Chapter 10

Dynamics of Acorn Production by Five Species of Southern Appalachian Oaks

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The management implications of fluctuations in acorn crop size underscore the need to better understand their patterns, causal factors, and predictability (both within a year and long term). Acorn yield has a demonstrable influence on the population dynamics of many wildlife species, both game (Eiler et al. 1989, Wentworth et al. 1992) and nongame (Hannon et al. 1987, Koenig and Mumme 1987, Smith and Scarlett 1987, Elkinton et al. 1996, Wolff 1996, McShea 2000). 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 ecosystems. White-footed mouse (*Peromyscus leucopus*) populations, which are directly influenced by acorn crop size, affect gypsy moth (*Lymantria dispar*) populations (Elkinton et al. 1996) and even the prevalence of Lyme disease (Jones et al. 1998). Also, oak regeneration has been shown to increase following large acorn crops (Marquis et al. 1976), although a host of other factors influence seedling establishment and success (Loftis and McGee 1993). The ability to predict the size of future acorn crops (Sork et al. 1993, Koenig, Mumme, et al. 1994) and to estimate current-year production (e.g., Koenig, Knops, et al. 1994, Whitehead 1969, 1980, Graves 1980, Sharp 1958, Christisen and Kearby 1984) has received considerable attention by forest managers and researchers because of its importance to wildlife and forest regeneration.

This chapter examines temporal patterns of acorn production within and among five species of southern Appalachian oaks. The data encompass the first five years (1993–1997) of an ongoing, long-term study. Variability in acorn production among individual trees and characteristics of fruit production that contribute to such variation will be addressed. The correlation between both the number of acorns on fruiting trees and the proportion of trees bearing acorns with annual crop size is evaluated, and a simple method for estimating acorn crop yield is proposed (number of acorns per square meter of basal area [BA]). Using visual survey information and a BA inventory for each oak species, land managers can apply crop size estimates (acorns/m^2 BA) to areas within the southern Appalachians to calculate the acorn crop by species within years. Finally, an acorn yield table based on five-year average acorn production is provided. These tables can be used with BA inventories to calculate mean annual acorn production by species on an area basis.

Acorn Sampling

Acorn production by 765 individuals of five oak species was sampled throughout the southern Appalachians from 1993 to 1997 (see Greenberg 2000, for details). Study species included northern red oak (*Q. rubra*) ($N = 148$), scarlet oak (*Q. coccinea*) ($N = 142$), and black oak (*Q. velutina*) ($N = 91$) in the red oak subgenus, and chestnut oak (*Q. prinus*) ($N = 201$) and white oak (*Q. alba*) ($N = 183$) in the white oak subgenus. Study trees were scattered in small groups throughout national forests (NFs) in three states: the Cherokee NF in Tennessee, the Pisgah NF in North Carolina, and the Chatahoochee NF in north Georgia. Study sites were distributed generally from northeast to southwest following the orientation of the mountains and separated by ≤ 220 km. Sample trees were located at elevations ranging from 850 to 1,180 m above sea level and over a wide range of topographic features (e.g., aspect, slope position, and percent slope).

Trees were selected to represent a wide range of size (9–133 cm dbh [diameter at breast height]) and age classes. Most trees were mature and in dominant or codominant crown positions (a few were intermediate). One stand of scarlet oak ($N = 20$) 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 m were felled) and was 26 years old at the start of the study.

Acorns were collected in circular, 0.5-m-diameter traps placed beneath the trees to obtain a representative sample of the crown. The number of traps per tree was approximately proportional to the BA (2–14 per tree; average 4.1 ± 2.2 standard deviation / tree). Crop-size estimates probably were conservative, because trap tallies did not account for acorns removed by squirrels or other arboreal consumers. Crown areas were measured with eight equally spaced radii from tree base to the canopy drip line, and area was computed as an octagon. Traps were checked at approximately two-week intervals from mid-August through the completion of acorn drop.

Statistical Analysis

Acorn production was calculated for each tree by multiplying the number of mature acorns collected per m^2 trap area by the crown area. All well-developed acorns were included in the analyses regardless of their condition (sound, animal- or insect-damaged). To standardize comparisons among different-sized trees and simplify for use by forest managers, the number of acorns per tree were converted to the number per m^2 basal area by dividing the total acorn production by the BA of each tree. Because of the correlation between BA and crown area, the number of acorns/m^2 BA is correlated with the number/m^2 crown. However, BA is more easily measured than crown area. This measure of acorn production can be tailored to stands (any size area) of varying oak composition and BA simply by multiplying the BA present by the number of acorns/m^2 BA for each species and summing.

The annual crop size for each species was ranked as "poor," "moderate" or "good" by comparing the mean number of acorns/m^2 BA for that year to its five-year mean (1993–1997). Good crop years were defined as $\geq$ the five-year mean, moderate as $\geq$ 60% of but $<$ 100% of the mean, and poor as $<$ 60% of the five-year species mean (adapted from Healy et al. 1999). Individual trees of each species were also ranked as poor, moderate, or good producers, by the same criteria.

