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Individual variation in acorn production by five species of southern Appalachian oaks

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Abstract

Acorns are an important wildlife food resource and seed source for oak regeneration. Most acorn production studies note wide and consistent differences in acorn productivity among individuals, but none clearly demonstrate determinants of productivity. Acorn production by black, northern red, scarlet, chestnut and white oak was measured from 1993 to 1997 in the southern Appalachians was measured and compared among species and individuals. 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/m^2 BA (basal area). On average, white oak produced the most acorns and chestnut oak the fewest. Northern red and white oak produced higher green weight and dry biomass than the other three species. There was a significant positive relationship between tree basal area and the number of acorns produced per crown for all species (r^2 between 0.10 and 0.27). However, this is because larger trees have greater crown areas for producing acorns, and not because they produce more acorns per unit area of crown. Alone, BA was significantly, positively correlated with the number of acorns/m^2 BA only in black, northern red ($p < 0.06$) and white oak (not in scarlet or chestnut oak) but explained little of the variation in acorn production among individuals. Trees $\leq$25 cm DBH of most species produced significantly fewer acorns/m^2 BA than their larger counterparts. However, many small (<23 cm DBH) scarlet oaks originating from a 1967 clear-cut were prolific producers, whereas white oaks (<25 cm DBH) in the same stand were not. Frequency of acorn production ranged from never to yearly among individuals. Good producers (trees producing $\geq$5-year species mean) composed 20% (chestnut oak) to 46% (northern red oak) of sample populations but contributed disproportionately to the acorn crop in moderate and good crop years. Good producers produced acorns more frequently and had more acorns/m^2 BA on fruiting trees than did poor producers. However, in any given year good and poor producers were similarly represented in the fruiting population. Hence, good producers could not be easily identified by the presence of acorns during poor crop years, nor could poor producers be identified by an absence of acorns in good crop years.

Keywords: Acorns; Oak; Southern appalachian oaks

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1. Introduction

Acorns represent a valuable food resource to numerous game and nongame wildlife species (Van Dersal, 1940; Martin et al., 1951). Highly erratic acorn production patterns have a demonstrable influence on the survival and/or recruitment of white-tailed deer (*Odocoileus virginianus*) (Wentworth et al., 1992), squirrels (*Sciurus* spp.) (Nixon et al., 1975), black bears (*Ursus americanus*) (Eiler et al., 1989), red headed woodpeckers (*Melanerpes erythrocephalus*) (Koenig and Mumme, 1987; Smith and Scarlett, 1987) and white-footed mice (*Peromyscus leucopus*) (Wolff, 1996) populations, among others. Wolff (1996) suggests that acorns function as a 'keystone' forest resource by influencing small mammal prey populations. Indeed, acorn production indirectly impacts gypsy moth (*Lymantria dispar*) populations (Elkinton et al., 1996) and even the prevalence of Lyme disease (Jones et al., 1998) through its direct influence on white-footed mouse populations. Oak regeneration is also dependent upon its seed source, along with many other factors that influence seedling establishment and success (Loftis and McGee, 1993). Because of its importance to wildlife and forest regeneration, acorn production has been the subject of considerable attention by forest managers.

Virtually all studies of acorn production note wide and consistent differences in acorn production performance among individuals (Downs and McQuilken, 1944; Burns et al., 1954; Gysel, 1956; Sharp and Sprague, 1967; Christisen and Kearby, 1984; Koenig et al., 1994; Sork et al., 1993). Some studies suggest that intrinsic features such as age or size (Goodrum et al., 1971) influence acorn production. Others demonstrate some relationship between external conditions such as stand density and acorn production (Healy, 1997). However, there remain no clear determinants of acorn production performance, leading most to conclude that genetics play a critical role.

The objectives of this study are to examine: (1) the range of variability in acorn production performance among five southern Appalachian oak species and individuals within species; (2) whether any measurable tree characteristics or fruiting patterns can be used to identify superior acorn producers; and (3) fruiting characteristics that contribute to the observed range of acorn production performance.

2. Methods

2.1. Acorn sampling

Acorn production by 765 individuals of five oak species was sampled throughout the southern Appalachians from 1993 to 1997 in an ongoing, long-term study. Study species included northern red oak (*Quercus rubra*) ($N = 148$), scarlet oak (*Q. coccinea*) ($N = 142$) and black oak (*Q. velutina*) ($N = 91$) in the red oak subgenus, and chestnut (*Q. prinus*) ($N = 201$) and white oak (*Q. alba*) ($n = 183$) 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 (NFs) in three states: the Cherokee NF in Tennessee, the Pisgah NF in North Carolina, and the Chatahoochee NF in north Georgia (Fig. 1).

Trees were selected haphazardly to represent a wide range of size (9–133 cm diameter at breast height (DBH)) and age classes. Most trees were mature and in dominant or codominant (a few were intermediate) crown positions. One stand composed of scarlet ($n = 20$) and white oak ($n = 18$) in the Pisgah NF originated following a clear-cut regeneration harvest in 1967 (when all trees taller than 1.4 m were felled). Sample trees were located at elevations ranging from 850 to 1180 m above sea level and at a wide range of topographic conditions such as aspect, slope position and percent slope.

