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# Acorn Production Characteristics of Southern Appalachian Oaks: A Simple Method to Predict Within-Year Acorn Crop Size

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### Abstract

Acorns are an important food resource for many wildlife species and the seed source for oak regeneration. Variability in acorn production within and among species is well known. Yet little is known about the population-level characteristics that contribute to crop size, or if such characteristics can be used to predict within-year crop size. We examined acorn production from 1993–97 by black oak (*Quercus velutina* Lam.), northern red oak (*Q. rubra* L.), scarlet oak (*Q. coccinea* Muenchh.), chestnut oak (*Q. prinus* L.), and white oak (*Q. alba* L.) in the Southern Appalachians to determine how frequency of acorn production, levels of intraspecific synchrony, and acorn density per tree influence crop size. We then developed a linear regression model for each species to quantitatively estimate acorn crop size within years using the proportion of trees bearing acorns as the independent variable. We also developed acorn yield tables for each species. Each species produced one to two good, one moderate, and two to three poor acorn crops. Acorn production was not synchronous among conspecifics. At least 29 percent of individuals produced acorns in all but the poorest crop year for all species. In good crop years, 70 to 90 percent of individuals produced acorns and 3 to 29 percent produced even during the poorest crop years. High year-to-year variability in the degree of fruiting synchrony and crop size within a population suggests that the term "masting" may not appropriately characterize the fruiting patterns of Southern Appalachian oaks. We found a strong relationship between the proportion of trees bearing acorns and crop size. Using these equations, land managers can quantitatively estimate within-year crop size per species if they know the proportion of fruiting trees as estimated by simple visual surveys (presence or absence of acorns or both). By applying the estimate (in units of number per square meter basal area) for each species to a basal area inventory of oaks in their area, managers can tailor within-year crop size estimates to specific land management units. Alternatively, acorn yield tables can be applied to oak basal area inventories to tailor estimates of acorn production (the sum of each species) on an average annual basis to any area. Yield tables also can be used to test how acorn production will be affected on an average annual basis using different basal area apportionment scenarios among oak species.

**Keywords:** Acorn production, hard mast, masting, oak, predicting acorn crop size, reduced major axis regression, Southern Appalachian oaks, visual acorn surveys.

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## Introduction

Acorns are an important food source for many wildlife species (Martin and others 1951, Van Dersal 1940) and the seed source for oak (*Quercus* spp.) regeneration. Acorn production varies tremendously from year to year and among species and individuals (Beck 1977; Burns and others 1954; Christisen and Kearby 1984; Downs and McQuilken 1944; Goodrum and others 1971; Greenberg, in press). Large among-year fluctuation in fruit production is often due to synchronous seed production among individuals within a population. Such fluctuations occur at irregular but periodic intervals characteristic of the species (Janzen 1971, Silvertown 1980). This fruiting pattern is termed masting (Silvertown 1980). However in many plant populations, seed production levels can vary dramatically without synchronized fruiting. The fruit crop produced by a population results from the number of fruiting plants, the number of fruits per plant, or both. Herrera and others (1998) suggest that there are no clear distinctions between masting and nonmasting plant species. The distinction between completely synchronized and partially synchronized fruit production is termed strict versus normal masting (Kelly 1994).

The practical applications and evolutionary implications of crop-size fluctuations underscore the need to better understand their patterns and causal factors. Acorn yield has a demonstrable influence on the population dynamics of many game (Eiler and others 1989, Wentworth and others 1992) and nongame (Elkinton and others 1996, Hannon and others 1987, Koenig and Mumme 1987, Smith and Scarlett 1987, Wolff 1996) wildlife species. Wolff (1996) suggests that acorns function as a keystone resource in forest-community dynamics by influencing small mammal prey populations. Indeed, acorn crop size has a far-reaching influence on the ecosystem. White-footed mouse (*Peromyscus leucopus* Rafinesque) populations, which are directly influenced by acorn crop size, affect gypsy moth (*Lymantria dispar* L.) populations (Elkinton and others 1996) and even the prevalence of Lyme disease (Jones and others 1998). Oak regeneration also has been shown to increase following large acorn crops (Marquis and others 1976), although a host of other factors influence seedling establishment and success. Because acorn crops impact wildlife and forest regeneration, the ability to predict the size of future acorn crops (Koenig and others 1994b, Sork and others 1993) and estimate current-year production (e.g., Christisen and Kearby 1984; Graves 1980; Koenig and others 1994a; Sharp 1958; Whitehead 1969, 1980) has received considerable attention.

Differences in the floral biology of the two subgenera of oaks probably contribute to some differences in acorn production patterns among species. Species in the white oak group or *Leptobalanus* subgenus, including chestnut oak (*Q. prinus* L.) and white oak (*Q. alba* L.), produce flowers in the spring. If they are fertilized, acorns develop by fall of the same year. Conversely, species in the red oak group or *Erythrobalanus* subgenus, including black oak (*Q. velutina* Lam.), northern red oak (*Q. rubra* L.), and scarlet oak (*Q. coccinea* Muenchh.), produce flowers in the spring but (if fertilized) do not develop acorns until the fall of the following year.

Most studies of eastern oaks describe the large fluctuations in acorn crop size as masting. However, despite large year-to-year fluctuations exhibited by most oak species, moderate crop sizes are also common (Beck 1977, Burns and others 1954, Christisen and Kearby 1984, Downs and McQuilken 1944, Goodrum and others 1971, Sork and others 1993). The degree of synchronized fruiting within a population of conspecifics is not directly addressed in most studies. Those that have addressed it indicate that oaks fruit in synchrony at species-specific intervals (Healy 1997, Koenig and others 1994b, Sork and others 1993).

In this paper we examine fruiting patterns to assess the level of synchronized acorn production among individuals within populations of five Southern Appalachian oak species from 1993–97. We also evaluate how the number of acorns on fruiting trees and the proportion of trees bearing acorns correlate with annual crop size. Further, we propose and use these data to evaluate a new and simple method for annually estimating acorn crop yield as acorns per square meter ($m^2$) basal area (BA). Using visual survey information and a BA inventory for each oak species, land managers can apply crop size estimates (number of acorns per $m^2$ BA) to areas within the Southern Appalachians to calculate the acorn crop by species within years. Finally, we provide acorn yield tables based on 5-year average acorn production that can be used with BA inventories to calculate mean annual acorn production by species on an area basis.