Using analysis of variance (ANOVA), the mean number of acorns/m^2 BA of fruiting trees (excluding nonfruiting individuals) was compared among years for each species, and pairwise contrasts were performed using least squares means tests (SAS Institute 1989). The number of acorns/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.

Reduced major axis (RMA) regression was used to predict within-year crop size using the proportion of acorn-bearing trees in the population as the independent variable (Greenberg and Parresol 2000). The RMA technique rather than ordinary least squares regression was selected because in this case the independent variable (x), the proportion of acorn bearing trees, is a sample-based estimate subject to error. In cases where both the x and y variables are subject to error, the RMA technique of fitting lines is recommended (Ricker 1973, 1984, Rayner 1985, Leduc 1987).

Are Some Species Better Producers than Others?

Acorn production (number and mass) is an important determinant of habitat quality for many species of wildlife and is a focus for many wildlife managers. Hence, understanding the frequency, timing, and relative contribution of acorn production by each oak species composing a forest could assist managers in planning for wildlife food supplies. Acorn production differed significantly among the five species studied (see Table 10.1). On average (±SE), white oak produced the most acorns per m^2 BA (4,216 ± 3,118) and chestnut oak the fewest (1,274 ± 841). Both northern red and white oak produced significantly higher green weight and dry biomass than chestnut, black, or scarlet oak. The distinction between acorn quantities versus mass (green weight and dry, edible biomass) is important for land managers who wish to maintain a specified mast capability in forest stands (Greenberg 2000). Damage to acorns by insect larvae was not examined here, but it can be very high; Beck (1977) estimated that an average of 35% of acorns, in a range of 29–67% depending on species and year, were infested in the southern Appalachians. If insect damage makes acorns nonviable or inedible, their relative contribution to the total crop may differ.

Despite the importance of acorns for wildlife, local and regional yield tables for acorns are unavailable. Table 10.2 summarizes acorn production estimates by this and other studies (although the list is not exhaustive) for the five study species. Comparison of acorn production among studies (Table 10.2) is confounded by a number of factors. Most pub-

Table 10.1
Average acorn production, green weight and dry biomass conversion factors for five species of southern Appalachian oaks, 1993–1997

Species	*N*	*Acorns (±SE) per m² BA*	*Green weight (±SE) (kg/m² BA)*	*Green weight conversion (kg/m² BA)*	*Dry biomass (kg/m² BA)*	*Dry biomass conversion (kg/m² BA)*
Black oak	88	2,045 ± 966^{a}	5.36 ± 2.53^{a}	0.00262	2.43 ± 1.15^{a,b}	0.00119
Northern red oak	111	2,511 ± 1,097^{a,b}	17.07 ± 7.46^{b}	0.00680	6.38 ± 2.79^{c}	0.00254
Scarlet oak	124	2,807 ± 1,401^{a,b}	8.48 ± 4.23^{c}	0.00302	3.59 ± 1.79^{a}	0.00128
Chestnut oak	161	1,274 ± 841^{c}	10.26 ± 6.77^{a}	0.00805	3.22 ± 2.13^{b}	0.00253
White oak	155	4,216 ± 3,118^{b}	13.32 ± 9.85^{d}	0.00316	5.31 ± 3.93^{d}	0.00126

Notes: Green weight and dry biomass conversion factors are based on a subsample of sound acorns drawn from all five years (1993–1997).
Superscript letters following acorn numbers or weights denote means within the column that are significantly different based on ANOVA.

Table 10.2
Comparison of studies of acorn production estimates for five eastern oak species.

Species	*Author*	*Number Acorns*	*Unit*	*N (sample size)*	*Duration of study*	*Location*
Black oak						
	Beck 1977	4,218	m^2 BA	by plot	1962–1973	Asheville, NC
	Burns et al. 1954[a]	900	tree	?	1947–1952	Dent Co., Missouri Ozarks
		1,500	tree	5	1948–1952	Butler Co., Missouri Ozarks
	Christisen and Kearby 1984	115	tree	37	1973–1976	Missouri Ozarks
	Downs 1944 (from Beck 1977)[b]	6,327	m^2 BA	by plot	1936–1942	Southern Appalachians
	Greenberg (this chapter)	2,045	m^2 BA	88	1993–1997	Southern Appalachians
	Sork et al. 1993	1,050	tree	13	1981–1988	St. Louis Co., MO
Northern red oak						
	Beck 1977	16,409	m^2 BA	by plot	1962–1973	Asheville, NC
	Christisen and Kearby 1984	50	tree	15	1973–1976	Missouri Ozarks
	Downs 1944 (from Beck 1977)[b]	4,745	m^2 BA	by plot	1936–1942	Southern Appalachians
	Greenberg (this chapter)	2,511	m^2 BA	111	1993–1997	Southern Appalachians
	Healy et al. 1999	16	m^2 crown	120	1986–1996	Central Massachusetts
	Sork et al. 1993	444	tree	12	1981–1988	St. Louis Co., MO