Acorns were collected in traps constructed with shade cloth attached to 0.5-m diameter ring of galvanized wire suspended by treated wooden stakes or rebar $\approx$1 m above the ground. Traps were placed beneath the trees so as to obtain a representative sample of the crown. The number of traps per tree was approximately proportional to the basal area (2–14 per tree).

Crown areas were measured from 1993 to 1997 and computed as an octagon using eight radii and azimuths from tree base to the canopy drip line. Traps were checked at $\approx$2-week intervals (collection intervals varied somewhat among NF districts) from mid-August through the completion of acorn drop. Traps do not measure acorns that are removed by arboreal consumers, or those that are occasionally removed from traps by acorn consumers, probably resulting in conservative crop size estimates.

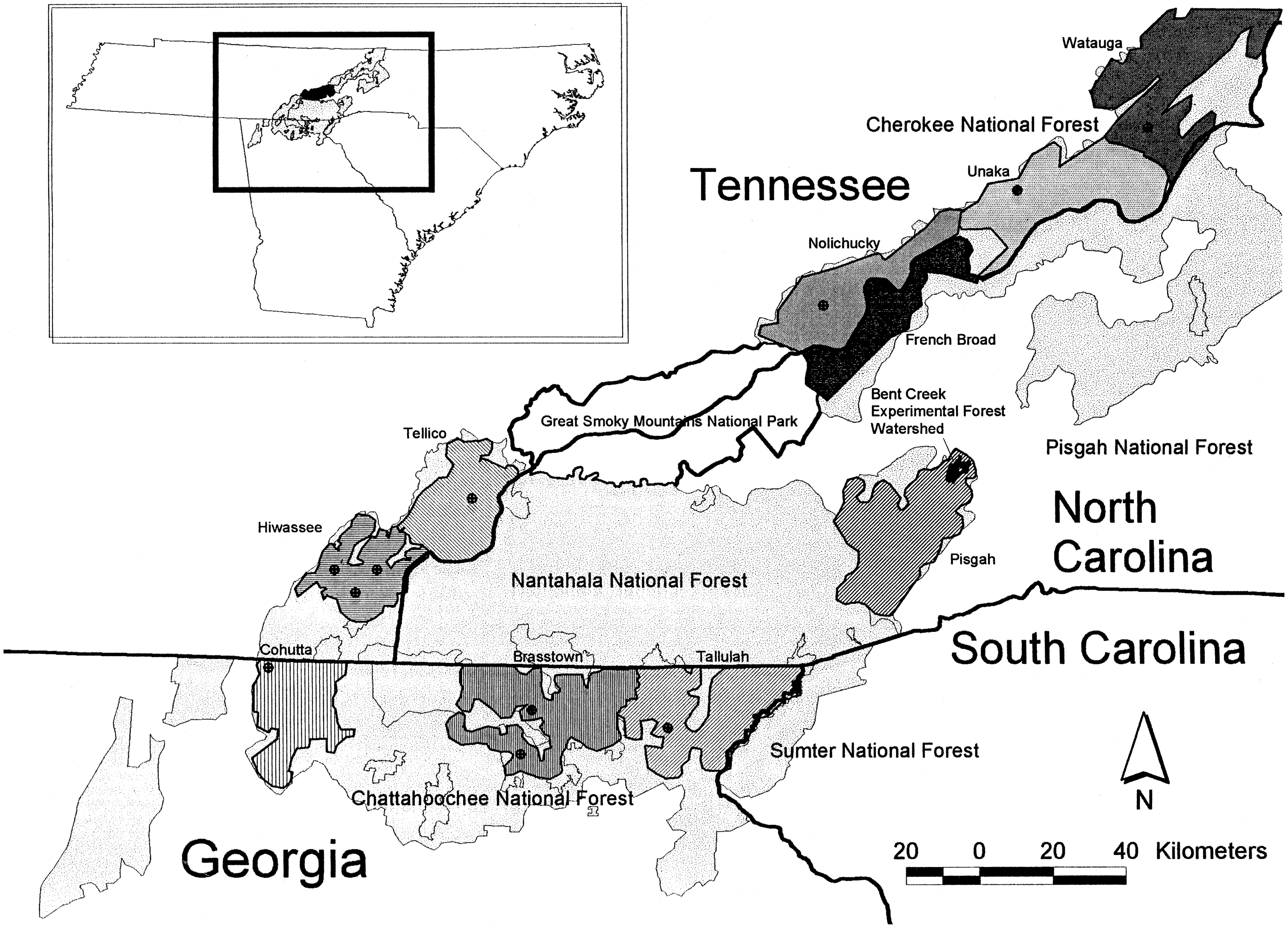

Fig. 1. General location of black, northern red, scarlet, chestnut and white oak study trees in the Chatahoochee National Forest (NF), north Georgia, Pisgah NF, North Carolina and Cherokee NF, Tennessee, southern Appalachian mountains.

Trap contents were sorted, counted and initially classified in the lab as aborted or well developed. Well-developed acorns were classified as intact or animal damaged. Well developed, intact acorns (or a subsample if $n > 25$ for a tree) were cut open and examined for internal insect damage. Sound acorns were weighed with hulls but without caps (green weight), dried at 50°C for five days and weighed again without hulls (dry biomass).

