop years, and more during moderate crop years. Even so, 30-second visual surveys of dozens to hundreds of trees per targeted subgroup (species, subgenera, or all oaks) to determine the presence or absence of acorns is simple; use of these models can yield results

otherwise attained only by trapping and collecting acorns at hundreds of oak trees each autumn.

MANAGEMENT IMPLICATIONS

I provide a method for forest and wildlife managers to convert annual visual acorn survey data to quantitative estimates

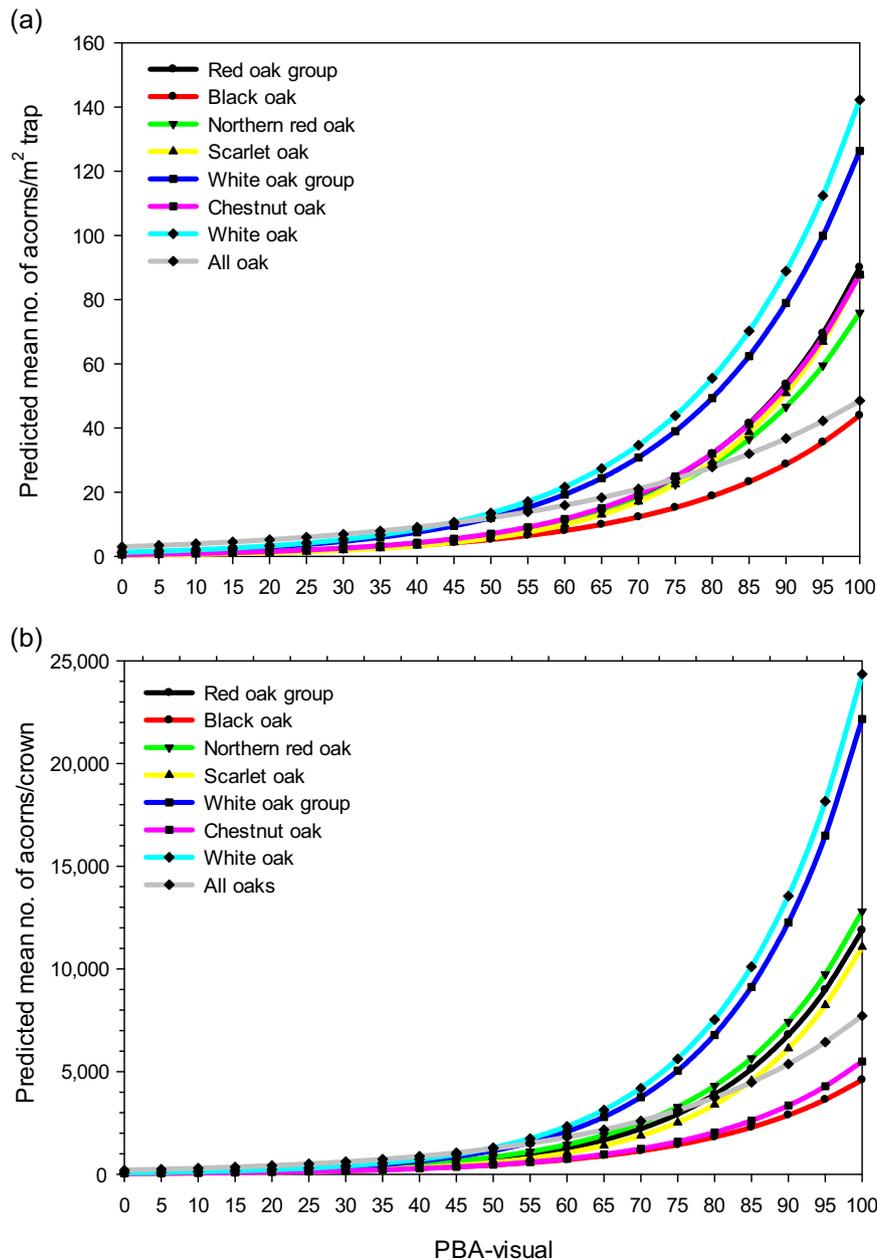


Figure 2. Predicted number of acorns per (a) m^2 trap and (b) tree crown, based on the visually determined proportion of oaks bearing acorns (PBA-visual) for 5 oak species, the red and white oak subgenera, and all oaks combined (for years 2006–2010, 2012, 2016), Pisgah National Forest, North Carolina, USA. Predictions are based on back-transformed results using equations presented in Table 6. Note that maximum PBA-visual ranged from 74.2 to 88.2 among oak subgroups during the years modelled; results using PBA-visual greater than the range of data used in modelling should be interpreted cautiously.

of acorn yield across large areas for 5 common eastern oak species, subgenera, or all oaks based on the proportion of oaks bearing acorns (presence or absence). Estimates are based on the average number of acorns/ m^2 trap or per crown; therefore, equations are not intended to predict production by individual trees, but can be applied at the population level in areas where oaks are abundant. Model results can be used alone as an index by comparing equation results among years or landscapes or applied to forest inventory data (e.g., multiplied by the no. of oaks per subgroup, assuming dbh values are similar to those used in model development) for estimates of annual acorn production tailored to specific land units.