Scarlet oak						
	Beck 1977	7,586	m² BA	by plot	1962–1973	Asheville, NC
	Burns et al. 1954[a]	500	tree	?	1947–1951	Dent Co., Missouri Ozarks
		2,400	tree	5	1948–1952	Butler Co., Missouri Ozarks
	Chritisen and Kearby 1984	38	tree	16	1973–1976	Missouri Ozarks
	Downs 1944 (from Beck 1977)[b]	11,126	m² BA	by plot	1936–1942	Southern Appalachians
	Greenberg (this chapter)	2,807	m² BA	124	1993–1997	Southern Appalachians
Chestnut oak						
	Beck 1977	2,582	m² BA	by plot	1962–1973	Asheville, NC
	Downs 1944 (from Beck 1977)[b]	2,582	m² BA	by plot	1936–1942	Southern Appalachians
	Goodrum et al. 1971	259	tree	?	1950–1954	Kisatchie Nat'l Forest, LA
	Greenberg (this chapter)	1,274	m² BA	161	1993–1997	Southern Appalachians
White oak						
	Beck 1977	10,717	m² BA	by plot	1962–1973	Asheville, NC
	Burns et al. 1954[a]	1,100	tree	?	1947–1952	Dent Co., Missouri Ozarks
		700	tree	5	1948–1952	Butler Co., Missouri Ozarks
	Christisen and Kearby 1984	112	tree	35	1973–1976	Missouri Ozarks
	Downs 1944 (from Beck 1977)[b]	5,552	m² BA	by plot	1936–1942	Southern Appalachians
	Goodrum et al. 1971	725	tree	10?	1950–1955	Kisatchie Nat'l Forest, LA
	Greenberg (this chapter)	4,216	m² BA	155	1993–1997	Southern Appalachians
	Sork et al. 1993	664	tree	15	1981–1988	St. Louis Co., MO

Note: Reported estimates were converted to number of acorns/m² BA if possible, and reported as in the original study if not.

[a]Same study used for Christisen and Korschgen 1955.

[b]Predicted estimates based on Beck's data and applying data on production by diameter class from Downs (see Beck 1977, Downs 1944).

lished studies are relatively short in duration (12 years is the maximum among those reviewed). Average production estimates differ dramatically depending upon which set of years was sampled, as well. For example, Healy et al. (1999) note that their perception of a "good" northern red oak acorn crop changed during the sixth and eighth years of their study; white oak produced a good crop only in the sixth year of another study (Sharp and Sprague 1967). Differences in geographic location, sampling strategies (individual tree versus area-based plots), sample sizes (often very small, not reported, or reported as combined N for all species studied), and the units in which averages are reported (number per unit crown area; per unit BA by plot; per tree; per ha) further confound comparisons among studies. Although many sources report productivity by diameter class, few note the sample size within diameter classes. These discrepancies highlight the need for long-term studies and for standardization in measurement and reporting methods.

Despite differences among estimates caused by these confounding factors, and despite potentially real regional variation in relative productivity within a species, it is clear that all species are capable of producing a crop that ranges from almost none to many thousands of acorns/m^2 BA. Estimates of average annual acorn production per unit area also vary widely among studies (Table 10.2). For example, in a hypothetical 1-ha stand composed of 0.8 m^2 black oak, 1.7 m^2 northern red oak, 0.5 m^2 scarlet oak, 1.0 m^2 chestnut oak, and 1.3 m^2 white oak, estimates of average annual number of acorns produced range from 51,576 acorns/ha (Beck 1977) to 29,906 acorns/ha (Beck 1977, using data from Downs 1944) to 14,064 acorns/ha (this study). Such large differences serve as a warning when comparing species; variability among years and locations could be misleading when computing average acorn production.

Temporal Patterns in Acorn Production

Many studies report that, in most years, acorn production by some species compensates for the effect of crop failure by others (Downs and McQuilken 1944, Burns et al. 1954, Christisen and Korschgen 1955, Gysel 1956, Beck and Olson 1968, Goodrum et al. 1971, Beck 1977, Christisen and Kearby 1984, Beck 1993, Sork et al. 1993, Koenig, Mumme, et al. 1994). Hence, it is important to remember that, although some species may outperform others on an average basis, averages do not insure a consistent supply of acorns.

Differences between 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 (*Leptobalanus* subgenus), including chestnut (*Quercus prinus*) and white oak (*Q. alba*), produce flowers in the spring. If they are fertilized, acorns develop by fall of the same year. Conversely, species in the red oak group (*Erythrobalanus* subgenus), including black oak (*Q. velutina*), northern red oak (*Q. rubra*), and scarlet oak (*Q. coccinea*), produce flowers in the spring but (if fertilized) do not develop acorns until the fall of the following year. Hence, the influence of weather or other external influences on acorn production might be expressed differently by species within the red oak versus white oak subgenera.