## Study Area and Methods

### Acorn Sampling

We sampled acorn production by 765 individuals of 5 oak species throughout the Southern Appalachians from 1993–97. Study species included northern red oak [total sample size ($N$) = 148], scarlet oak ($N$ = 142), and black oak ($N$ = 91) in the red oak subgenus and chestnut oak ($N$ = 201) and white oak ($N$ = 183) in the white oak subgenus. Some trees were not sampled in all years, resulting in slight differences in sample size among years. Study trees were scattered throughout national forests (NF's) in three States: the Cherokee NF in Tennessee, the Pisgah NF in North Carolina, and the Chattahoochee NF in north Georgia (fig. 1).

We selected trees haphazardly to represent a wide range of size (9 to 133 centimeters diameter at breast height) and age classes. Most trees were mature and in dominant or codominant (a few were intermediate) crown positions. One stand of scarlet [stand size ($n$) = 20] and white oak ($n$ = 18) in the Pisgah NF was established following a clearcut regeneration harvest in 1967 [when all trees taller than 1.4 meters (m) were felled]. Sample trees were located at elevations ranging from 850 to 1180 m above sea level and over a wide range of topographic features, i.e., aspect, slope position, and percent slope.

We collected acorns in traps constructed with shade cloth attached to a 0.5-m diameter ring of galvanized wire suspended by treated wooden stakes or rebar approximately 1 m above the ground. Traps were placed beneath the trees to obtain a representative sample of the crown. The number of traps per tree was approximately proportional to the BA (2 to 14 per tree, average $4.1 \pm 2.2$ standard deviation per tree). Trap tallies did not account for acorns removed from the crown by squirrels or other arboreal consumers or acorns that were occasionally removed from the traps by such animals. As a result, our crop size estimates probably were conservative.

We measured crown areas using eight radii and azimuths from tree base to the canopy drip line and computed them as an octagon. Traps were checked at 2-week intervals (collection intervals varied somewhat among NF ranger districts) from mid-August through the completion of acorn drop.

### Statistical Analysis

We calculated acorn production for each tree by multiplying the number of mature acorns collected per $m^2$ trap area by the crown area. We included all well-developed acorns in our analyses regardless of their condition (sound, animal or insect damaged). To standardize comparisons among different sized trees and to simplify formulas for use by forest managers, we converted the number of acorns per tree to the number per $m^2$ BA by dividing the total acorn production of each tree by the respective tree BA. The number of acorns per $m^2$ BA is proportional to the number

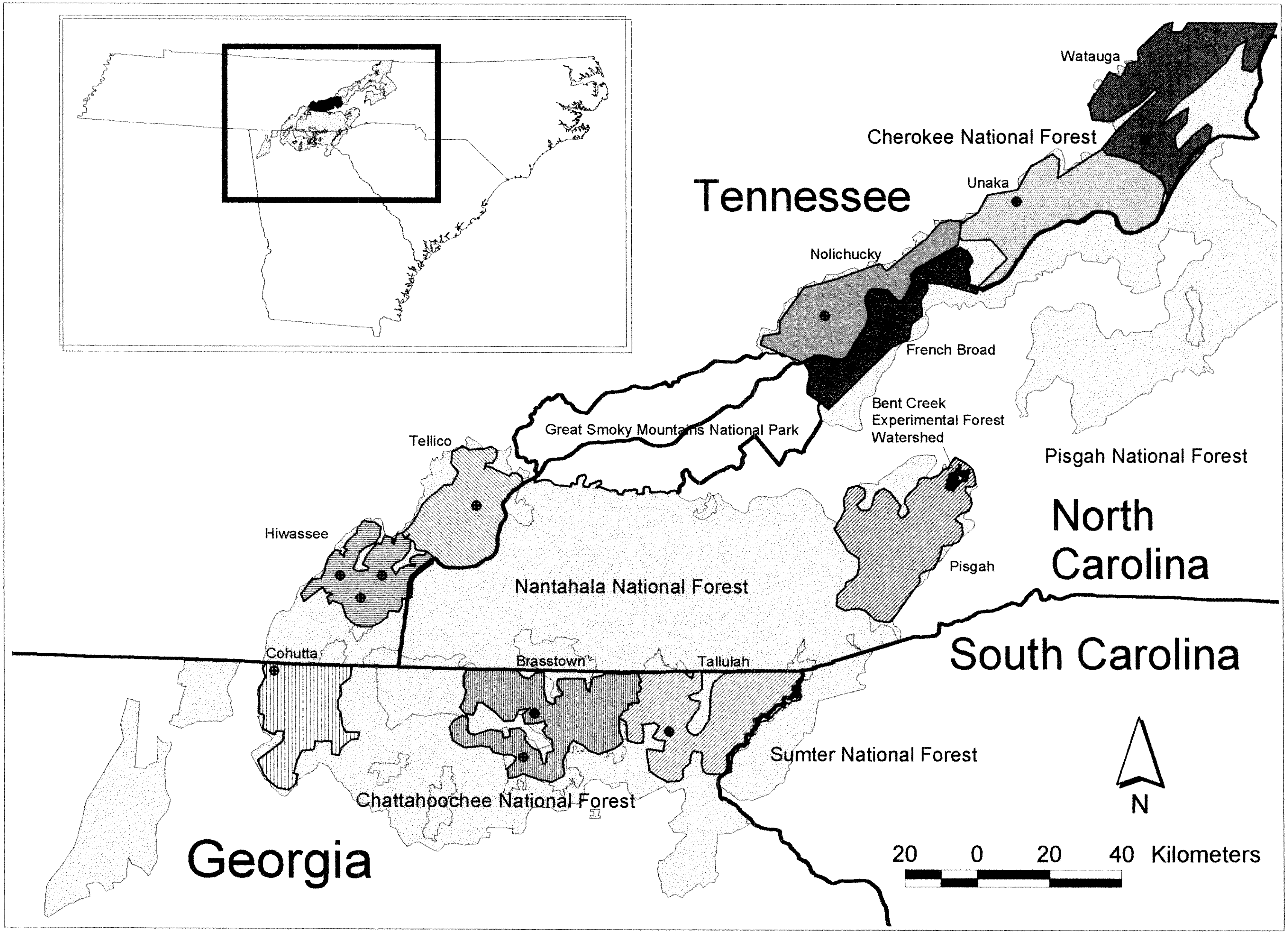


Figure 1—General location of five species of oak trees sampled from 1993–97 in the Chattahoochee National Forest in north Georgia, Pisgah National Forest in North Carolina, and Cherokee National Forest in Tennessee.

per $m^2$ crown and is easier to use because BA is more easily measured than crown area.

