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ACORN PRODUCTION BY OAKS IN CENTRAL COASTAL CALIFORNIA: VARIATION WITHIN AND AMONG YEARS[1]

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Abstract. We measured acorn production by individual oaks of five different species at Hastings Reservation in central coastal California between 1980 and 1991. Variation in acorn production was considerable both within and among years and was generally uncorrelated between species. Compared to expected values, variance within years in the size of acorn crops was small, while variance among years was high. Crop failures occurred fairly frequently and large crops in successive years were observed, but no more than expected by chance. Individual trees masted at species-specific intervals, but these patterns did not result in regular masting cycles at the population level.

We compared these patterns to predictions of four hypotheses for the evolution of seed production patterns. Observations did not support the hypotheses that production patterns track resource availability (the "resource matching" hypothesis) or that they have evolved to attract seed dispersers (the "seed dispersal" hypothesis). However, they are generally consistent with two additional hypotheses, that masting in these wind-pollinated species evolved because of a proportional increase in fertilization and seed set during mast years (the "wind pollination" hypothesis) and that masting has evolved to maximize the probability of avoiding predation via predator satiation (the "predator satiation" hypothesis).

Key words: acorns; California; Fagaceae; masting; oaks; predator satiation; Quercus; *reproductive effort; resource matching; seed production; wind pollination.*

INTRODUCTION

The size and constancy of acorn crops are not only basic to the life history of oaks but also important to the diverse assemblage of birds and mammals that rely on acorns as a major food resource. However, little is known about acorn production patterns except for studies in the eastern United States that describe periodic years of synchronous production, or mast years, followed by periods of very low production (Downs and McQuilken 1944, Burns et al. 1954, Christisen and Korschgen 1955, Goodrum et al. 1971, Sork et al. 1993) and work demonstrating considerable variability in acorn production among individual trees (Downs 1944, Gysel 1956, Sharp and Sprague 1967, Griffin 1976, Feret et al. 1982). Understanding acorn production patterns is of particular interest in California where oaks dominate millions of hectares (Griffin and Critchfield 1972, Bolsinger 1987) but are declining due to habitat loss and poor regeneration by several key species (Pavlik et al. 1991).

This paper expands on earlier preliminary reports (Carmen et al. 1987, Koenig et al. 1991) and is the first of a series devoted to understanding seed production patterns of oaks in central coastal California. We examined five species: *Quercus lobata, Q. douglasii, Q. agrifolia, Q. kelloggii,* and *Q. chrysolepis.* These species are all common in this region but differ in many characteristics, the most salient of which are summarized in Table 1. Here we examine four hypotheses for the evolution of the seed production patterns observed in these species. Tests are made with respect to five aspects of reproduction: the extent of within- and among-year variation, bimodality in reproductive effort, the incidence of crop failures, whether large crops occur in successive years, and the existence of masting cycles.

We first briefly discuss the two levels at which we analyze our data and then outline the hypotheses and their predictions.

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TABLE 1. Names and characteristics of oak species used in this study.

	Q. lobata	*Q. douglasii*	*Q. chrysolepis*	*Q. kelloggii*	*Q. agrifolia*
Common name	Valley oak	Blue oak	Canyon oak	Black oak	Coast live oak
Subgenus	*Quercus* ("white")	*Quercus* ("white")	*Protobalanus* ("intermediate")	*Erythrobalanus* ("black")	*Erythrobalanus* ("black")
Deciduous?	Yes	Yes	No	Yes	No
Growing seasons required to mature acorns	1	1	2	2	1
Sample size (No. trees)	86	56	21	20	63

LEVELS OF VARIATION IN ACORN PRODUCTION

We address variation in seed production at two levels.

Among individuals, within years.—Values are the crop sizes of individual trees in year *i*. Sample size within years is the number of individuals. Each species yields *n* samples, where *n* is the number of years of the study (in our case, $n = 12$ through 1991). For example, the mean variance in within-year acorn production of species *a* is calculated as $\sum_{i=1}^{n} \sigma^2_{i,a})/n$ where $\sigma^2_{i,a}$ is the variance in acorn production in year *i* of all individual trees of species *a* included in the survey.

Among years.—Crop sizes for all trees of species *a* are averaged for each year *i* to yield *n* values, $\bar{X}_{i,a}$, where *i* ranges from 1 to *n*. These $\bar{X}_{i,a}$ values then provide the basis for analysis, with each species ultimately yielding a single number.

HYPOTHESES AND PREDICTIONS

Masting may result from either of two major processes: resource matching and economies of scale (Norton and Kelly 1988). According to the "resource matching" hypothesis, seed crop size tracks current resource levels and thus annual variation in resources causes masting patterns. Alternatively, masting may result from the reallocation of resources among years so as to increase the efficiency with which seeds escape predation (the "predator satiation" hypothesis; Janzen 1971, Ims 1990*a*, *b*), attract seed dispersers (the "seed dispersal" hypothesis; Barnett 1977, Givnish 1980, Sork 1983), or are fertilized; the latter is particularly relevant to wind-pollinated species (the "wind-pollination" hypothesis; Norton and Kelly 1988, Smith et al. 1990).