If external factors such as weather (Sork et al. 1993) influence flower fertilization or acorn development, it might be predicted that, regionally, species within subgenera should perform similarly. Indeed, northern red oak and scarlet oak of the red oak group exhibited similar temporal patterns of acorn production during the five-year study period (Figure 10.1). However, black oak differed, by having a poor crop year in 1994 (northern red oak and scarlet oak had moderate crops) and a moderate crop year in 1996 (northern red oak and scarlet oak had poor crops). White oak and chestnut oak exhibited similar temporal patterns of acorn production, although white oak outperformed chestnut oak in both 1994 and 1996 (the other years were poor crop years for both species). Crop failure occurred only once during the five-year study period for each species.

Indeed, poor acorn production by some species was offset by good or moderate production by others during most years. In some years (1993 and 1995), species of the red oak group produced acorns when those of the white oak group did not, whereas white oak and chestnut oak produced acorns when red oak species performed poorly (1996). In 1994 all species except black oak produced moderate acorn crops. In only one of the five years studied (1997) was there a complete crop failure (Greenberg and Parresol 2000). This and numerous other studies emphasize the importance of maintaining mixed oak stands that include multiple species within both the white oak and red oak subgenera, to enhance the likelihood of a constant acorn supply.

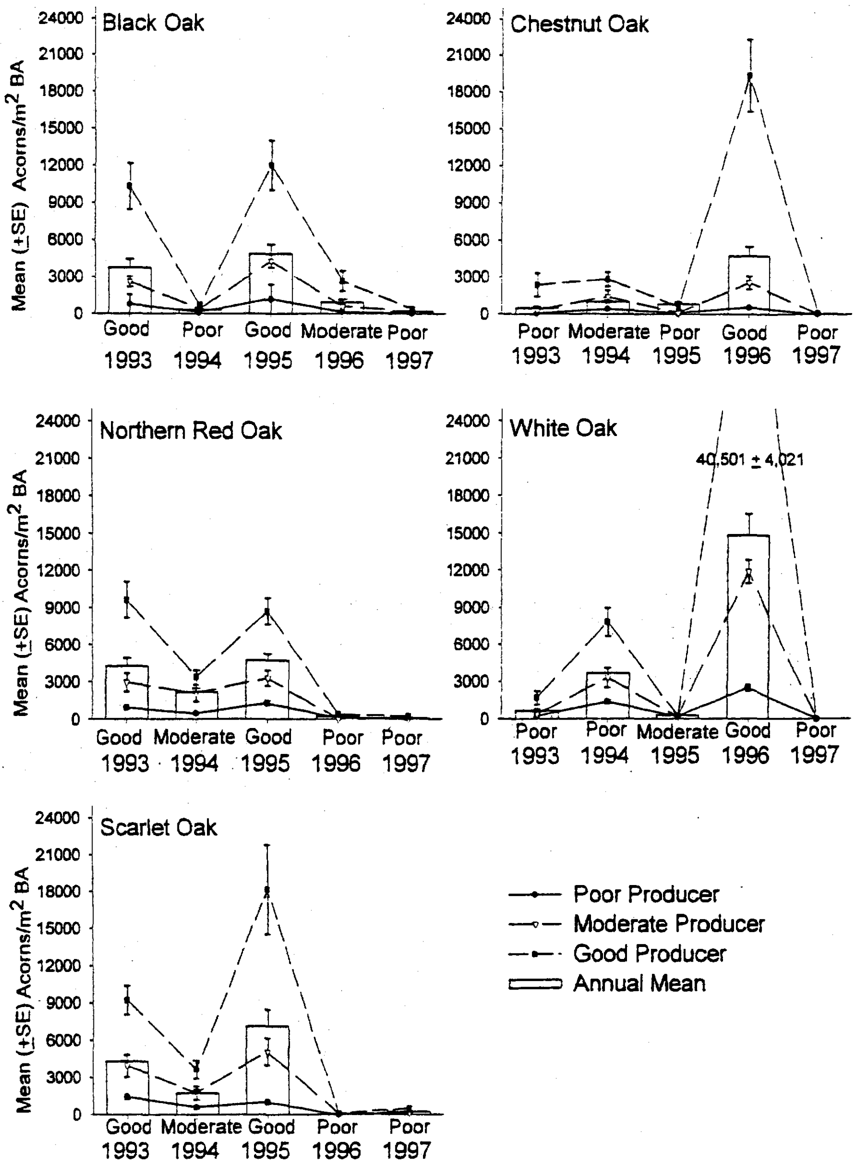

FIGURE 10.1. Annual crop size (mean ± SE number of acorns/m² BA) and relative contribution (mean ± SE number of acorns/m² BA) by good, moderate, and poor producers of five oak species 1993–1997 in the southern Appalachians. Crop-year rating is denoted for each year.

Individual Tree Variation in Acorn Production

Frequency of acorn production also varies among individuals within species. A small proportion of individuals in each species never produced acorns during the study period (1993–1997). With the exception of white oak, a few individuals bore acorns every year (Greenberg 2000).