We ranked the annual crop size for each species as poor, moderate, or good by comparing the mean number of acorns per $m^2$ BA for that year to its 5-year (1993–97) mean. Good crop years were defined as $\geq$ the 5-year mean, moderate as $\geq$ 60 percent of but < the mean, and poor as < 60 percent of the 5-year species mean (adapted from Healy and others 1999).

Using analysis of variance (ANOVA), we compared the mean number of acorns per $m^2$ BA of fruiting trees (excluding nonfruiting individuals) among years for each species and performed pair-wise contrasts using least squares means tests (SAS Institute Inc. 1989). The number of acorns per $m^2$ BA was natural-log transformed for ANOVA to reduce the correlation between the mean and variance (Sokal and Rohlf 1981). Statistical significance is reported at the $P < 0.05$ level unless otherwise stated.

In regression analysis, if two predictor variables are highly correlated ($r > 0.8$), then resultant parameter estimates are usually unstable. The condition is called multicollinearity and a simple remedy is to exclude one of the predictor variables, because both variables provide essentially the same information (Judge and others 1988). We determined Pearson correlation coefficients (PROC CORR, SAS Institute Inc. 1989) between the proportion of trees bearing acorns and the number of acorns per fruiting tree for each year to determine whether they were collinear.

For each year of the study, we used graphs to examine the relationship between mean crop yield (number of acorns per $m^2$ BA) and the proportion of acorn-bearing trees in the Southern Appalachian region. From these graphs, we hypothesized the following linear functional relation:

$$Y = \beta_0 + \beta_1 X, \qquad (1)$$

where

$Y$ = the natural logarithm of mean crop yield (number of acorns per $m^2$ BA),
$X$ = the proportion of acorn-bearing trees in the population (independent variable), and
$\beta_0$, $\beta_1$ = the parameters.

Ordinary least squares (OLS) regression analysis assumes that the regressand, or independent variable, is a controlled or fixed variable that is observed with no error, but the observed regressor ($y$) is a random variable and subject to error ($\varepsilon$), that is,

$$y = Y + \varepsilon .$$

The model used with OLS is then

$$y = \beta_0 + \beta_1 X + \varepsilon . \qquad (2)$$

However, the independent variable values from this study are sample-based estimates. Thus $X$ also must be considered as a random variable subject to error, expressed as

$$x = X + \phi , \qquad (3)$$

where

$x$ = the observed regressand, and
$\phi$ = the observed regressand's associated error.

Substituting equation (3) into equation (2) gives an appropriate model to estimate the hypothesized functional relation in equation (1), that is,

$$y = \beta_0 + \beta_1 x + (\varepsilon - \beta_1 \phi) . \qquad (4)$$

Ordinary least squares is not appropriate for estimating the parameters of equation (4). If used, OLS gives biased estimates (Ricker 1984). Equation (4) is known variously as an errors-in-variables model, a measurement error model, or a stochastic predictor model (Fuller 1987). For mutually variable data of the kind just described, Leduc (1987), Rayner (1985), and Ricker (1973, 1984) recommend the reduced major axis (RMA) technique of fitting lines. The equation (Ricker 1973, 1984; Sokal and Rohlf 1981) for the point estimate of the RMA slope ($b_1$) is

$$b_1 = \left[ \frac{S_{yy}}{S_{xx}} \right]^{0.5},$$

where

$$S_{yy} = \sum_{i=1}^{N} (y_i - \bar{y})^2 ; \quad S_{xx} = \sum_{i=1}^{N} (x_i - \bar{x})^2 ,$$

where

$N$ = the total sample size,
$y$ = the dependent variable, and
$x$ = the independent variable.

The estimate ($b_0$) of $\beta_0$ is obtained in the same manner as that of OLS:

$$b_0 = \bar{y} - b_1\bar{x} \cdot$$

To test the significance of equation (4), we must use the correlation coefficient, $r$. If $r$ is significant, then $\beta_1$ is significantly different from zero (Ricker 1984). In the Application and Reliability section of this paper, we show how to determine an adequate sample of trees to obtain a reasonable value for $X$ (the proportion of acorn-bearing trees in the population). Also, we demonstrate use of equation (4) and construction of a confidence interval about a prediction.

Using the same strategy, we also examined the relationship between the mean number of acorns per $m^2$ BA of fruiting trees (excluding nonacorn bearing individuals in any given year) and mean crop yield (number of acorns per $m^2$ BA of all trees). For these variables, the functional relation appeared linear on their original scales, so no transformations were needed.

**Results**

Acorn production varied dramatically among years and species (fig. 2). Species within subgenera followed similar but not identical production patterns. Within the red oak group, northern red oak, scarlet oak, and black oak produced good crops in 1993 and 1995. However in 1994 the black oak crop was poor, but the oak crops were moderate for the other two species. In the white oak group, chestnut oak and white oak also exhibited similar patterns, but the magnitude of the white oak crop in 1994 (a moderate crop year for both species) and 1996 (a good crop year for both species) was much greater than the chestnut oak crop. Within each species, crop failure occurred only once during the 5-year study period. Year-to-year differences in acorn production among species prevented complete acorn crop failure in all years except one (1997) (fig. 2).

Regionally, acorn production by individual trees was not synchronous within years for any species. Within a species, the proportion of trees bearing acorns ranged from 70 percent (chestnut oak, 1996) to 90 percent (white oak, 1996) during the maximum crop year, and from 3 percent (white oak, 1997) to 29 percent (black oak, 1996) during the poorest crop year (scarlet oak, 1996; all other species, 1997). At least 29 percent of individuals of all species produced acorns every year except the poorest crop year for that species (fig. 3).

Average number of acorns per $m^2$ BA of fruiting trees (excluding nonfruiting individuals) differed significantly among years for all species (fig. 3). There was a significant correlation between mean annual crop size and the number of acorns on fruiting individuals ($r \geq 0.97$, $P \leq 0.0069$) for all species. Additionally, correlation analysis established that the two potentially independent variables—proportion of fruiting trees and the number of acorns on fruiting trees—were highly and significantly correlated for all species except chestnut oak (fig. 3; table 1). Because of this serendipitous multicollinearity, it was unnecessary to include both variables in regression analysis. For simple linear regression, we chose to focus only on the proportion of acorn-bearing trees because of its simplicity and utility to land managers.