Resource matching.—This hypothesis proposes that seed production tracks some resource. It is likely that the critical resource, whatever it is, should at least be correlated with weather (Sork et al. 1993). Because annual weather conditions vary relatively little (seasonal rainfall, for example, varies by a factor of only 4.3 between the wettest and the driest years at our study site), fluctuations in seed crops are likely to be moderate (Norton and Kelly 1988). There is also no a priori reason to expect that critical resources, and thus the frequency of seed crop sizes either within or among years, will be bimodally distributed (that is, consist primarily of trees or years of high and low acorn production with few intermediate values). Because crop sizes should track resources on a year-to-year basis, crop failures at the population level should be rare. Large seed crops in successive years are possible depending on the pattern of resource availability. Finally, regular masting cycles should not occur at either the individual or population levels. Such cycles would suggest that trees alternate in the allocation of resources between mast and nonmast years (Norton and Kelly 1988) rather than track resources, unless the relevant critical resource also cycles (Sork et al. 1993).

Predator satiation.—As usually envisioned, this hypothesis predicts that individuals should mast synchronously, since this maximizes the probability of swamping predators in mast years and starving them in nonmast years (Silvertown 1980). Thus, the frequency distribution of crop sizes among individuals within years should be unimodal and within-year variance in acorn production should be low. Among years, acorn production values should be bimodally distributed with large variance. Crop failures are expected and individual trees should produce large crops cyclically and synchronously to ensure the reduction of seed predator populations between mast years. However, masting cycles should either be long relative to the time needed for predator numbers to decline, as in periodical cicadas, or of irregular length, making it difficult for predators to track cycles over ecological or evolutionary time. Because high predator population sizes following a good mast year are likely to lead to heavy seed losses in a succeeding mast year (Norton and Kelly 1988), large seed crops should not occur successively.

Ims (1990*a*, *b*) has recently pointed out that many of the predictions of the predator satiation hypothesis are dependent on the functional response of seed predators. If, for example, predators are generalists switching from alternative food resources only when seeds are abundant, reproductive synchrony might lead to the most intense predation, thus selecting for highly asynchronous seed production within years and low variation among years. Unfortunately, major predators of acorns in California include a large number of species ranging from short-lived insects specializing on acorns such as filbert weevils (*Curculio* spp.) to long-lived generalists such as mule deer (*Odocoileus hemionus*). Thus, it is difficult to determine a priori what pattern of acorn production would result in the fewest acorns being attacked. We therefore confine ourselves to the traditional view of predator satiation described above. However, a potential role for predators cannot be rejected even if the predictions based on this view are not met.

Wind pollination.—Because of its undirected nature, concentration of pollen production in mast years should increase the efficiency of wind pollination. Therefore, reproduction will be most efficient if investment in male and female reproduction is restricted to particular years (Nilsson and Wästljung 1987, Norton and Kelly 1988).

Smith et al. (1990) examined the assumptions necessary for masting to be related to wind pollination and concluded that this should primarily be true in boreal forest trees that have seeds grouped in catkins whose extensive woody tissue is produced regardless of the frequency of seed set. Such trees might gain considerable energy advantages by concentrating pollen production in years of mast flowering. In contrast, many temperate forest trees, including oaks, commit energy to female growth only after pollination and thus are able to abort large numbers of female flowers with relatively little energy loss if pollination is poor (Smith et al. 1990, Sork et al. 1993). In these species the potential advantages of investing simultaneously in male and female reproduction are reduced but may not be eliminated, especially if climatic conditions conducive to successful seed development can also be used as cues for high pollen production (C. C. Smith, *personal communication*). To the extent this is the case, the wind pollination hypothesis would involve an element of resource matching as well.

Pollination efficiency is likely to be maximized if within-year acorn production is synchronous with low variance while among-year acorn production is bimodally distributed with high variance. Crop failures should occur in years when trees reallocate resources to nonreproductive functions. These predictions are the same as for the predator satiation hypothesis. In contrast to this latter hypothesis, however, the wind pollination hypothesis is compatible with regular masting cycles and with the production of large crops in successive years, since the advantages of masting do not automatically diminish following a year of high acorn production if this phenomenon serves primarily to enhance the efficiency of pollination and reproductive effort.

Attraction of seed dispersers.—This hypothesis focuses on potential competition among trees for animals to disperse their seeds. Similar to the predator satiation hypothesis, the optimal pattern of seed production depends on the functional response of dispersers to large seed crops and the potentially complex relationships between the proportion of seeds cached by animals and both the reproductive effort of an individual tree and the overall seed availability in a particular year (Ims 1990*a*).

If seed dispersal is the major factor driving seed production patterns, there should be some trees each year that invest highly in reproduction so as to outcompete others for the attraction of dispersers. Thus, within years there should be moderate to high variance in acorn production and possibly a bimodal distribution of reproduction, while among years, fluctuations in seed crops should be moderate to low. Seed production should not be bimodal among years, and crop failures at the population level should be rare or absent. Masting in successive years is possible, as are masting cycles by individual trees. However, masting cycles should not occur at the population level.

The likely importance of this hypothesis depends in part on the kind of reward provided to dispersers. True fruits consist of a fleshy pericarp whose consumption often provides an incentive for animals to remove and disperse the enclosed seeds, whereas in the case of acorns, the embryo itself is the "reward" and dispersal is generally an incidental side-effect of predation (Barnett 1977). Nonetheless, if the rare, accidental dispersal afforded by acorn predators is of paramount importance, seed dispersal could exert a greater selective influence on production patterns than might be expected given the extensive predation that might accompany a small amount of dispersal.