Good producers composed between 20% (chestnut oak) and 46% (northern red oak) of the sample populations (see Table 10.3). Poor producers composed over 50% of the population for every species except northern red oak. Despite their relatively low representation, good producers of all species outperformed poor and moderate producers by a wide margin of acorn production (Figure 10.1) (Greenberg 2000). Differences were most apparent during good crop years and were negligible in poor crop years. Such disparities in production performance have been reported in numerous studies (Downs and McQuilken 1944, Burns et al. 1954, Gysel 1956, Sharp and Sprague 1967, Christisen and Kearby 1984, Koenig et al. 1991, Sork et al. 1993).

Good producers were characterized by having a higher frequency of acorn-bearing years and producing more acorns/m^2 BA on fruiting trees during good or moderate crop years (Greenberg 2000). However, in any given year, good, moderate, and poor producers were represented similarly in the fruiting population. Hence, the presence of acorns during poor or moderate crop years did not distinguish good from poor producers, nor did an absence of acorns distinguish poor from good producers during good crop years (Greenberg 2000).

Acorn production potentially could be enhanced following silvicul-

Table 10.3
Proportion of poor, moderate, and good acorn producers of five oak species sampled in the southern Appalachians

		Poor	*Moderate*	*Good*
Species	*N*	*(Percentage of individuals)*		
Black oak	135	51.7	19.1	29.2
Northern red oak	111	40.4	13.5	45.9
Scarlet oak	124	53.2	12.1	34.7
Chestnut oak	162	72.2	7.4	20.4
White oak	155	54.2	12.3	33.5

tural treatments such as thinning or two-age harvesting if good producers could be identified and retained. However, three to five years (Healy et al. 1999) or more (Johnson 1994a) of monitoring individual trees for acorn production are necessary to identify good producers. Such difficulty in identifying good producers may in part explain differences in findings among studies of how thinning influences acorn production. If more good than poor producers are removed in one study and more poor than good producers are removed in another, results may differ. Results may be especially confounded when factoring in variability in acorn production among years and species (Healy 1997b).

Does Bigger Mean Better?

Acorn production per tree is significantly positively correlated with basal area in all species (Table 10.4). This is not surprising, given the close positive relationship between crown area and BA. Acorn production increases with tree size at least in part simply because larger trees have greater crown areas for producing acorns. It is not surprising then that some studies report increasing acorn production per tree with increasing tree diameter (Goodrum et al. 1971). However, if this were the only influence of tree size on acorn production then the same volume of acorns could be produced by a few large trees or by the same area of crown distributed among several smaller-diameter trees. The key question is whether larger-diameter trees produce more acorns per unit BA (or per unit crown area) than smaller diameter trees.

Table 10.4

Correlation between basal area and mean number of acorns per tree and between basal area and crown area for five species of southern Appalachian oaks, 1993–1997

	BA (m^2) vs. acrorns/tree		*BA (m^2) vs. crown area (m^2)*	
Species	*N*	r^2	*N*	r^2
Black oak	88	0.2706	91	0.4957
Northern red oak	111	0.2387	148	0.5152
Scarlet oak	124	0.2051	142	0.7481
Chestnut oak	162	0.1013	201	0.7328
White oak	154	0.2677	183	0.7122

Note: All correlations are significant ($p < 0.0001$).

Alone, basal area was significantly positively correlated with the number of acorns/m^2 BA in black oak ($p = 0.0003$; $r^2 = 0.14$), northern red oak ($p = 0.0581$; $r^2 = 0.03$), and white oak ($p = 0.0098$; $r^2 = 0.04$), but not in chestnut or scarlet oak. However, size of BA explained little of the variation in acorn production among individuals (Greenberg 2000). A weak relationship between tree diameter and acorn production has been observed in numerous studies (Downs and McQuilken 1944, Burns et al. 1954, Gysel 1956, Sharp and Sprague 1967, Christisen and Kearby 1984, Koenig et al. 1991, Sork et al. 1993). Healy et al. (1999) report that thinning promoted crown and diameter growth in northern red oaks and also increased acorn production per m^2 crown. However, they note that variation among individuals and years had a much greater effect on acorn production than thinning. Given the high variability in acorn production among individual trees it is not surprising that any potential relationship between tree size and the number of acorns/m^2 BA is obscured.

However, when trees are grouped into diameter classes, some differences in acorn production among size classes are apparent (Figure 10.2). ANOVA indicated that in black oak, northern red oak, and white oak, trees ≤ 25 cm dbh produce significantly fewer acorns/m^2 BA than their larger-diameter counterparts. Acorn production appears to taper off in northern red oak and white oak trees > 76 cm (Greenberg 2000). This has been observed in other studies of acorn production (Downs and McQuilken 1944, Goodrum et al. 1971).