Visual determination of acorn presence for estimating PBA-visual is rapid and low-cost compared with acorn-trapping, enabling managers to sample the large number of trees required for accurate PBA-visual and crop size estimation. These models provide a tool for users to estimate and compare the number of acorns produced within specific years and landscapes, rather than rely on relative comparisons of crop yield provided by hard-mast indices.

ACKNOWLEDGMENTS

My study was funded by the U.S. Department of Agriculture Forest Service, Southern Research Station, Bent

Creek Experimental Forest. Special thanks to J. Adams, K. Frick, B. Benz, M. Wind, and T. Roof, for fieldwork, and many other forestry technicians and volunteers for assisting with visual surveys or 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. T. L. Keyser, E. B. Arnett and 2 anonymous reviewers helped to improve this manuscript. The author has no conflict of interest.

LITERATURE CITED

- Bechtold, W. A. 2003. Crown-diameter prediction models for 87 species of stand-grown trees in the eastern United States. *Southern Journal of Applied Forestry* 27:269–278.
- Christisen, D. M., and W. H. Kearby. 1984. Mast measurement and production in Missouri (with special reference to acorns). Missouri Department of Conservation Terrestrial Series 13, Jefferson City, USA.
- Clark, J. D., F. T. van Manen, and M. R. Pelton. 2005. Bait stations, hard mast, and black bear population growth in the Great Smoky Mountains National Park. *Journal of Wildlife Management* 69:1633–1640.
- Feldhamer, G. A. 2002. Acorns and white-tailed deer: interrelationships in forest ecosystems. Pages 215–223 in W. J. McShea and W. M. Healy, editors. *Oak forest ecosystems: ecology and management for wildlife*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Garrison, B. A., R. L. Wachs, J. S. Jones, and M. L. Triggs. 1998. Visual counts of acorns of California black oak (*Quercus kelloggii*) as an indicator of mast production. *Western Journal of Applied Forestry* 13:27–31.
- Graves, W. C. 1980. Annual oak mast yields from visual estimates. Pages 270–274 in T. R. Plumb, technical coordinator. *Proceedings of the symposium on the ecology, management, and utilization of California oaks*. U.S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-44, Albany, California, USA.
- Greenberg, C. H., C. E. Keyser, L. C. Rathbun, A. K. Rose, T. M. Fearer, and W. H. McNab. 2014. Forecasting long-term acorn production with and without oak decline using forest inventory data. *Forest Science* 60:222–230.
- Greenberg, C. H., and B. R. Parresol. 2000. Acorn production characteristics of southern Appalachian oaks: a simple method to predict within-year acorn crop size. U.S. Department of Agriculture Forest Service, Research Paper SRS-RP-20, Asheville, North Carolina, 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: ecology and management for wildlife*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Greenberg, C. H., and G. S. Warburton. 2007. A rapid hard-mast index from acorn presence-absence tallies. *Journal of Wildlife Management* 71:1654–1661.
- Gysel, L. W. 1956. Measurement of acorn crops. *Forest Science* 2:305–313.
- Koenig, W. D., J. M. H. Knops, W. J. Carmen, M. T. Stanback, and R. L. Mumme. 1994. Estimating acorn crops using visual surveys. *Canadian Journal of Forest Research* 24:2105–2112.
- Loftis, D. L., and C. E. McGee, editors. 1993. *Oak regeneration: serious problems, practical recommendations*. U.S. Department of Agriculture Forest Service, General Technical Report SE-GTR-84, Asheville, North Carolina, USA.
- McNab, W. H. 2011. Subregional variation in upland hardwood forest composition and disturbance regimes of the central hardwood region. Pages 11–26 in C. H. Greenberg, B. Collins, and F. R. Thompson, editors. *Sustaining young forest communities—ecology and management of early successional habitats in the US central hardwood region*. Springer, New York, New York, USA.
- Perry, R. W., and R. E. Thill. 1999. Estimating mast production: an evaluation of visual surveys and comparison with seed traps using white oaks. *Southern Journal of Applied Forestry* 23:164–169.
- Pittillo, J. D., R. D. Hatcher, Jr., and S. W. Buol. 1998. Introduction to the environment and vegetation of the Southern Blue Ridge Province. *Castanea* 1998:202–216.
- Ricker, W. E. 1984. Computation and uses of central trend lines. *Canadian Journal of Zoology* 62:1897–1905.
- Rose, A. K., C. H. Greenberg, and T. M. Fearer. 2012. Acorn production prediction models for five common oak species of the eastern United States. *Journal of Wildlife Management* 76:750–758.
- Sharp, W. M. 1958. Evaluating mast yields in the oaks. *Pennsylvania State University Agriculture Experiment Station Bulletin* 635, University Park, USA.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry: the principles and practice of statistics in biological research*. Second edition. W. H. Freeman, San Francisco, California, USA.
- Steffen, D. E., N. W. Lafon, and G. W. Norman. 2002. Turkeys, acorns, and oaks. Pages 241–255 in W. J. McShea and W. M. Healy, editors. *Oak forest ecosystems: ecology and management for wildlife*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Whitehead, C. J. 1969. Oak mast yields on wildlife management areas in Tennessee. Tennessee Game and Fish Commission, Nashville, USA.
- Wolff, J. O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy* 77: 850–856.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Associate Editor: Arnett.