A summary of the predictions of the four hypotheses is provided in Table 2.

STUDY AREA AND METHODS

Study area

The study was conducted at Hastings Reservation, a 900-ha reserve located in the Santa Lucia Mountains of central coastal California, ≈40 km inland. Elevation of the reserve ranges from 460 to 950 m. This area experiences a mediterranean climate in which virtually no rain falls during the summer and early fall (June–September). Annual rainfall ranges from 26 to 111 cm, with a 50-yr mean of 55 cm. *Quercus* is the dominant genus of tree in all areas of the study site. At lower elevations three species (*Quercus lobata, Q. douglasii,* and *Q. agrifolia*) are common, joined at higher elevations (mostly above 800 m) by *Q. chrysolepis* and *Q. kelloggii.* These five species include all three subgenera of oaks, both evergreen and deciduous species, and species that require one vs. two growing seasons to mature acorns (Table 1).

Acorn censuses

Beginning in 1980, we tagged and sampled 249 individual oaks including 87 *Q. lobata,* 57 *Q. douglasii,*

TABLE 2. Predictions of hypotheses potentially influencing masting patterns tested in this paper.

		Economies of scale			
	Resource matching	Predator satiation	Wind pollination	Attraction of seed dispersers	Observed relationship
Within years					
Variation in acorn production	Moderate	Low	Low	Moderate to high	Low
Bimodal distribution of reproductive effort?	No	No	No	Probably	No
Among years					
Variation in acorn production	Moderate	High	High	Moderate to low	High
Bimodal distribution of reproductive effort?	No	Yes	Yes	No	Yes (4 of 5 spp.)
Crop failures?	No	Yes	Yes	No	Yes
Masting in successive years?	Possibly	No	Yes	Yes	Yes, but no more than expected by chance
Regular masting cycles by individuals?	No	No	Possibly	Possibly	Yes
Regular masting cycles within populations?	No	No	Possibly	No	No

63 *Q. agrifolia,* 21 *Q. kelloggii,* and 21 *Q. chrysolepis.* Trees sampled are spread throughout the reserve but are all within 3.5 km of each other. By 1991, one individual each of *Q. lobata, Q. douglasii,* and *Q. kelloggii* had died, decreasing sample sizes slightly.

Each autumn between mid-September and early October, just prior to acorn fall, we measured the relative abundance of acorns on each tree using two methods. First, two observers scanned different areas of the tree's canopy and counted as many acorns as possible in 15 s. These counts were added to yield acorns per 30 s (hereafter "N30"). Second, the two observers agreed on a score between 0 and 4 describing the overall size of the acorn crop for each tree. These categories (hereafter "acorn score"), modified from the visual estimate scale proposed by Graves (1980), were as follows: 0 (no acorns), 1 (a few seen after close scrutiny), 2 (a fair number), 3 (a good crop), and 4 (a bumper crop; many acorns seen almost everywhere on the tree). At least one of the original observers participated in the counts each year since the study was initiated.

We chose to use visual surveys over the more commonly used methods of seed traps or quadrat counts for three reasons. First, because of the high variability of acorn production within and between years, we required the large sample sizes made possible by relatively rapid visual surveys. Second, visual surveys are not confounded by seed predation prior to acorn fall (Gysel 1956). Third, our survey methods allowed us to effectively sample a much higher proportion of the tree than would have been possible by seed trapping. Consequently, we believe that our methods offer not only a more efficient but a more accurate assessment of acorn production patterns than any feasible alternative.

Nonetheless, visual estimates suffer from several potential shortcomings, including variation due to differing amounts of foliage on trees and truncation due to limited counting speed at very high densities. As a preliminary calibration of our visual surveys, we compared N30 values with the number of apparently viable acorns captured in seed traps placed below eight large *Q. lobata* at Hastings Reservation in 1992. Traps consisted of four 0.25-m^2 buckets per tree placed approximately halfway between the trunk and the edge of the tree's canopy and were checked weekly throughout the period of acorn fall. Because 1992 was a very good acorn year at Hastings, it is likely that the proportion of acorns removed arboreally prior to acorn fall was small.

The Spearman rank correlation between the values obtained from the traps and the visual surveys was 0.976 ($P < .001$). After log transformation, 84.2% of the variance (r^2 from a linear regression) in the number of acorns trapped was explained by the number counted visually.

Statistical methods

For most of the statistical analyses we used the number of acorns counted in 30 s, transformed logarithmically (ln[N30 + 1]; these will be referred to below as A values) in order to reduce the correlation between the mean and variance (Sokal and Rolf 1969). Acorn scores were used when a categorical, rather than continuous, measure was preferable. We used nonparametric two-tailed tests except when a one-tailed test was specifically appropriate. A critical α of .05 was used in significance tests except for the autocorrelation analyses where multiple tests were performed for each species. In order to reduce the probability of Type I errors under these conditions, we adopted a critical α of .01 for these latter analyses.