Differences among species in the performance of small-diameter individuals make it impossible to generalize. The fecundity of small dominant or codominant white oaks (10–25 cm dbh) and scarlet oaks (9–22 cm dbh) originating after a 1967 clearcut differed considerably. From 1993 through 1997 scarlet oak produced an average (±SE) of 4,077 ± 2,549 acorns/m^2 BA. Nearly half (45%) of the trees ($N = 20$) were good producers, and 45% were poor producers. However, white oaks ($N = 18$) produced an average of 1,535 ± 924 acorns/m^2 BA. Good producers composed only 11% of the trees, and 83% were poor producers (Greenberg 2000).

Do All Oaks Mast?

Acorn production patterns are often characterized as *masting*, a term that implies synchronous acorn production that results in boom or bust

Sharp 1958, Christisen and Kearby 1984). However, visual surveys are time consuming and provide only categorical estimates of acorn crop yield, which may be biased by differences among observers.

By itself, the proportion of trees bearing acorns was a significant and strong predictor of acorn crop size (mean number/m^2 BA) in any given year of this study (Table 10.5) (Greenberg and Parresol 2000). This provides an expedient tool for forest and wildlife managers or planners to quantify acorn crop sizes within years. Because the proportion of acorn-bearing trees and the number of acorns/m^2 BA of fruiting trees are correlated with one another it is inappropriate to include both in regression analysis. 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/m^2 BA of fruiting trees.

Greenberg and Parresol (2000) detail a method for determining the required sample size to estimate the proportion of trees bearing acorns within a given year, and regression equations (using reduced major axis regression) for five species to estimate within-year crop size with confidence intervals. Methods are as follows:

Estimating the Proportion of Acorn-Bearing Trees to Predict Yield

The natural logarithm of acorn crop yield is estimated as

$$\hat{y} = b_0 + b_1\hat{x} \tag{1}$$

where $\hat{y}$ is the predicted logarithm of acorn crop yield, the b's are equation coefficients (from Table 10.5), and $\hat{x}$ is an estimate of the percentage 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, that is, 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, it is desirable 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 is (Zar 1984)

$$n = \frac{Z^2_{\alpha/2}\tilde{p}\tilde{q}}{d^2} \tag{2}$$

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

Table 10.5
Reduced major axis regression of the natural logarithm of acorn yield (acorns/m^2 BA) on the proportion of trees bearing acorns for five species of southern Appalachian oaks

Species	b_0	b_1	r	*p-value*	$\bar{x}$	S_{xx}	$\hat{\sigma}^2_\epsilon$
Black oak	3.56472	0.055905	0.9942	0.0005	60.3	2,569.41	0.03113
Northern red oak	3.66069	0.060747	0.9861	0.0020	54.3	3,102.63	0.10617
Scarlet oak	3.51901	0.064498	0.9918	0.0009	51.8	3,952.09	0.09008
Chestnut oak	3.78155	0.064998	0.8658	0.0578	39.6	3,184.57	1.20371
White oak	2.58029	0.080842	0.9526	0.0123	47.1	5,095.65	1.05248

Note: See Greenberg and Parresol 2000.

$\hat{p}$. The use of this formula will be demonstrated in the examples following Equation 7 and in Table 10.7.

The antilogarithm of $\hat{y}$ yields the estimated crop size ($\widehat{cs}$) (number of acorns/m^2 BA) in arithmetic (untransformed) units, that is,

$$\widehat{cs} = \exp(\hat{y}) \tag{3}$$

Confidence Intervals

Placing bounds on the predictions of acorn yield is useful, since point estimates from regression equations such as (1) are subject to error. In this case, the variance of y is a function of both residual error and the variance of X. It is given by (Madansky 1959, Kendall and Stuart 1979)

$$\hat{\sigma}_y^2 = b_1^2 \hat{\sigma}_x^2 + \hat{\sigma}_\varepsilon \tag{4}$$

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

$$100^2 \hat{p}\,(1-\hat{p})/n \tag{5}$$

The construction of confidence intervals on the predictions requires the standard errors of the predictions ($s[\hat{y}_i]$) and a t-value. The interval boundary points are obtained from

$$\hat{y} \pm t_{\alpha/2,\, n_r-2} \times s(\hat{y}_i) \tag{6}$$

where n_r is the number of regression observations ($n_r = 5$). The standard errors are calculated as

$$s(\hat{y}_i) = \sqrt{\sigma_y^2\left[\frac{1}{n_r} + \frac{(x_i - \bar{x})^2}{S_{xx}}\right]} \tag{7}$$

Example

A manager wishes to estimate acorn production in a hypothetical forest stand composed of black oak (0.8 m^2), northern red oak (1.7 m^2), scarlet oak (0.5 m^2), chestnut oak (1.0 m^2), and white oak (1.3 m^2). A preliminary walk-through indicates that about 50% of black oak, 90% of northern red oak and scarlet oak, 30% of chestnut oak, and 20% of white oak are producing acorns that year (see Table 10.6).