2.2. 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. For purposes of this paper all well-developed acorns were included in 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 (BA) per tree by dividing the total acorn production of each tree by its BA.

Acorn production performance of each tree was ranked as 'poor', 'moderate' or 'good' by comparing its five-year (1993–1997) mean number of acorns/m^2 BA to the five-year mean of its species. A tree was defined as a good producer if it produced ≥5-year mean of its species, moderate if it produced ≥60% of, but less than the mean, and poor if it produced <60% of the five-year mean for the species (adapted from Healy et al., 1999). Only individuals that were sampled in all five years were included in the ranking. Annual acorn crops were also ranked as poor, moderate or good by comparing the mean number of acorns/m^2 BA for a given to year to the five-year average for the species.

The mean number of acorns/m^2 BA of fruiting trees (excluding non-fruiting individuals) was compared among production classes for each year and species using ANOVA. Pairwise contrasts were performed using least-squares means tests (SAS Institute,

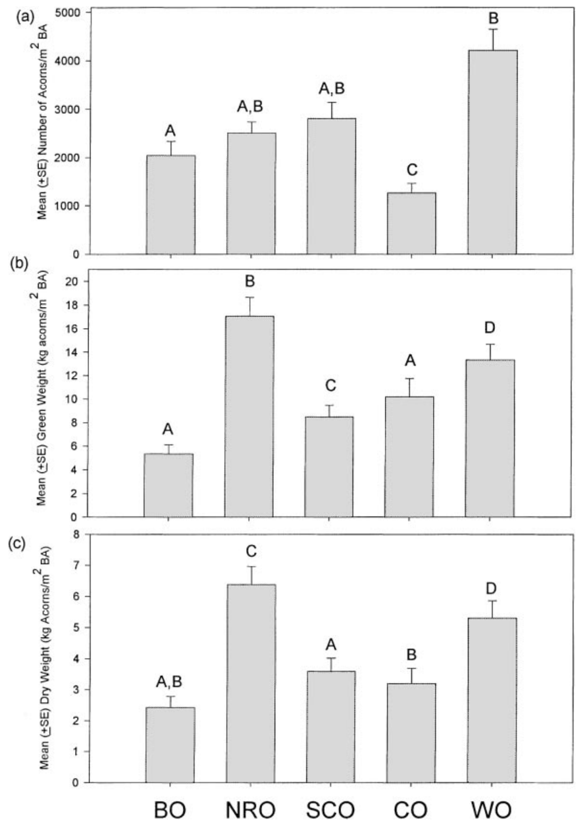

Fig. 2. Mean (1993–1997) (±SE) (a) number; $F = 23.4$; $p = 0.0001$ (b) green weight; $F = 17.4$; $p = 0.0001$ and, (c) dry biomass; $F = 17.8$; $p = 0.0001$, of acorns/m^2 BA produced by five oak species in the southern Appalachians. Significant differences in mean acorn production are denoted by different letters among species. Acorn data were natural log transformed for ANOVA, but are presented as actual means.

Table 1
Correlation between basal area (m^2) and the mean (1993–1997) number of acorns produced per tree crown for five species of southern Appalachian oaks

Species	n	r^2	p-Value	F-Value	Equation[a]
Black oak	88	0.2706	<0.0001	31.91	$Y = (-365.35) + 4603.37(x)$
Northern red oak	111	0.2387	<0.0001	34.17	$Y = -135.06 + 2344.87(x)$
Scarlet oak	124	0.2051	<0.0001	31.49	$Y = (-15.21) + 3148.10(x)$
Chestnut oak	162	0.1013	<0.0001	18.04	$Y = (-49.09) + 997.18(x)$
White oak	154	0.2677	<0.0001	55.94	$Y = (-26.88) + 5239.61(x)$

[a] Y is the the mean (1993–1997) number of acorns produced per crown and x the basal area (m^2).

Table 2
Correlation between basal area (m^2) and crown area (m^2) for five species of southern Appalachian oaks

Species	n	r^2	p-Value	F-Value	Equation[a]
Black oak	91	0.4957	<0.0001	87.49	$Y = 0.7181 + 241.56(x)$
Northern red oak	148	0.5152	<0.0001	155.18	$Y = 19.97 + 206.25(x)$
Scarlet oak	142	0.7481	<0.0001	415.83	$Y = 3.62 + 327.35(x)$
Chestnut oak	201	0.7328	<0.0001	545.81	$Y = 10.41 + 233.11(x)$
White oak	183	0.7122	<0.0001	447.82	$Y = 6.96 + 257.61(x)$

[a] Y is the mean crown area (m^2) and x the basal area (m^2).