Pattern of acorn production.—To visualize similarities in acorn production by the different species, we calculated the mean annual A values for each species. We then used the 12 mean annual values as characters and clustered the five species using the UGPMA algorithm, based on the correlation coefficients between them (Sokal and Sneath 1963).

Bimodality of reproductive effort within years.—We performed a cluster analysis within species using each of the 12 annual A values for the individual trees of that species as characters. Conspecifics were divided into three groups according to the similarities in their acorn production patterns as determined by the CLUSTER procedure of SPSSPC+ (Norušis 1986). Three groups were chosen so as to yield clusters with reasonably large samples, but the results were unchanged if species were divided instead into two or four clusters. We determined the mean crop size for individuals within each cluster for each year and then calculated the correlation coefficients between them (three per species, one for each pair of clusters).

The goal of this analysis was to determine whether there are definable sets of conspecifics sharing similar masting patterns possibly, but not necessarily, independent of the masting patterns of other conspecifics. One possible result would be that there exist two or more subgroups of trees within each species that exhibit completely different patterns of acorn production, or perhaps the same pattern but out of phase with each other. To the extent that either of these was true, at least some of the correlations between the mean acorn production values of different clusters would be zero or negative, indicating within-year bimodality of reproductive effort. Alternatively, subgroups might all covary synchronously and differ quantitatively rather than qualitatively; that is, each cluster might consist of trees that produce crops synchronously, but cluster 1 might consist of good producers while cluster 2 might consist of poor producers. This pattern would produce positive correlations between mean acorn production values of different clusters and indicate a unimodal pattern of within-year reproductive effort.

Bimodality of reproductive effort among years.—First we determined how many of the 12 A values for each individual fell in the lower, middle, and upper third of the range of A values observed for that particular tree. Trees in which the range of acorn production was 0 (that is, trees that failed to produce any acorns over the 12-yr period) were eliminated, leaving 240 trees.

The criterion for bimodality was that the number of years that A fell in the middle third of the range for that individual be less than both the number of years that A fell in the lower and upper thirds. This criterion was tested using one-tailed Wilcoxon matched-pairs signed-ranks tests.

Randomization tests

We used randomization tests (Manly 1991) to quantitatively compare observed data to distributions predicted by the relevant hypotheses (Table 2). All tests used the distributions of acorn productivity observed in our data rather than any predetermined distribution (e.g., uniform or normal).

1. *Variance in acorn production within years.*—Simulated "pseudo-years" were generated using the actual matrix of A values. The matrix consisted of 246 rows (for the individual trees) by 12 columns (for each year). For each of the trees, one of its 12 A values was selected at random in order to generate one pseudo-year. A total of 1000 simulated years was generated and the simulated within-year variance in A values was calculated for trees of each of the five species. These expected variances were compared to observed values. The mean variance of the simulated data was compared to the 12 individual annual values for each species using a two-tailed Wilcoxon signed-ranks test. Results are not biased by using variances, since the means of the randomizations are identical to those of the actual data.

2. *Bimodality of reproductive effort within years.*—We tested for bimodality within years by both the cluster analysis described earlier and with a randomization test. For the latter, we compared the frequencies of individuals with acorn scores of 0 (no acorns seen), 1 (a few acorns seen), and 2 or more (a fair crop or better) within years for each species. Acorn production was considered to be bimodal whenever both extreme categories were greater than the intermediate category, that is, when more individuals within a year failed to produce acorns and produced at least a fair crop than the number that produced only a few acorns.

We tested the observed proportion of years that acorn production within a species was bimodal against the expected bimodality as follows. Pseudo-years of data were generated as described in (1), above, using the acorn scores rather than A values. For each pseudo-year, we summed the number of trees for a given species whose score was 0, 1, and 2+. If the number of trees in each of the extreme categories was greater than the intermediate one, the trial was scored as having yielded a bimodal distribution. The expected proportion of bimodality was based on 1000 trials, and the observed and expected values compared with two-tailed binomial tests.

3. *Variance in acorn production among years.*—Trials were performed as described in (1), above. Mean acorn production within each species was then calculated for 12 randomly generated pseudo-years, and the among-year variance was computed for each of the five species. This process was repeated 1000 times, from which we calculated the expected null distribution of among-year variance for each species. This null distribution was compared to the single observed value for each species.

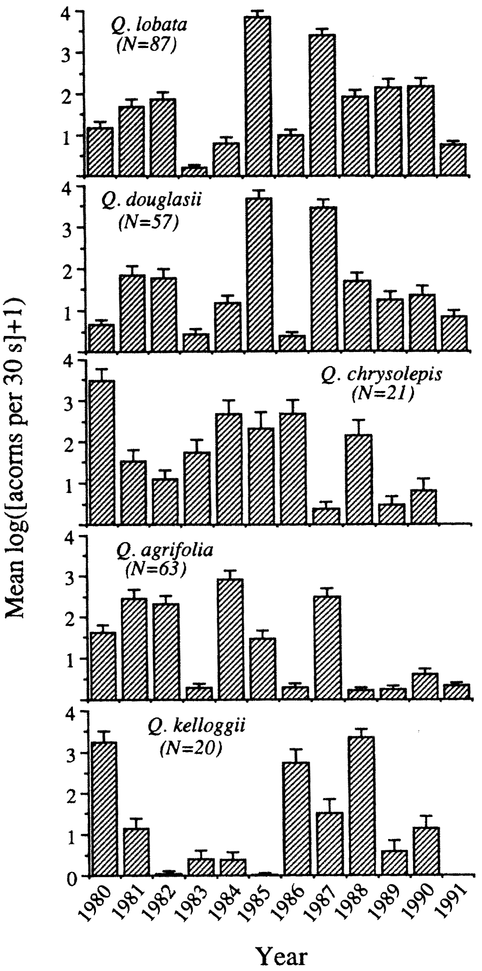

FIG. 1. Annual natural-log-transformed number of acorns counted in 30 s for five species of oaks between 1980 and 1991 at Hastings Reservation (mean ± 1 SE). Sample sizes as listed.