Beginning with black oak, equation 2 is used to determine how many trees must be surveyed to be within 3% ($d = 0.03$) of the true fruiting proportion (approximated at 50%) at the 80% confidence level ($\alpha = 0.2$, therefore $Z = 1.28$):

$$n = \frac{1.28^2 \times 0.50 \times 0.50}{0.03^2} = 455$$

The required sample size is reduced dramatically if a 5% margin of error is used, that is

$$n = \frac{1.28^2 \times 0.50 \times 0.50}{0.05^2} = 164$$

Slightly more trees should be sampled than predicted from equation 2. Since $\hat{p}$ often is not equal to the initial guess $\tilde{p}$, and if $\hat{p}$ is closer than $\tilde{p}$ to 0.5, n will be slightly larger (variance is maximized at $p = 0.5$). After surveying 174 trees for presence or absence of acorns, it is determined that $\hat{p} = 0.52$, using a 5% margin of error (for this p, the required n also is 164, so a survey of 174 is adequate). Using the coefficients from Table 10.5, for black oak the estimated yield of acorns per m² tree BA in logarithmic units is

$$y = 3.56472 + (0.055905 \times 52) = 6.4718$$

To place bounds on this prediction, $\hat{\sigma}_y^2$ must be calculated first, using equation 4. This yields the following result:

$$\hat{\sigma}_{\bar{y}}^2 = 0.0559^2 \frac{100^2 \times 0.52 \times 0.48}{174} + 0.0311 = 0.0449$$

where b_i and $\hat{\sigma}_\varepsilon^2$ come from Table 10.5. From equation 7 the standard error is computed as

$$s(\hat{y}_i) = \sqrt{0.0449\left[\frac{1}{5} + \frac{(52 - 60.3)^2}{2{,}569.41}\right]} = 0.1009$$

where $\bar{x}$ and S_{xx} are from Table 10.5. From equation 6 the 90% confidence interval is

Table 10.6
Hypothetical forest stand of five southern Appalachian oak species illustrating use of equations 1–7 to predict within-year acorn crop size

Species	BA (m^2/stand)	Estimated % fruiting	Required sample (n)[a] $n = \frac{Z^2_{\alpha/2}\tilde{p}\tilde{q}}{d^2}$	Actual % fruiting	Acorn crop $\hat{y} = b_0 + b_1\hat{x}$	Bounds[b] $\hat{\sigma}^2_{\hat{y}} = b_1^2\hat{\sigma}^2_x + \hat{\sigma}_\varepsilon$
Black oak	0.8	50	164	52	6.4718	0.0449
Northern red oak	1.7	90	60	89	9.0672	0.0516
Scarlet oak	0.5	90	60	92	9.4528	0.0437
Chestnut oak	1.0	30	138	29	5.6665	0.0588
White oak	1.3	20	105	22	4.3588	0.0975
Total	5.3					

Note: First the required sample size for trees used to determine the proportion of fruiting trees must be estimated.

[a]Slightly more trees should be sampled than predicted from equation 2. Since $\hat{p}$ often is not equal to the initial guess $\tilde{p}$, and if $\hat{p}$ is closer than $\tilde{p}$ to 0.5, n will be slightly larger (variance is maximized at p = 0.5).

[b]The variance of variable x, $\hat{\sigma}^2_x$ (equation 5) and used in equation 4 to calculate bounds was calculated here using the required sample size (n) + 10.

$$6.4718 \pm 0.1009\ (2.353) = 6.2344 \leq \hat{y} \leq 6.7092$$

Values are converted from logarithmic to arithmetic units by applying equation 3. Black oak crop size (number of acorns/m^2 BA) from a 52% fruiting population is predicted to be

$$\widehat{cs} = \exp(6.4718) = 646.65 \text{ acorns/m}^2 \text{ BA}$$

Applying equation 3 to the confidence limit values, the following interval is obtained:

$$510 \leq \widehat{cs} \leq 819.9$$

Using the same set of equations, the minimum required number of sample trees is determined for each species, and (using the minimum required number + 10 for the n value in calculations) the crop size (number of acorns/m^2 BA) with confidence intervals is predicted. Crop size values, now in numbers per m^2 BA, must now be expanded to the

SE $s(\hat{y}_i) = \sqrt{\hat{\sigma}^2_{\hat{y}}\left(\frac{1}{n} + \frac{(x_i - \bar{x})^2}{S_{xx}}\right)}$	90% confidence interval $\hat{y} \pm t_{\alpha/2, n_r - 2} \times s(\hat{y}_i)$	Crop size (acorns/ m^2 BA) $\hat{cs} = exp(\hat{y})$	Acorns/stand BA × $\hat{cs}$
0.1009	$\hat{y} \pm 0.2374$	510 ≤ 647 ≤ 820	408 ≤ 518 ≤ 656
0.1742	$\hat{y} \pm 0.4099$	5,752 ≤ 8,666 ≤ 13,057	9,776 ≤ 14,732 ≤ 22,197
0.1631	$\hat{y} \pm 0.3838$	8,682 ≤ 12,744 ≤ 18,706	4,341 ≤ 6,372 ≤ 9,353
0.1176	$\hat{y} \pm 0.2767$	219 ≤ 289 ≤ 381	219 ≤ 289 ≤ 381
0.1776	$\hat{y} \pm 0.4179$	51 ≤ 78 ≤ 119	66 ≤ 101 ≤ 155
			22,012

whole stand. The number of acorns produced in the stand is calculated by multiplying crop size ($\hat{cs}$) for each species by the BA of that species and summing (Table 10.6).