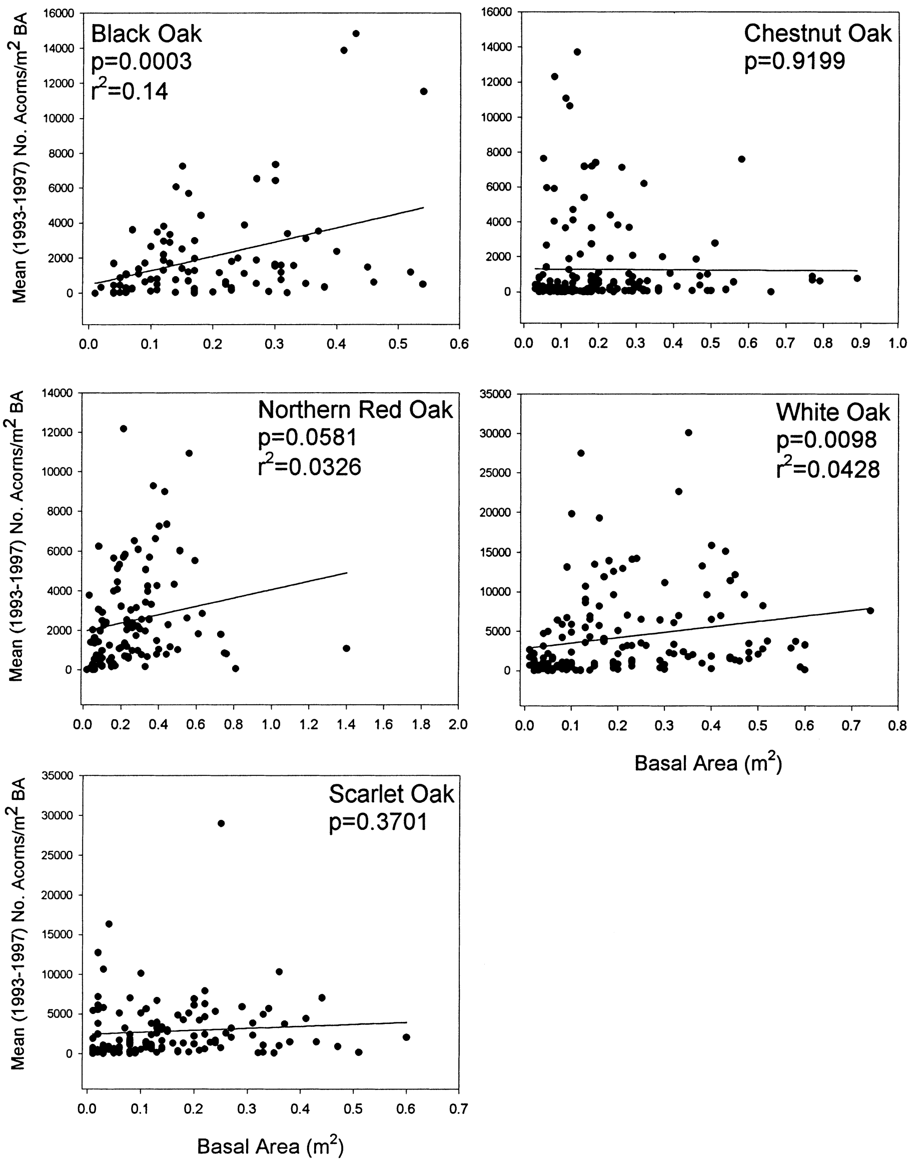

Fig. 3. Simple linear regression of basal area (m^2) and mean (1993–1997) number of acorns/m^2 BA for five species of southern Appalachian oaks.

1989). The number of acorns/m^2 BA was natural log transformed for ANOVA to reduce the correlation between the mean and variance (Zar, 1984). Statistical significance is reported at the $p < 0.05$ level unless otherwise stated. Simple linear regression was performed to explore the relationship between tree BA, crown size and mean acorn production.

3. Results

The average (1993–1997) number of acorns produced/m^2 BA differed significantly among species (Fig. 2). On average, white oak produced the most acorns and chestnut oak the fewest. Both northern red and white oak produced significantly higher green

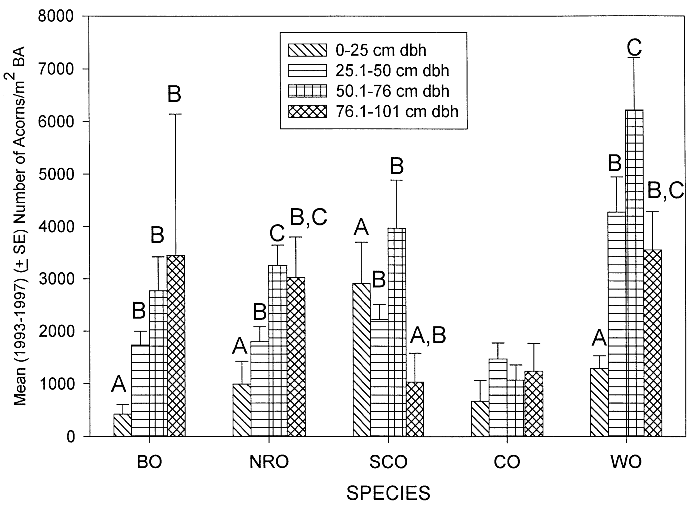

Fig. 4. Mean (1993–1997) (±SE) number of acorns/m^2 BA produced by four diameter classes of black oak ($F = 5.8$; $p = 0.0012$), northern red oak ($F = 11.8$, $p = 0.0001$), scarlet oak ($F = 3.85$; $p = 0.0013$), chestnut oak ($F = 1.1$; $p = 0.3509$) and white oak ($F = 6.71$; $p = 0.0003$) in the southern Appalachians. Different letters denotes significant differences in mean acorn production among diameter classes. Acorn data were natural log transformed for ANOVA, but are presented as actual means.