4. *Masting in successive years.*—For this test, we considered a score of 3 or 4 a mast year and only included trees that masted at least twice during the 12 yr of the study. This resulted in a sample size of 149 trees. For each species, the number of trees with a given number of mast years was determined; the maximum number of mast years for any tree was 10. We then designed the following null model to test whether a tree's *m* mast years were randomly distributed or tended to occur in successive years. For each *m*, we simulated 1000 trees with *m* mast years by randomly assigning mast years among the 12 yr of the study. From these 1000 trees, we counted the number of runs (consecutive mast years) of 1, 2, . . . , 10 yr. For example, among the 1000 simulated trees with four mast years there were 2164 runs of 1 yr, 645 runs of 2 yr, 158 runs of 3 yr, and 18 runs of four consecutive mast years. From these numbers, we estimated the number of runs of *m* years that would be expected if mast years were distributed at random in the actual trees and tested the observed against the expected values with a χ^2 one-sample test.

5. *Masting cycles.*—We looked for masting cycles both at the individual and population levels. At the individual level, we calculated autocorrelation coefficients (Pearson *r* values) of the acorn crops of individual trees with the acorn crop of the same tree in prior years. That is, for each year *y*, the log-transformed numbers of acorns counted per 30 s (A_y) were correlated with A_{y-1} for a 1-yr lag, A_{y-2} for a 2-yr lag, and so on up to A_{y-8} for an 8-yr lag. Sample sizes decline by one for each successive autocorrelation as the limits of the study are reached; thus, for a 1-yr lag the sample size is 11 (the study length minus one), while for an 8-yr lag the sample size is 4.

For each tree, we obtained expected autocorrelation coefficients by randomizing the actual set of *A* values for that tree and calculating autocorrelation coefficients from the new reorganized data set. We calculated the mean autocorrelation coefficients for 500 such trials for each tree and compared the observed with the expected values for all trees of a given species with two-tailed Wilcoxon matched-pairs signed-ranks tests.

At the population level, we averaged the crop size for all conspecifics within years and calculated autocorrelation coefficients for lag times up to 8 yr as above. We derived expected values using the same randomization procedure just described, calculating the mean of 500 trials. The observed value was considered significant if its absolute value was >95% of autocorrelation coefficients obtained from the randomization trials.

By comparing the two analyses just described we gain an essential piece of information. Individual trees may produce crops cyclically, but cycles may or may not be synchronous with those of others in the population. If individual trees produce acorns synchronously, crop cycles will be evident both at the individual and population levels. If individuals cycle, but are not synchronous with each other, then cycles will not be observed at the population level but may or may not be evident at the individual level, depending on whether they are of the same length in different trees.

RESULTS

Pattern of acorn production

Acorn production varied considerably among years and species (Fig. 1). With the exception of *Q. lobata* and *Q. douglasii*, closely related species whose among-year acorn production patterns are very similar, there was no significant correlation between species in mean annual acorn production (Table 3). Using the correlation coefficients from Table 3, species masting patterns clustered together according to the number of years required to mature acorns rather than by subgenus or deciduousness (Fig. 2).

TABLE 3. Spearman rank correlation coefficients of acorn production by five species of oaks over a period of 12 yr at Hastings Reservation using mean annual number of acorns counted per 30 s.

	Q. lobata	*Q. douglasii*	*Q. chrysolepis*	*Q. agrifolia*
Q. lobata				
Q. douglasii	0.79**			
Q. chrysolepis	−0.22	−0.32		
Q. agrifolia	0.06	0.39	0.02	
Q. kelloggii	0.16	−0.15	0.35	−0.24

** $P < .01$; other $P > .05$.

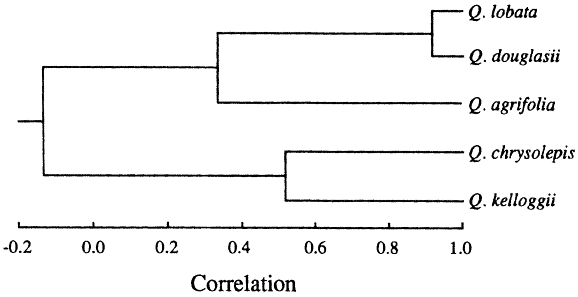

FIG. 2. Clustering of the five species of oaks in the study according to the correlations between their mean annual masting patterns as measured by the UPGMA algorithm.