The proportion of trees bearing acorns was a significant and strong predictor of acorn crop size (mean number per $m^2$ BA) in any given year (fig. 4; table 2). Because of the relative facility with which the proportion of fruiting trees can be ascertained, these equations are of greater use to forest managers than equations that use estimates of mean number of acorns per $m^2$ BA of fruiting trees. Using the proportion of trees bearing acorns (determined from visual survey), the equations presented in the Application and Reliability section, and the values shown in table 2, we were able to calculate the within-year crop size for each species by multiplying the antilog of $\hat{y}_{\text{species A}}$ by the $BA_{\text{species A}}$ ($m^2$). To calculate total acorn production by the five oak species within an area, we summed the species values. Crop yield estimates described in numbers of acorns can be converted to green weight or dry biomass (no hulls) using the conversion values presented in table 3.

Average acorn yield (1993–97) for the five species studied is presented in table 3. This information cannot be used to predict or even estimate within-year acorn crops; as indicated in figure 2, actual production varies dramatically from year to year. However, table 3 can be used to estimate long-term acorn production capability. Mean acorn production by species can be calculated on an area basis by

**Table 1—Correlation between the annual (1993–97) proportion of trees bearing acorns and the number of acorns per fruiting tree (natural-log transformed) for five species of Southern Appalachian oaks**

| Species | $n$ | $r$ | $P$-value |
|---|---|---|---|
| Black oak | 5 | 0.98 | 0.0028 |
| Northern red oak | 5 | .96 | .0106 |
| Scarlet oak | 5 | .91 | .0296 |
| Chestnut oak | 5 | .68 | .2045 |
| White oak | 5 | .95 | .0120 |

$n$ = number of years; $r$ = correlation coefficient.

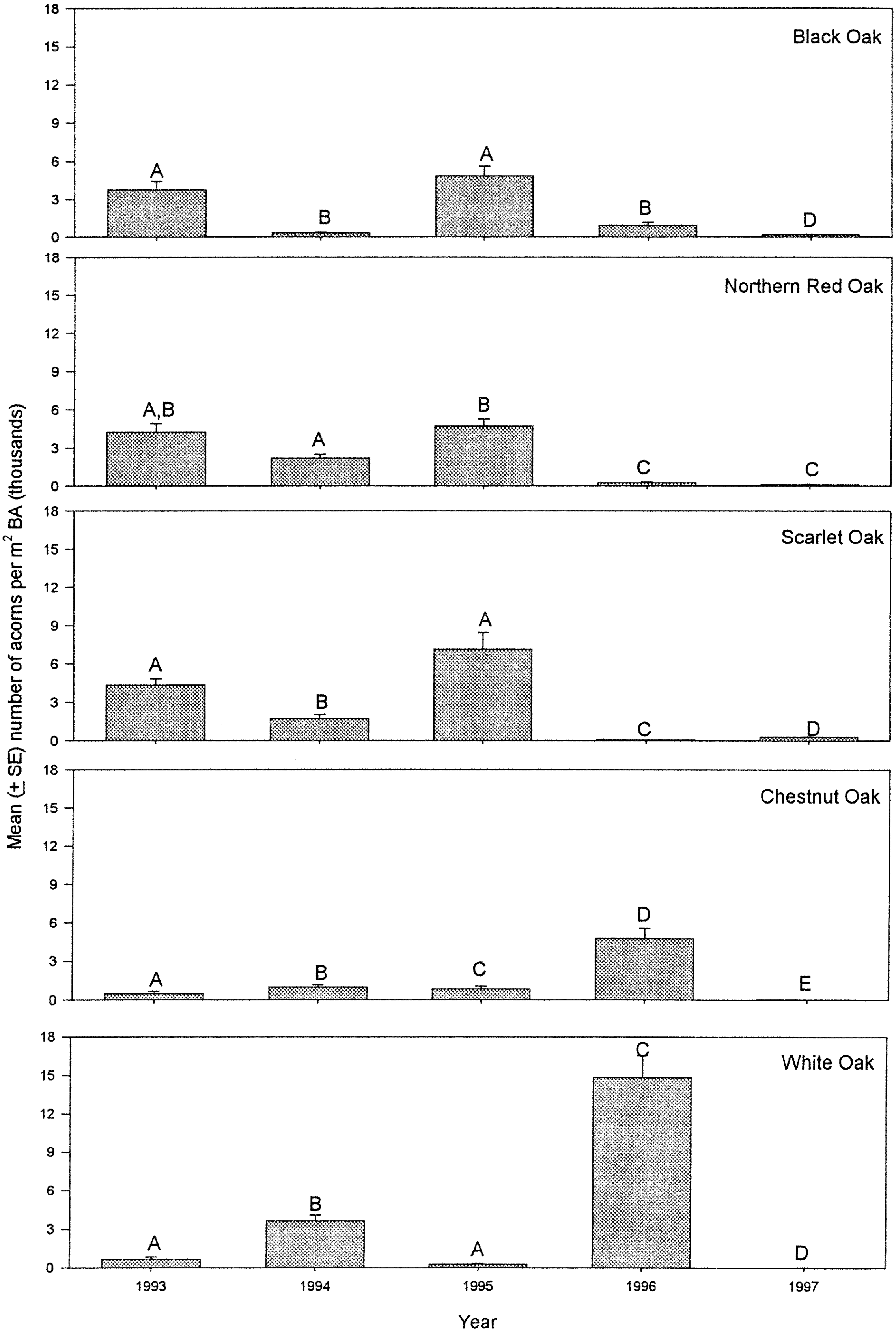


Figure 2—Annual (1993–97) crop size {mean [± standard error (SE)] number of acorns per $m^2$ basal area [BA]} produced by five oak species in the Southern Appalachians. Different letters within a species denote significant among-year differences in number of acorns. I denotes standard error.