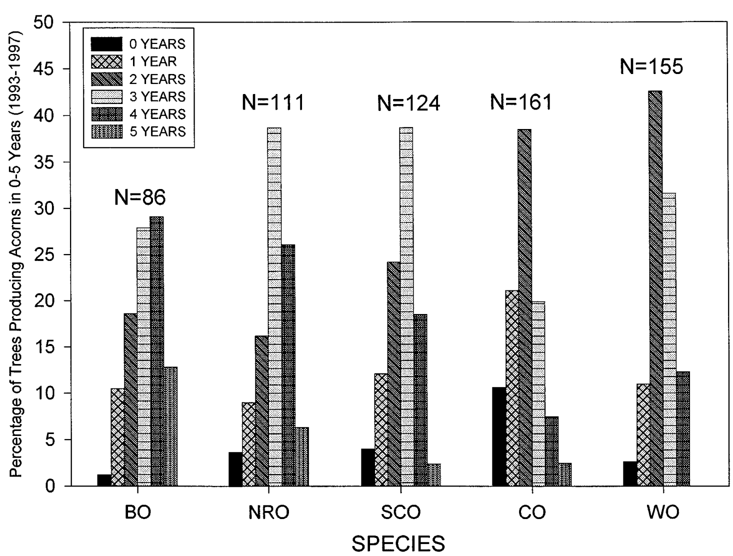

Fig. 5. Fruiting frequency (% of years sampled) of five oak species sampled from 1993 to 1997 in the southern Appalachians.

weight and dry biomass than chestnut, black or scarlet oak (Fig. 2).

Acorn production per tree crown was significantly, positively correlated with BA in all species (Table 1). This is not surprising in view of the close positive relationship between crown area and BA (Table 2). Acorn production increases with tree size at least in part simply because larger trees have greater crown areas for producing acorns. A key question is whether larger trees produce more acorns per unit area of crown (or BA) than smaller trees. Alone, BA was significantly, positively correlated with the number of acorns/m^2 BA only in black, northern red ($p < 0.06$) and white oak (not in scarlet or chestnut oak) but explained little of the variation in acorn production among individuals (Fig. 3).

However, when trees are grouped into diameter classes some differences in acorn production among size classes are apparent (Fig. 4). ANOVA indicated that in black oak, northern red oak and white oak, trees $\leq$25 cm DBH produce significantly fewer acorns/m^2 BA than their larger counterparts. Acorn production appeared to taper off in northern red oak and white oak trees >76 cm.

The fecundity of small dominant or codominant white (10–25 cm DBH) and scarlet oaks (9–22 cm DBH) originating following a 1967 clear-cut differed considerably. From 1993 to 1997 scarlet oak produced an average of 4077 $\pm$ 2549 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 1535 $\pm$ 924 acorns/m^2 BA. Good producers composed only 11% of the trees, and 83% were poor producers.

Fruiting frequency varied among individuals within species. A small proportion of individuals in each species never produced acorns during the study period (1993–1997) (Fig. 5). Conversely, a few individuals bore acorns every year.

Good producers composed 20% (chestnut oak) to 46% (northern red oak) of the sample populations (Fig. 6). Conversely, poor producers composed over 50% of the population for all species except northern red oak (Fig. 6). Despite their relatively low representation good producers of all species outperformed poor and moderate producers by a wide margin of acorn production (Fig. 7). Differences were most apparent during good crop years and were negligible in poor crop years.

Good producers were characterized by having a higher frequency of acorn-bearing years (Fig. 8) and more acorns/m^2 BA on fruiting trees (Fig. 9).

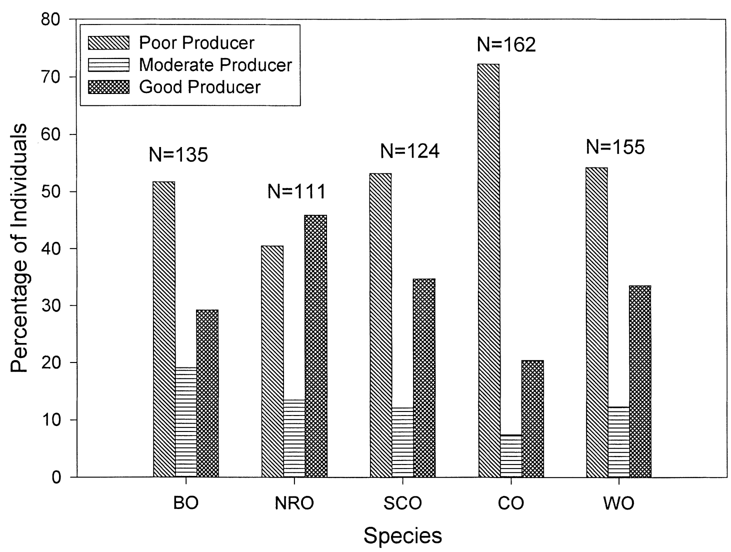

Fig. 6. Proportion of poor, moderate and good acorn producers of five oak species sampled in the southern Appalachians.