Within-year patterns

Variation in acorn production.—Within-year variation in acorn production was often high; coefficients of variation of individual *A* values averaged between 102.1% for *Q. chrysolepis* and 178.5% for *Q. kelloggii* (Table 4). However, variances were all significantly smaller than expected from randomization test number 1. Comparing each year individually for each of the five species, 53 out of 60 observed variances (88%) were less than expected under the null model (Table 4).

Bimodality of reproductive effort.—Results from randomization test number 2 clearly demonstrated that bimodality of acorn production within years was less than expected: the observed incidence ranged from 8.3% (1 of 12 yr) for *Q. kelloggii* to 41.7% (5 of 12 yr) for *Q. lobata*; these values were all significantly ($P < .01$) less than the expected values, which ranged from 66.8 to 95.2%. We also examined the data for bimodality with a cluster analysis of the acorn production patterns of conspecifics (see *Methods*). The results, graphed in Fig. 3, were also unambiguous: all 15 Spearman rank correlations (r_s) between clusters were positive, ranging from 0.54 to 0.95, and 13 (87%) were significant at the .05 level or higher. Thus, among-year patterns of acorn production are quite similar within species; the primary differences between clusters are quantitative rather than qualitative. This supports the conclusion that within-year acorn production is not bimodal.

Among-year variation

Variation in mean acorn production.—Acorn production also varied considerably among years (Fig. 1). Coefficients of variation (CV) in mean annual acorn productivity as measured by *A* values ranged from 61.1% for *Q. lobata* to 101.6% for *Q. kelloggii*; variances ranged from 1.12 to 1.54. These latter values were all significantly greater ($P < .001$) than the expected variances based on randomization test number 3. Expected variances ranged from 0.025 (*Q. lobata*) to 0.106 (*Q. kelloggii*).

Bimodality of reproductive effort.—Results from the tests for among-year bimodality are shown in Table 5. Four of the five species showed significant bimodality. *Q. chrysolepis* was the exception, and it approached significance as well.

Crop failures.—In only one year did we fail to count any acorns among one or more of the five species (*Q. chrysolepis* and *Q. kelloggii* in 1991). Thus, total crop failures occurred in only 2 of 60 (3.3%) species by year combinations. However, years in which acorn production by a particular species was poor were common. Using a less restrictive definition of a crop failure as a year in which the mean N30 value was less than one per tree, failures occurred once (8.3% of years) for *Q. lobata,* three times (25% of years) for *Q. douglasii* and *Q. chrysolepis,* and six times (50% of years) for *Q. agrifolia* and *Q. kelloggii,* for a total of 19 of 60 (31.7%) species by year combinations.

Masting in successive years.—Individual trees sometimes produced large crops several years in a row. One *Q. lobata* individual, for example, produced a large crop (acorn score of 3 or 4) in 10 of the 12 yr, including five successive years between 1987 and 1991. How-

TABLE 4. Within-year variation in acorn production compared to expected values as derived by randomization.

Species	Observed mean CV (%)	Observed mean σ^2 (mean ± 1 SD)	Expected σ^2 (mean ± 1 SD)	*z* value†	No. years obs < exp (max = 12)
Q. lobata	111.7	2.06 ± 0.87	3.10 ± 0.27	2.9**	11
Q. douglasii	112.8	1.84 ± 0.81	2.86 ± 0.35	3.1**	12
Q. chrysolepis	102.1	1.72 ± 0.98	2.74 ± 0.52	2.7**	10
Q. agrifolia	155.4	1.59 ± 1.13	2.60 ± 0.35	2.0*	8
Q. kelloggii	178.5	1.02 ± 0.75	2.40 ± 0.58	3.1**	12

* $P < .05$; ** $P < .01$.

† Two-tailed Wilcoxon signed-ranks test of 12 observed values compared to expected mean value.

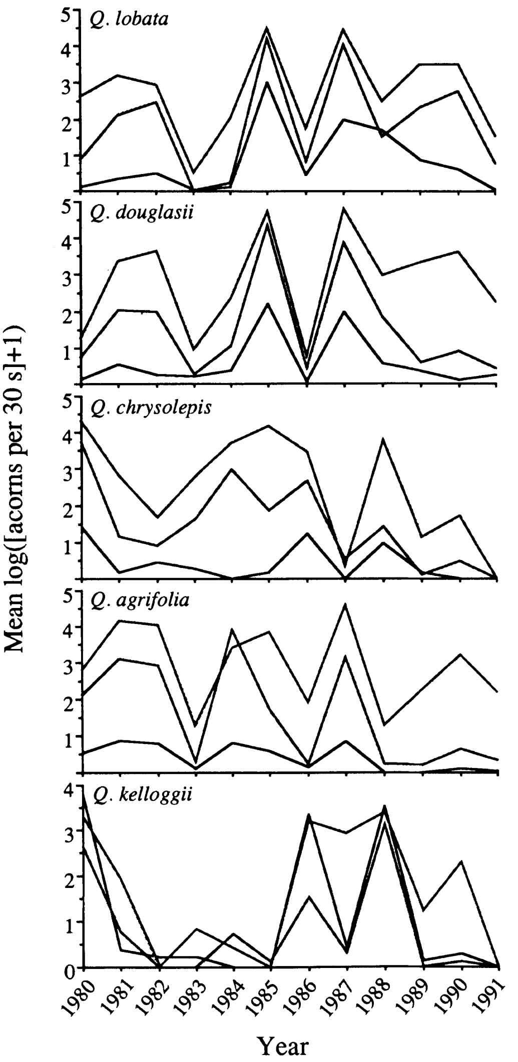

FIG. 3. The mean annual natural-log-transformed number of acorns counted per 30 s for each of three subgroups of individuals within each species, where subgroups were determined from a cluster analysis.

ever, results from randomization test number 4 demonstrate that in no case did the observed number of runs of mast years by individuals differ significantly from what would be expected under the null model (Table 6). Thus, despite a few extraordinary trees, individuals did not produce large crops in successive years more frequently than expected by chance.