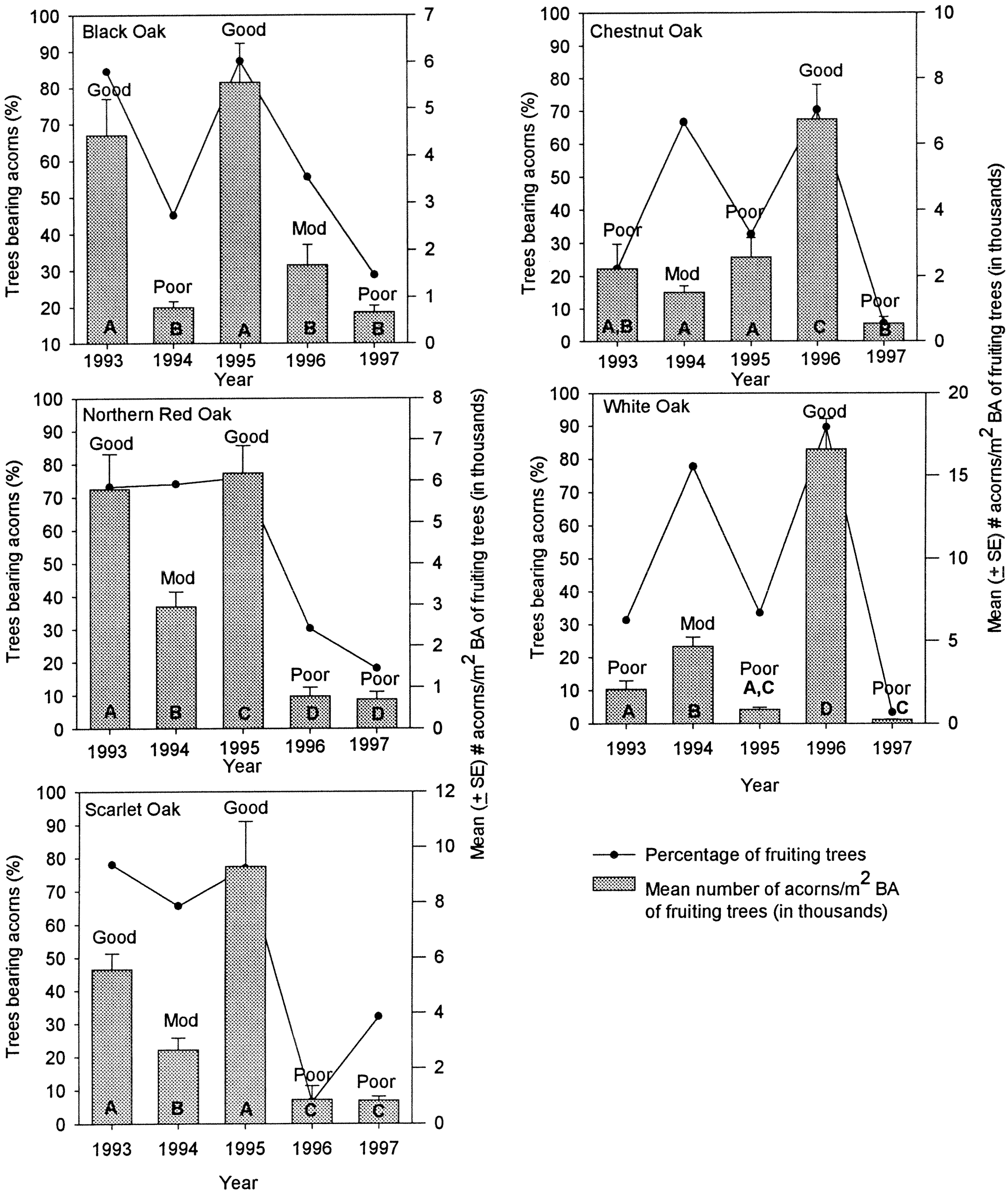


Figure 3—Annual (1993–97) proportion of trees bearing acorns and mean [± standarad error (SE)] number of acorns per $m^2$ basal area (BA) of fruiting individuals of five oak species in the Southern Appalachians. Acorn numbers data were natural-log transformed [in (value + 1)] for analysis of variance but are presented as actual means. Different letters within a species denote significant among-year differences in number of acorns. I denotes standard error.

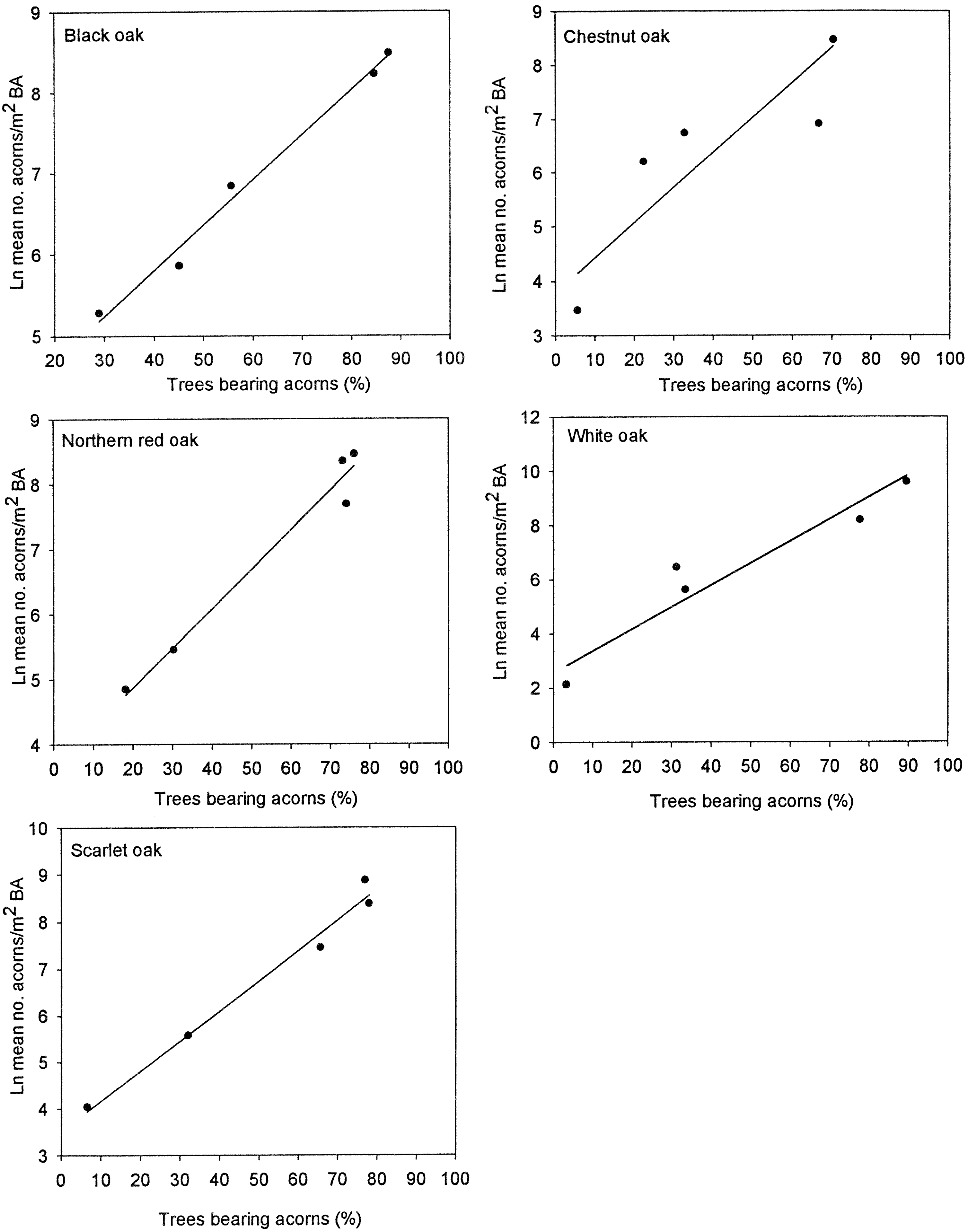


Figure 4—Reduced major axis regression of the natural logarithm (ln) of acorn yield [number of acorns per $m^2$ basal area (BA)] on the proportion of oak trees bearing acorns in the Southern Appalachians.