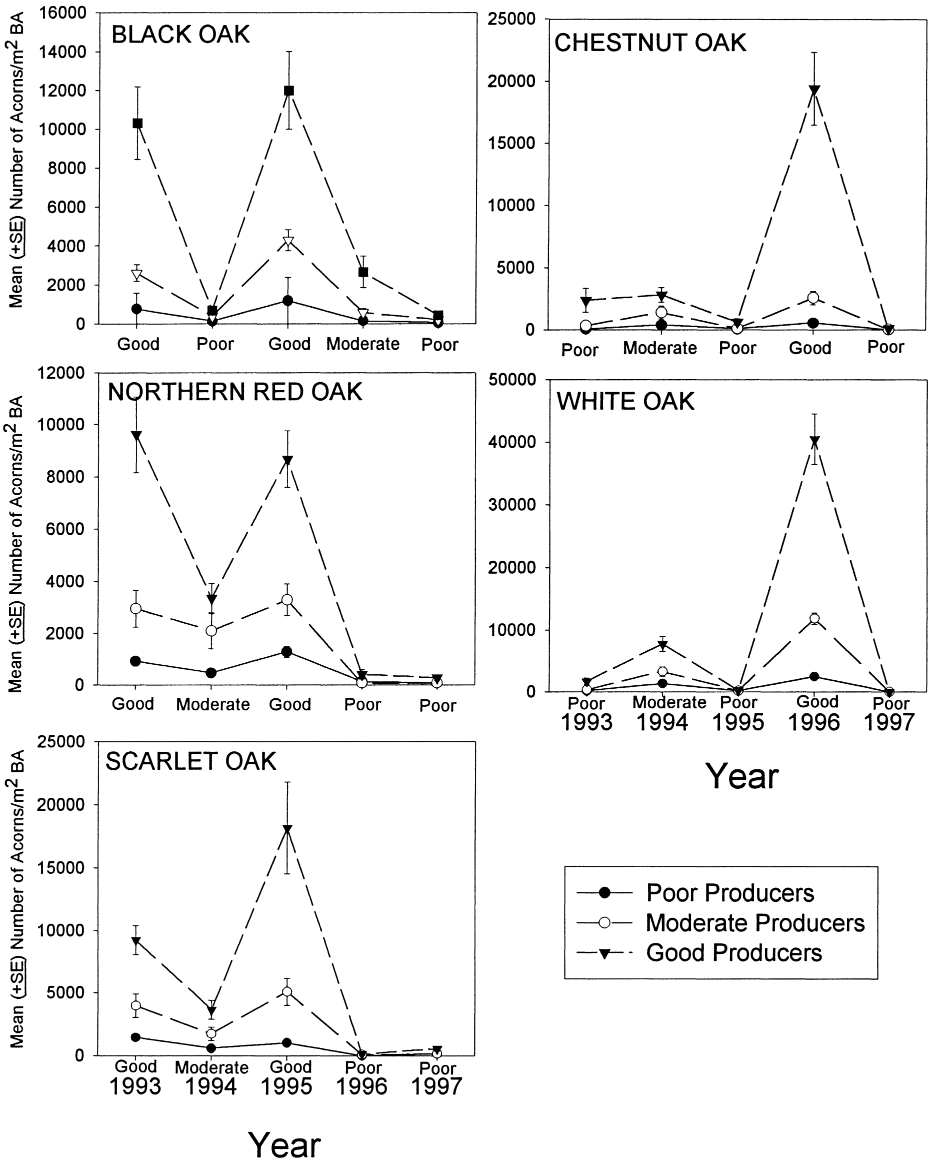

Fig. 7. Mean (±SE) annual acorn production by good, moderate and poor producers of five oak species from 1993 to 1997 in the southern Appalachians. Crop-year rating is denoted for each year.

However, in any given year good, moderate and poor producers were represented similarly in the fruiting population (Fig. 10). 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.

4. Discussion

Results of this study confirm Beck's (1977) findings that on average, northern red and white oak are superior acorn producers. However, this study among others clearly illustrate the importance of maintaining mixed oak stands, since interspecific differences in temporal

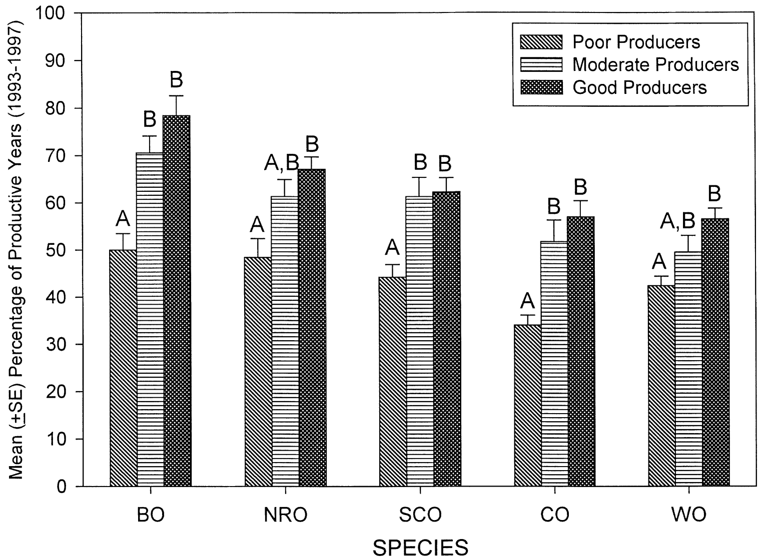

Fig. 8. Mean (±SE) percentage of productive years by poor, moderate and good acorn producers of five oak species in the southern Appalachians. Different letters among production classes within a species denotes significant differences.