Masting cycles among individuals.—Results of the autocorrelation analyses for individual trees are summarized in Fig. 4. Acorn production patterns of all five species exhibited significant autocorrelations, even to a lag time of 8 yr, indicating masting at species-specific intervals. All three of the species requiring 1 yr to mature acorns (*Q. lobata*, *Q. douglasii*, and *Q. agrifolia*) had strong cycles varying between 2 and 3 yr in length. In addition, both *Q. lobata* and *Q. douglasii* showed highly significant inverse autocorrelations with a 1-yr lag; that is, large seed production negatively affected production the following year. *Q. chrysolepis* trees tended to alternate regularly between good and bad years suggesting a 2-yr cycle, but only two of the autocorrelations were significant. In *Q. kelloggii* the pattern is not clear, but the tendency for several autocorrelations in the same direction to follow one another is suggestive of a very long cycle of at least 5 yr in length.

Population masting cycles.—At the population level, none of the 40 autocorrelation coefficients (year y with years $y-1, y-2, \ldots, y-8$ for each of the five species) was significantly different from that expected based on the randomization trials. Thus, we found no evidence of regular masting cycles at the population level.

DISCUSSION

As in other studies of acorn productivity, all five species studied here showed considerable variation in seed production both within (Table 4) and among (Fig. 1) years. Among-year patterns were more similar in species requiring the same number of years to mature acorns (Fig. 2) but were generally uncorrelated among species (Table 3) with the exception of *Q. lobata* and *Q. douglasii*, two closely related species in the same subgenus that are both deciduous and both require 1 yr to mature acorns. Thus, as found by Sork et al.

TABLE 5. Test for among-year bimodality of acorn production. Listed are the mean number of years ln(N30 + 1) values were in the lower, middle, and upper third of the range of acorn production for individual trees (mean ± 1 SD). $N = 12$ yr.

Species	No. years in Lower ⅓ of range	 Middle ⅓ of range	 Upper ⅓ of range	*P* value (comparison to middle third) Lower ⅓	 Upper ⅓
Q. lobata	6.24 ± 2.42	2.13 ± 1.43	3.63 ± 1.82	<.001	<.001
Q. douglasii	6.72 ± 2.69	2.15 ± 1.52	3.13 ± 1.93	<.001	<.01
Q. chrysolepis	5.76 ± 2.32	2.71 ± 1.42	3.52 ± 2.14	<.001	=.14
Q. agrifolia	7.23 ± 1.87	1.62 ± 1.28	3.15 ± 1.61	<.001	<.001
Q. kelloggii	7.23 ± 1.90	1.20 ± 1.15	3.20 ± 1.61	<.001	<.001

* Trees that did not produce any acorns excluded. Statistical comparisons are by one-tailed Wilcoxon matched-pairs signed-rank tests.

TABLE 6. Observed and expected number of runs of mast years by species. For each species, the largest category of runs includes all runs of that length and longer. Individuals with <2 mast years excluded. Expected values derived by randomization.

Species	Observed or expected	No. consecutive mast years 1	2	3	4	χ^2	df	P
Q. lobata	O	131	35	11	6	3.6	3	.31
	E	113.5	35.6	11.6	8.7			
Q. douglasii	O	55	20	7	3	1.4	3	.69
	E	53.8	17.0	6.2	5.0			
Q. chrysolepis	O	27	8	...	...	0.8	1	.37
	E	23.7	9.8	...	...			
Q. agrifolia	O	67	12	8	...	3.9	2	.14
	E	63.4	18.6	5.3	...			
Q. kelloggii	O	16	2	...	...	0.8	1	.36
	E	14.7	3.6	...	...			

(1993) for three species of oaks in Missouri, acorn production among species in the community was asynchronous. Within populations, however, among-year acorn production was relatively synchronous despite considerable differences in the quantity of acorns produced by different individuals (Fig. 3).

We investigated the patterns of acorn production using randomization models to test whether they were consistent with four hypotheses for the evolution of masting. Within-year variance in acorn production was significantly less than expected by chance (Table 4) and not bimodally distributed (Fig. 3), while among-year variance was significantly greater than expected and bimodal (Table 5). Near total crop failures were relatively common and masting occurred in successive years, but not more frequently than expected by chance (Table 6). We did not observe regular masting cycles at the population level but found significant cycles at the individual level for all species (Fig. 4). Masting cycles among individuals appeared to be 2–3 yr in length for four of the species and possibly of much longer length in one. Both *Q. lobata* and *Q. douglasii* showed significant inverse correlations between the acorn crop in 1 yr and that of the prior year, suggesting that individuals of these species require at least 1 yr to recover following a large investment in acorn production.