**Table 2—Reduced major axis regression of the natural logarithm of acorn yield (number of acorns per m² basal area) on the proportion of oak trees bearing acorns for five species of Southern Appalachian oaks**

| Species | $b_0$ | $b_1$ | $r$ | *P*-value | $\bar{x}$ | $S_{xx}$ | $\hat{\sigma}^2_\varepsilon$ |
|---|---|---|---|---|---|---|---|
| Black oak | 3.56472 | 0.055905 | 0.9942 | 0.0005 | 60.3 | 2569.41 | 0.03113 |
| Northern red oak | 3.66069 | .060747 | .9861 | .0020 | 54.3 | 3102.63 | .10617 |
| Scarlet oak | 3.51901 | .064498 | .9918 | .0009 | 51.8 | 3952.09 | .09008 |
| Chestnut oak | 3.78155 | .064998 | .8658 | .0578 | 39.6 | 3184.57 | 1.20371 |
| White oak | 2.58029 | .080842 | .9526 | .0123 | 47.1 | 5095.65 | 1.05248 |

$b_0$, $b_1$ = equation coefficients; $r$ = correlation coefficient; $\bar{X}$ = mean proportion of trees bearing acorns; $S_{xx}$ = variance of $X$; $X$ = the proportion of acorn-bearing trees in the population; $\hat{\sigma}^2_\varepsilon$ = residual error.

**Table 3—Average acorn production with green weight and dry biomass conversion factors for five species of Southern Appalachian oaks, 1993–97**

| | | | | Conversion factors[b] | |
|---|---|---|---|---|---|
| Species | $N$[a] | Mean | SE | Green weight | Dry biomass[c] |
| | | *No./m² BA* | | ------- *Kg/m² BA* ------- | |
| Black oak | 88 | 2044.5 | 966.2 | 0.00262 | 0.00119 |
| Northern red oak | 111 | 2510.9 | 1096.9 | .00680 | .00254 |
| Scarlet oak | 124 | 2807.1 | 1400.6 | .00302 | .00128 |
| Chestnut oak | 161 | 1274.0 | 840.9 | .00805 | .00253 |
| White oak | 155 | 4216.4 | 3117.6 | .00316 | .00126 |

$N$ = number of trees sampled; SE = standard error; BA = basal area.
[a] Only trees that were sampled all 5 years were included in estimates.
[b] Acorn weights based on a subsample of sound acorns drawn from all 5 years.
[c] No hulls included in this measurement.

multiplying the total BA of a species within an area by the mean acorn production per m² BA for that species. By summing these values, we can calculate total average acorn production of the five species.

## Application and Reliability

### Estimating the Proportion of Acorn-Bearing Trees to Predict Yield

The natural logarithm of acorn crop yield is estimated as

$$\hat{y} = b_0 + b_1 \hat{x} , \qquad (5)$$

where

$\hat{y}$ = the predicted logarithm of acorn crop yield,
$b_0$, $b_1$ = equation coefficients (from table 2), and
$\hat{x}$, = an estimate of the percent of acorn-bearing trees.

To compute $\hat{x}$, it is necessary to draw a random sample of trees of size ($n$) and count the number of successes ($s$) of trees bearing acorns. The proportion ($p$) of acorn-bearing trees is unbiasedly estimated as $\hat{p} = s/n$ , thus $\hat{x} = 100 \times \hat{p}$ . Of course, we want to estimate $p$ within some margin of error ($d$) at the (1 - $\alpha$) confidence limits. The sample size required to achieve the desired level of precision (Zar 1984) is

$$n = \frac{Z^2_{\alpha/2}\, \tilde{p}\, \tilde{q}}{d^2} , \qquad (6)$$

where

$Z$ = a standard normal variate (Zar 1984: 483),
$\alpha$ = Type I error rate,
$\tilde{p}$ = an initial guess of $p$ (based on intuition or, preferably, a pilot survey), and
$\tilde{q} = 1 - \tilde{p}$.

We demonstrate use of this formula in the Examples subsection.

When one uses the logarithmic transformation, he or she usually wants estimated values expressed in arithmetic, i.e., untransformed, units. The antilogarithm of $\hat{y}$ yields the estimated crop size ($\hat{cs}$) (number of acorns per $m^2$ BA), that is,

$$\hat{cs} = \exp(\hat{y}) \ . \tag{7}$$

A number of ecologists, e.g., Baskerville 1972, Sprugel 1983, suggest applying a correction factor (CF) to the antilog values; we have chosen to disregard the CF because there is evidence that the CF overcorrects (Hepp and Brister 1982, Snowdon 1985). To convert $\hat{cs}$ from Standard International units to English units, multiply by 0.092903, that is,

$$\hat{cs}_{\text{English}} = 0.092903 \times \hat{cs} = \text{number of acorns/ft}^2 \text{ BA} \ , \tag{8}$$

where

$ft^2$ = square feet.

**Confidence Intervals**

Regression equations, such as equation (5), give point estimates of potential acorn yield. Because point estimates are subject to error, it would be useful to place bounds on the predictions. From the structural relation in equation (4), it is obvious the variance of $y$ ($\hat{\sigma}_y^2$) is not simply residual error, but also a function of the variance of $X$. It is given by (Kendall and Stuart 1979, Madansky 1959)

$$\hat{\sigma}_y^2 = b_1^2 \hat{\sigma}_X^2 + \hat{\sigma}_\varepsilon^2 \ , \tag{9}$$

where

$\hat{\sigma}_X^2$ = variance of X and

$\hat{\sigma}_\varepsilon^2$ = residual error.