masting patterns often offset complete mast failures (Beck and Olson, 1968; Beck's, 1977; Christisen and Kearby, 1984; Koenig et al., 1994). Further the distinction between numbers versus green weight and dry, edible biomass of acorns produced is important for land managers who wish to maintain a specified mast capability in forest stands.

Given the enormous variation in fecundity among individuals, it is not surprising that larger trees produce more acorns; this is primarily by virtue of their proportionately larger crowns. Tree diameter alone contributed little to differences in fecundity among individual trees.

High variability in acorn production among individual trees obscures any potential relationship between tree size and the number of acorns/m^2 BA. The weak to non-existent relationship between tree BA alone and acorn productivity has been noted in other 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).

However, when grouped into diameter classes, it becomes clear that in black, white and northern red oak trees $\leq$25 cm DBH tend to produce fewer acorns/m^2 BA than their larger counterparts. Scarlet oak appears to be an exception. The proportion of good producers in a stand of small (<23 cm DBH) scarlet oaks originating from a 1967 clear-cut was similar to that of the entire sample of mature scarlet oaks. Size appears to have little influence on acorn production in chestnut oak. Acorn production in this study as in others appears to taper off somewhat in very large trees of northern red and white oak species. This has been observed in many other studies of acorn production (Downs and McQuilken, 1944; Goodrum et al., 1971). Hence a similar acorn productivity can be apparently attained by distributing the same BA among several smaller (>25 cm) oaks as among fewer larger oaks. This has the further benefit of reducing the risk that a few retained oaks are poor producers.

Superior acorn producers composed less than half of the oak population for all species, but produced many times more acorns than the other trees during good or moderate 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 produced acorns more fre-

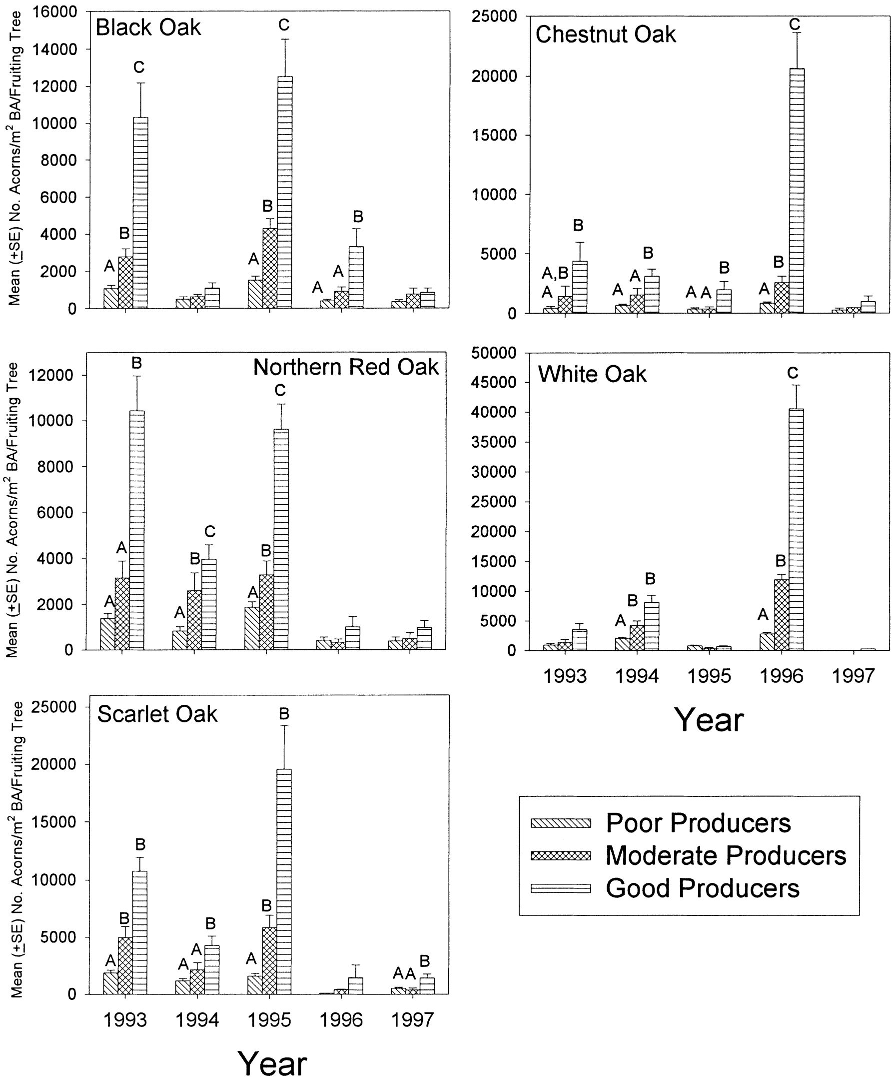

Fig. 9. Mean (±SE) number of acorns/m^2 BA produced by fruiting trees of poor, moderate and good producers of five oak species from 1993 to 1997 in the southern Appalachians. Significant differences ($p < 0.05$) are denoted by different letters among production classes within a year. Acorn data were natural log transformed for ANOVA, but are presented as actual means.