Using these equations, managers can estimate within-year acorn crop size, knowing for each species only the proportion of trees bearing acorns and the BA inventory within the survey area, 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 the species values are summed. 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 10.1. Estimates can be applied to surveyed areas of any size within the southern Appalachian region.

In order 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 depends 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% margin of error and 80% confidence level, if 50% are fruiting), while poor or good crop years require the least (as few as 59 trees if 10% or 90% of a given species are fruiting).

The relationship between acorn crop size and the proportion of acorn-bearing trees described in our study is based on data from acorn traps. It is probable that there will be some discrepancy in acorn detection (presence/absence) 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 higher (although more accurate) estimate of the proportion of fruiting trees and, therefore, would inflate crop-yield estimates. Until that issue is better addressed, visual surveys of trees having very few acorns should be considered as without acorns for these calculations.

Acorn Yield Tables

Table 10.1 is a tool that managers in the southern Appalachians can use to determine or maintain a specified acorn production capability on an area basis. It is possible to test a variety of BA apportionment scenarios among oak species. Average acorn yield for the five study species is presented in Table 10.1. This information cannot be used to predict or even estimate within-year acorn crops, because actual production varies considerably from year to year (Figure 10.1). In addition, mean values are likely to change, perhaps even substantially, with additional years of data (see above discussion under "Are Some Species Better Producers than Others?"). However, given these words of caution, Table 10.1 can be used to estimate long-term acorn production capability. Mean acorn production by species can be calculated on an area basis by multiplying the total BA of a species within an area by the mean acorn production/m^2 BA for that species. By summing these values, we can calculate total average acorn production by the five species.

Conclusions

The ecological and land management implications of acorn crop size underscore the need to better understand acorn production patterns within and among oak species and production characteristics among individuals. For this study, the data indicated that, on average, white oak produced more acorns and biomass (along with northern red oak) than black oak, scarlet oak, or chestnut oak. However, other studies rank species differently in their production capacity. This almost certainly is in part due to differences among studies in the number of years sampled, which years were sampled, how the data are reported (per tree, per m^2 crown area, per m^2 BA by plot, etc.), and the number of trees sampled. These difficulties in comparing studies also highlight the need for long-term studies that use standardized measurement and reporting methodologies. Poor acorn production by some species in this study was offset by good or moderate production by others during most years. Hence, even if some species produce more acorns per m^2 BA, it is important for managers to retain multiple oak species within both the red oak and white oak subgenera, to enhance the likelihood of a constant acorn supply.

Individuals varied in frequency of production and quantity of acorns produced per m^2 BA. Good producers tended to produce more acorns more frequently than poor producers. Although good producers composed 20% (chestnut oak) to 46% (northern red oak) of sample populations, they contributed disproportionately to the acorn crop. However, good producers could not be identified by the presence of acorns during poor crop year nor could poor producers be identified by an absence of acorns during good crop years.

Acorn production increased with tree size, at least in part simply because larger trees have bigger crowns. If that were the primary influence of tree size on acorn production, then the same number of acorns could be produced by a few large trees or by the same area of crown distributed among several smaller-diameter trees. A more pertinent question is whether larger-diameter trees produce more acorns per unit BA than smaller-diameter trees. For the five species studied, the correlation between BA and acorn production/m^2 BA is very weak and/or nonsignificant. It becomes clear that, when grouped into diameter classes, for most species, trees $\leq$ 25 cm produce fewer acorns/m^2 BA than trees > 25 cm. However, the performance of small-diameter trees differs among species.

The term *masting* may not appropriately characterize the fruiting patterns of southern Appalachian oaks. Although most individuals within species in the study produced acorns in some years, or did not produce in others, one-third to two-thirds of individuals produced acorns in other years. This suggests that acorn production is not synchronous among individuals within a population.

Acorn crop size is strongly correlated with both the proportion of individuals in the population that produce acorns and the number of acorns/m^2 BA of acorn-bearing trees. Good crop years are characterized by both more trees producing acorns and more acorns/m^2 BA on fruiting trees. The relationship between acorn crop size and the proportion of individuals in the population that produce acorns provides an expedient tool for land managers to quantify crop size within years. Using the equations presented, land managers can predict acorn crop size for the five study species if they have an inventory of oak BA by species (within any size of area) and if they know the proportion of trees bearing acorns as estimated by simple visual surveys (presence/absence of acorns).

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