The variable $X$, i.e., $100 \times s/n$, is based on a binomial random variable. Thus, its estimated variance is

$$100^2 \hat{p}(1-\hat{p})/n \ .$$

The construction of confidence intervals is straightforward. Two quantities are needed to construct bounds on the predictions: (1) the standard errors of the predictions [$s(\hat{y}_i)$] and (2) a $t$-value. The interval boundary points are obtained from

$$\hat{y} \pm t_{\alpha/2, n_r - 2} \times s(\hat{y}_i) \ , \tag{10}$$

where

$n_r$ = number of regression observations ($n_r = 5$).

The standard errors are calculated as

$$s(\hat{y}_i) = \sqrt{\hat{\sigma}_y^2 \left( \frac{1}{n_r} + \frac{(x_i - \bar{x})^2}{S_{xx}} \right)} \ . \tag{11}$$

**Examples**

We shall start by determining some sample sizes required to achieve a specified level of precision. Suppose that after visiting field sites, we believe there will be a moderate acorn crop yield. Suppose we are willing to be within 3 percent ($d$ = 0.03) of the true fruiting proportion at the 80-percent confidence level ($\alpha = 0.2$, therefore $Z = 1.28$), and that a small pilot survey suggests $\tilde{p}$ is about 0.42 for black oak. From equation (6) we obtain

$$n = \frac{1.28^2 \times 0.42 \times 0.58}{0.03^2} = 444 \ .$$

If we are willing to accept a larger margin of error, say 5 percent, the required sample size is reduced dramatically, that is,

$$n = \frac{1.28^2 \times 0.42 \times 0.58}{0.05^2} = 160 \ .$$

One should attempt to sample a slightly larger number of trees than predicted from equation (6), because $\hat{p}$ in general will not be equal to the initial guess $\tilde{p}$, and if $\hat{p}$ is closer than $\tilde{p}$ to 0.5, $n$ will be slightly larger (note that variance is maximized at $p = 0.5$). Now, suppose we feel comfortable with the 5-percent margin of error on our estimate of $p$. We do a visual survey of 170 trees for presence or absence of acorns, or both, and determine that $\hat{p} = 0.45$ (for this $p$ the required $n$

is 163, so our survey of 170 is adequate). Using the coefficients from table 2 for black oak, the estimated yield of acorns per $m^2$ BA of trees in logarithmic units is

$$\hat{y} = 3.56472 + 0.055905 \times 45 = 6.0804 .$$

To place bounds on this prediction, we must first calculate $\hat{\sigma}_y^2$ using equation (9). This yields the following result:

$$\hat{\sigma}_y^2 = 0.0559^2 \frac{100^2 \times 0.45 \times 0.55}{170} + 0.0311 = 0.0766 ,$$

where $b_1$ and $\hat{\sigma}_\varepsilon^2$ come from table 2.

From equation (11), the standard error is computed as

$$s(\hat{y}) = \sqrt{0.0766\left(\frac{1}{5} + \frac{(45 - 60.3)^2}{2569.41}\right)} = 0.1493 ,$$

where $\bar{x}$ and $S_{xx}$ are from table 2. From equation (10), the 90-percent confidence interval is

$$6.0804 \pm 0.1493(2.353) = 5.7291 \le \hat{y} \le 6.4317 .$$

To convert logarithmic values to arithmetic units, we apply equation (7). For the predicted mean acorn yield per $m^2$ BA from a 45-percent fruiting population of black oak, we obtain

$$\hat{cs} = \exp(6.0804) = 437.2 .$$

By applying equation (7) to the confidence limit values, we obtain the following interval:

$$307.7 \le \hat{cs} \le 621.2 .$$

To convert these values to English units, one must apply equation (8). This results in

$$\hat{cs}_{\text{English}} = 0.092903 \times 437.2 = 40.6 \text{ acorns/ft}^2 \text{ BA} ,$$

with limit values of

$$28.6 \le \hat{cs}_{\text{English}} \le 57.7 .$$

Suppose from a recent inventory we know that black oak occupies, on average, 20 $ft^2$ BA per acre. To convert to per-acre values, we simply multiply by 20, obtaining

$$\hat{cs}_{\text{acre}} = 20 \times 40.6 = 812 \text{ acorns/acre} ,$$

with limit values of

$$572 \le \hat{cs}_{\text{acre}} \le 1{,}154 .$$

As another example, let us consider calculations for northern red oak. Suppose a preliminary survey indicates $\tilde{p}$ is 0.70. Setting $d = 0.05$ and using the 80-percent confidence level, we obtain a sample size of

$$n = \frac{1.28^2 \times 0.70 \times 0.30}{0.05^2} = 138 .$$

Now suppose a visual survey of 145 trees results in $\hat{p} = 0.74$. Using the coefficients for northern red oak in table 2, the natural logarithm of crop yield is

$$\hat{y} = 3.66069 + 0.060747 \times 74 = 8.1560 .$$

The variance of y is

$$\hat{\sigma}_y^2 = 0.0607^2 \frac{100^2 \times 0.74 \times 0.26}{145} + 0.1062 = 0.1551 .$$

The standard error is computed as

$$s(\hat{y}) = \sqrt{0.1551\left(\frac{1}{5} + \frac{(74 - 54.3)^2}{3102.63}\right)} = 0.2245 .$$

The 90-percent confidence interval is

$$8.1560 \pm 0.2245(2.353) = 7.6278 \le \hat{y} \le 8.6842 .$$

Transforming to arithmetic units, we obtain

$$\hat{cs} = \exp(8.1560) = 3{,}484.2 \text{ acorns/m}^2 \text{ BA} ,$$

with confidence limit values of

$$2{,}054.5 \le \hat{cs} \le 5{,}908.8 .$$

Converting these values to English units, we obtain

$$\hat{cs}_{\text{English}} = 0.092903 \times 3{,}484.2 = 323.7 \text{ acorns/ft}^2 \text{ BA} ,$$

with limit values of

$$190.9 \le \hat{cs}_{\text{English}} \le 548.9 .$$

Suppose from the same recent inventory we know that northern red oak occupies, on average, 10 $ft^2$ BA per acre. To convert to per-acre values, we simply multiply by 10, obtaining

$$\hat{cs}_{\text{acre}} = 10 \times 323.7 = 3{,}237 \text{ acorns/acre} ,$$

with limit values of

$$1{,}909 \le \hat{cs}_{\text{acre}} \le 5{,}489 .$$

It is likely that one will want to sum the values across species to obtain total per-hectare or total per-acre acorn crop yields and confidence limits on the sum. For the two species illustrated, the combined total yield per-acre of black oak and northern red oak is:

$$\hat{cs}_{\text{total/acre}} = 812 + 3,237 = 4,049 \text{ acorns/acre},$$

with limit values of

$$(572 + 1,909) = 2,481 \leq \hat{cs}_{\text{total/acre}} \leq 6,643 = (1,154 + 5,489).$$

One could compute values for the remaining three species and sum them to obtain the total yield value and concomitant confidence interval for all five species.