quently, and fruiting trees produced more acorns/m^2 BA than their less prolific counterparts.

Identification of good producers would be useful to land managers wishing to enhance mast production capability. Healy et al. (1999) describe a method for identifying good producers. However, identifying most good producers requires three years of observing and marking individual trees. Unfortunately, a quick method is not readily apparent.

5. Conclusion

Acorn production performance varies among species and among individuals within species. However, measurable tree characteristics such as size do not appear to offer sufficient information to identify individual trees of superior production ability. Forest stands composed of multiple oak species have a higher likelihood of sustained acorn yield than single-species

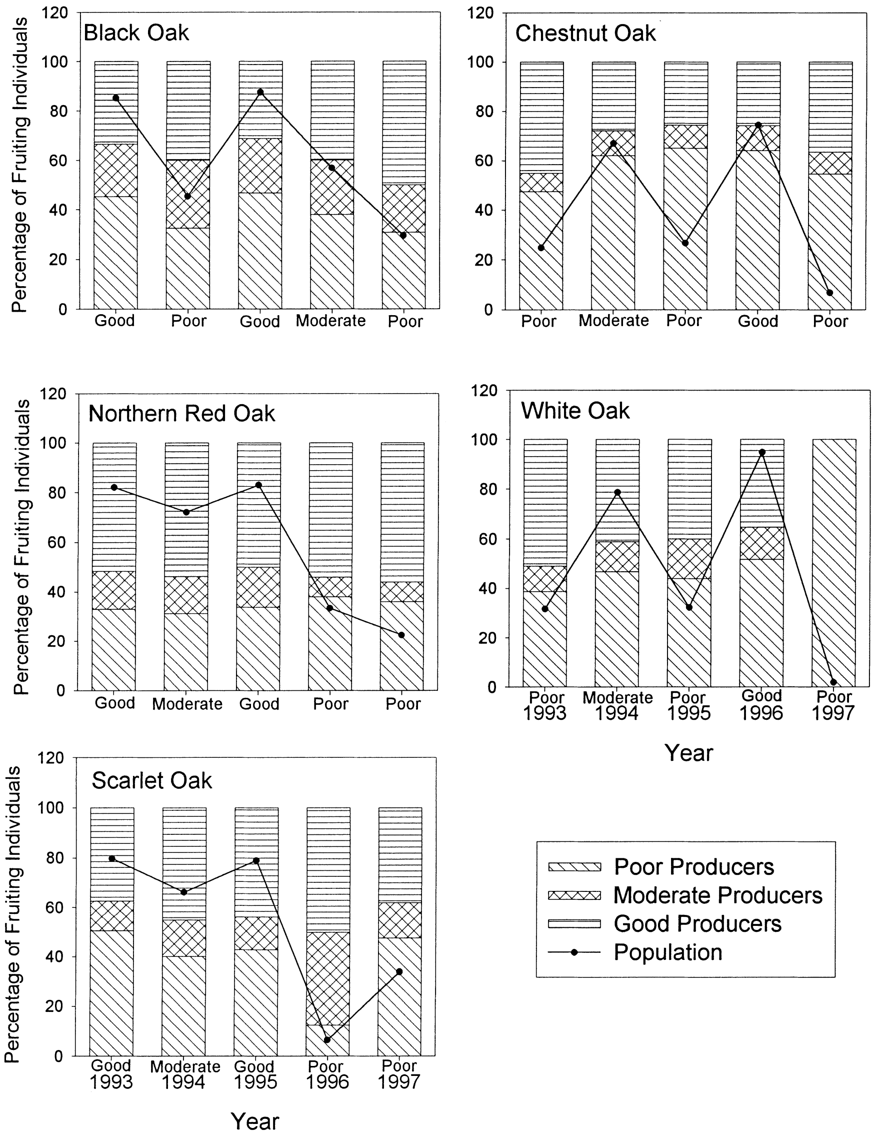

Fig. 10. Proportion of poor, moderate and good producers composing the annual (1993–1997) fruiting population of five species of southern Appalachian oaks.

stands since the effect of crop failure by one species is often dampened by others. For most species, trees >25 cm DBH tend to produce more acorns than smaller trees. Although there is a minimal effect of tree BA on acorn production, individual variation is extremely high such that size alone is a poor predictor of production performance. Retaining good producers in each species could enhance acorn production. However, only by noting individual differences in the frequency of fruiting and number of acorns produced/m^2 BA can superior acorn producers be identified.

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