Masting cycles at the individual level have also been found in three species of Missouri oaks by Sork et al. (1993). Our combined results suggest that individuals of many, if not most, oaks may mast at species-specific intervals. Despite cyclic behavior at the individual level, however, we did not detect regular cycles at the population level (Fig. 1). Olson (1974) lists an "interval between seed crops" of various lengths for several oak species, but the information on which these values are based appears to be circumstantial. Regular masting cycles have yet to be demonstrated for any species in the genus *Quercus*.

A summary of the observed patterns of acorn production is presented in Table 2. The observed patterns

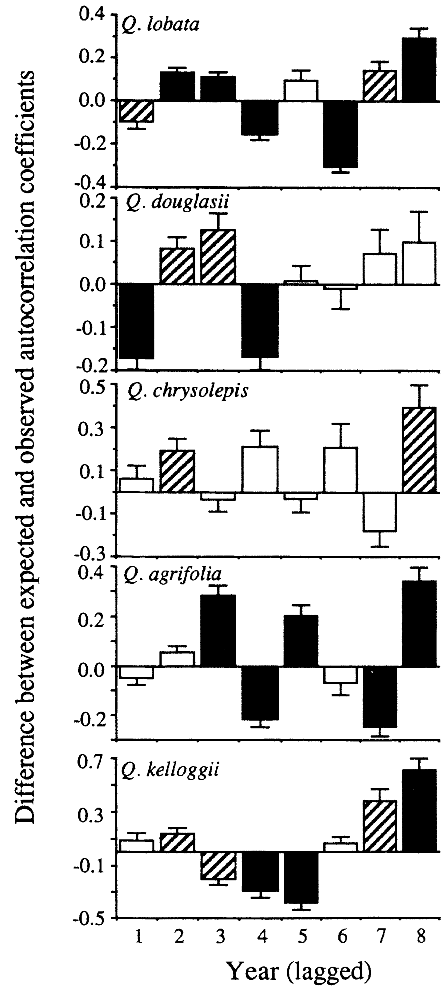

FIG. 4. The difference between the observed and expected autocorrelation coefficients between the natural-log-transformed number of acorns counted per 30 s lagged 1–8 yr (mean ± 1 SE). Values were tested using a Wilcoxon matched-pairs signed-ranks test. Significance levels are indicated by the bars as follows: black = $P < .001$; cross-hatched = $P < .01$; white = $P > .01$.

did not support most of the predictions of either the resource matching or the attraction of seed dispersers hypotheses. In contrast, most of the predictions of the predator satiation and all of the predictions of the wind pollination hypothesis were met. Only two differences between these hypotheses were expected among the predictions tested: the predator satiation hypothesis does not predict masting in successive years or regular masting cycles, whereas neither of these are excluded by the wind pollination hypothesis. With respect to the first of these predictions, successive runs of mast years by the same individual occurred, but not more frequently than expected by chance. This is slightly more consistent with the wind pollination hypothesis. As for the second prediction, regular masting cycles among individuals were found for all species, a result not in keeping with the predator satiation hypothesis, at least in its usual form.

The patterns of acorn production within and among years are thus most consistent with the hypotheses that mast-fruiting in oaks in central coastal California functions to increase pollination efficiency and/or to satiate predators. That predator satiation may provide an important selective factor favoring masting in these species is not surprising given the large numbers of seed predators, both vertebrate and invertebrate, dependent on acorns (Pavlik et al. 1991). However, the success of the wind pollination hypothesis is surprising given that oaks commit most of the energy to female growth only after pollination, thereby apparently eliminating the potential advantages of synchronous investment in male and female reproduction (Smith et al. 1990). Sork (*in press*) directly examined fertilization efficiency in three species of oaks in Missouri and found that the number of female flowers did not correlate with male catkin biomass and that percent fertilization was not greater in years of high pistillate or pollen production; neither of these findings supports the wind pollination hypothesis. Similar data from our population would clearly be desirable.

Results from other recent work provide no consensus as to the ultimate causes of masting in trees. Norton and Kelly (1988) found that wind pollination provided the best fit to a 33-yr data set on mast seeding by the rimu tree (*Dacrydium cupressinum*) in New Zealand. However, their study did not measure seed production by individuals, nor did they compare the population patterns of seed production against appropriate null models. Thus, it is difficult to compare their results with ours. More detailed work on three species of oaks in Missouri (Sork et al. 1993) found masting patterns to be strongly correlated with weather and cyclic at the individual level. Although the former result is consistent with the resource matching hypothesis, the latter is not, and these authors conclude that among-year variation is not solely due to resource matching. Additional results from their study, summarized by Sork (*in press*), generally support the importance of predator satiation rather than the wind pollination hypothesis. Based on these findings and additional indirect evidence, Sork (*in press*) proposed that predator satiation is likely to be the major factor selecting for mast-seeding in temperate oaks, but that both predator satiation and increased pollination efficiency may be important in tropical oak species.

Perhaps no single ecological factor will account for seed production patterns in all species or even in any one taxon, at least one as extensive and diverse as *Quercus*. Additional studies and tests, based on carefully quantified data and appropriate null models, will be necessary to sort out the relative importance of different factors to mast-fruiting patterns within this genus.

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