## Discussion

Fruiting (or nonfruiting) synchrony does not occur reliably among years within species, so there are large fluctuations in acorn production. Although most (> 70 percent) individuals produced acorns in some years and very few (3 to 29 percent) in others, at least 1 to 2 years (differing for each species) of the 5-year study were characterized by approximately one-third to two-thirds of sample trees producing acorns. Given the huge range of variability in acorn production among individuals and species (Greenberg, in press), this is not surprising. Koenig and others (1994b) found evidence of species-specific masting intervals at the individual level but not at the population level. Conversely, Sork and others (1993) found that most northern red oak and white oak conspecifics (and to a lesser degree, black oak) produced acorns in the same years. In most years we found, as did others, that acorn production by some species will compensate for the effect of crop failure by others (Beck 1977, Burns and others 1954, Christisen and Kearby 1984, Downs and McQuilken 1944, Goodrum and others 1971).

Many other studies report boom-and-bust acorn production patterns for southeastern oaks (Beck 1977, Burns and others 1954, Christisen and Kearby 1984, Downs and McQuilken 1944, Goodrum and others 1971). However, moderate crop years also occurred frequently in each of these studies—a fact that is underemphasized in discussions of masting in oaks. Indeed, high year-to-year variability in the degree of fruiting synchrony and crop size within a population suggests that the term masting may not appropriately characterize the fruiting patterns of Southern Appalachian oaks.

The results of our study indicate that acorn crop size is strongly correlated with the proportion of individuals in the population that produce acorns and the number of acorns per $m^2$ BA of fruiting trees. Annual changes in each of these factors are highly and significantly correlated in all species except chestnut oak. Healy and others (1999) also observed that more northern red oak trees bore acorns and there were more acorns per tree during good crop years. Both the proportion of fruiting trees and the number of acorns on fruiting trees are independently strong and are significant predictors of crop size within a given year for all species except chestnut oak. However, additional years of research will probably show these factors to be significant predictors for chestnut oak crop size as well.

In the Examples subsection, confidence intervals may seem remarkably wide. They are reasonable, however, given that there is high natural variability in $y$, especially with $\hat{\sigma}_y^2$ being the sum of two variance components, and $n_r$ is small. Additional points of data will have the effect of reducing standard errors, and with increasing degrees of freedom the $t$-value will also be reduced. The overall result will be tighter confidence intervals on the predictions.

Several visual survey methods are commonly used for estimating acorn yield (Christisen and Kearby 1984; Graves 1980; Koenig and others 1994a; Sharp 1958; Whitehead 1969, 1980). However, visual surveys are time consuming and provide only categorical estimates of acorn crop yield, which may be biased by differences among observers. The strong relationship between the proportion of individuals bearing acorns and mean crop size provides an expedient tool for forest and wildlife managers or planners to quantify acorn crop sizes within years.

To ensure a precise estimate of the proportion of acorn-bearing trees, it may be necessary to sample large numbers of trees per species. The sample size required will depend on the proportion of fruiting trees, the margin of error, and the confidence level one is willing to accept. Moderate crop years require the highest sampling effort (164 trees with a 5-percent margin of error and 80-percent confidence level, if 50 percent are fruiting), while poor or good crop years require the least (as few as 59 trees if 10 percent or 90 percent of a given species are fruiting).

Using the equations provided in the Statistical Analysis subsection, we can estimate within-year acorn crop size knowing only the proportion of trees bearing acorns and the BA inventory within the survey area for each species. Estimates can be applied to surveyed areas of any size within the Southern Appalachian region.

The relationship between acorn crop size and the proportion of acorn-bearing trees described in our study are based on data from acorn traps. It is probable that there will be some discrepancy in acorn detection (presence or absence, or both) between visual surveys and trap data (Gysel 1956), especially in years of poor crop yield. Visual surveys in which tree canopies are closely scrutinized may detect the presence of very small numbers of acorns that could be missed by acorn traps. Relative to the trap data that our equations are based upon, visual surveys would probably provide an inflated (although more accurate) estimate of the proportion of fruiting trees and, therefore, inflated crop-yield estimates. Until that issue is better addressed, we suggest that visual surveys of trees having very few acorns be considered as trees without acorns for these calculations.

## Management Implications

The equations we developed based on the relationship between the proportion of trees bearing acorns and crop size enable managers to quantitatively estimate within-year crop size for specific management areas. The estimate, in units of number of acorns per $m^2$ BA by species, can be calculated based on the proportion of fruiting trees as estimated by simple visual surveys (presence or absence of acorns, or both). It then can be applied to a BA inventory of each oak species in the survey area. In this way, managers can tailor within-year crop size estimates to specific areas.

Alternatively, acorn yield tables can be applied to oak BA inventories to tailor estimates of acorn production on an average annual basis to any area in the Southern Appalachians. Yield tables also can be used to test how acorn production will be affected on an average annual basis using different BA apportionment scenarios among oak species. This will be useful in developing land management plans that include the goal of maintaining specified average annual acorn yields for wildlife.

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We examined acorn production from 1993–97 by black oak (Quercus velutina Lam.), northern red oak (Q. rubra L.), scarlet oak (Q. coccinea Muenchh.), chestnut oak (Q. prinus L.), and white oak (Q. alba L.) in the Southern Appalachians to determine how frequency of acorn production, levels of intraspecific synchrony, and acorn density per tree influence crop size. We then developed a linear regression model for each species to quantitatively estimate acorn crop size within years using the proportion of trees bearing acorns as the independent variable. We also developed acorn yield tables for each species. Using these equations, land managers can quantitatively estimate within-year crop size per species if they know the proportion of fruiting trees as estimated by simple visual surveys (presence or absence of acorns or both). By applying the estimate (in units of number per square meter basal area) for each species to a basal area inventory of oaks in their area, managers can tailor within-year crop size estimates to specific land management units. Alternatively, acorn yield tables can be applied to oak basal area inventories to tailor estimates of acorn production (the sum of each species) on an average annual basis to any area. Yield tables also can be used to test how acorn production will be affected on an average annual basis using different basal area apportionment scenarios among oak species.

**Keywords:** Acorn production, hard mast, masting, oak, predicting acorn crop size, reduced major axis regression, Southern Appalachian oaks, visual acorn surveys.