Patterns of Geographic Synchrony in Growth and Reproduction of Oaks within California and Beyond[1]

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Abstract: *We measured patterns of spatial synchrony in growth and reproduction by oaks using direct acorn surveys, published data on acorn production, and tree-ring chronologies. The two data sets involving acorn production both indicate that acorn crops are detectably synchronous over areas of at least 500 to 1,000 km not only within individual species but among species that require the same number of years to mature acorns. Although no tree-ring data are available for California oaks, growth patterns among oaks elsewhere are statistically correlated between sites up to 2,500 km apart. These results indicate that both tree growth and acorn production patterns covary over large geographic scales and support the hypothesis that large-scale weather patterns play an important role in determining these life-history parameters of California oaks. They also have important implications for the population biology of wildlife that live in California's oak woodlands.*

Oaks are a dominant hardwood genus in a variety of temperate and semi-tropical regions throughout the world. Here in California, considerable work has been devoted to understanding the environmental factors influencing growth and reproduction by individuals and within local populations. However, virtually nothing is known concerning the factors influencing these life-history parameters on larger geographic scales. For example, our long-term work on acorn production at Hastings Reservation in central coastal California has revealed that a significant amount of variation in annual acorn crop size of blue oaks (*Quercus douglasii*) is correlated with weather conditions during the spring flowering period, with large crops associated with warm, dry springs and small crops associated with cold, wet springs (Koenig and others 1996). Although such results may eventually allow us to predict acorn crop size in particular localities based on local conditions, they do little to address the question of how synchronous acorn crops of valley or blue oaks are on larger geographic scales. This paper addresses this issue by asking the question: How synchronous is acorn production and other life-history parameters of oaks throughout California and beyond?

Study Area and Methods

We used three sets of data to address the degree of spatial autocorrelation in growth and reproduction of oaks. These are detailed below.

Patterns of Acorn Production within California

Data on acorn production by California oaks is currently being obtained by annual surveys of populations in 14 localities throughout California (*fig. 1; table 1*). Surveys at Hastings Reservation of *Quercus lobata, Q. douglasii, Q. agrifolia, Q. kelloggii*, and *Q. chrysolepis* were initiated in 1980 (Koenig and others 1994b). Surveys at two other central coastal sites of *Q. lobata, Q. douglasii*, and *Q. agrifolia* were begun in 1989. All other sites include 1 to 3 of the above species (plus one site for *Q. engelmannii*) and were set up in 1994. Thus, results presented here are preliminary.

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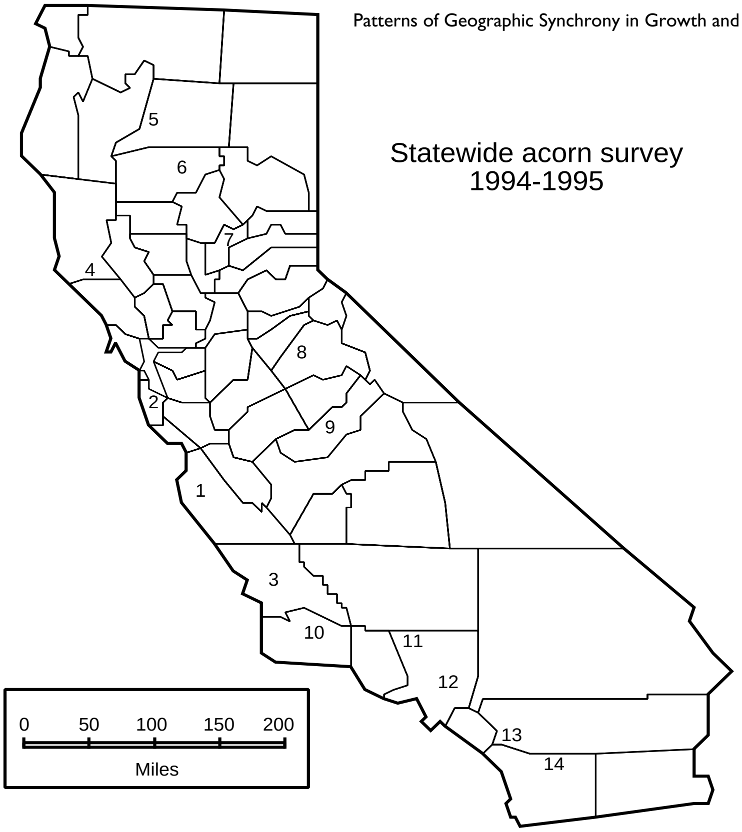

Figure 1—Sites used for the statewide acorn survey. Sites are numbered and listed in table 1.

Table 1—Sites and species of **Quercus** *surveyed during the 1994-1995 statewide acorn survey*[1]

Site	l	d	e	a	k	c
1. Hastings Reservation (Monterey Co.)	X	X		X	X	X
2. Jasper Ridge (San Mateo Co.)	X	X		X		
3. Pozo (San Luis Obispo Co.)	X	X		X		
4. Hopland Field Station (Mendocino Co.)		X			X	X
5. Tower House (Shasta Co.)	X				X	X
6. Dye Creek (Tehama Co.)	X	X				
7. Sierra Foothills Station (Yuba Co.)		X				
8. Yosemite Valley (Mariposa Co.)					X	X
9. San Joaquin Exp. Range (Madera Co.)		X				
10. Sedgwick Ranch (Santa Barbara Co.)	X	X		X		
11. Liebre Mtn. (Los Angeles Co.)		X			X	
12. Switzer's Camp (Los Angeles Co.)				X		X
13. Santa Rosa Plateau (Riverside Co.)			X	X		
14. Mt. Palomar (San Diego Co.)					X	X

[1] l = *Q. lobata*, d = *Q. douglasii*, e = *Q. engelmanii* , a = *Q. agrifolia*, k = *Q. kelloggii*, and c = *Q. chrysolepis*.

Sampling is done in September at the height of the acorn crop and includes at least 20 individuals of each species at each site. To reduce among-individual variation, the same individuals are surveyed each year (Koenig and others 1994a).

Relative abundance of acorns on each tree was assessed using a modification of the visual survey method proposed by Graves (1980) and detailed by Koenig and others (1994a). In brief, each of two observers scanned different areas of the tree canopy and counted as many acorns as possible in 15 seconds. These counts were summed to yield "acorns per 30 seconds," referred to as N30. N30 values were log-transformed (*ln*[N30+1]) and then averaged to yield a mean estimate of the acorn crop for each species. At least in California, this method is not only efficient but also yields data that are superior in quality to those obtained by alternative methods, including seed traps (Koenig and others 1994a). Samples of 20 to 25 individual trees per site are sufficient to yield good estimates of annual acorn production, especially if the same individuals are counted each year and sampling continues for at least 7 years (Koenig and others 1994a).

Among-years synchrony of the three central coastal California sites for which we have 7 years of data was tested with a Kendall coefficient of concordance test (Siegel 1956). With only 2 years of data for the remaining sites, we are currently able to see only whether acorn crops tended to be uniformly larger or smaller across sites from 1994 to 1995.

Large-Scale Geographic Patterns of Acorn Production

The data we are accumulating on acorn production within California are a first step toward answering the question: What is the pattern of synchrony in acorn production on a global scale? To answer this, we searched the literature for studies conducted anywhere in the world that provided multiple years of data on acorn production. Ninety-seven data sets from 33 separate studies were found yielding a total of 849 years of acorn production data between the years 1934 and 1993. Studies were divided according to whether the species of oak being examined required 1 (n = 47) or 12 (n = 49) years to mature acorns. The majority (n = 86, or 89 percent) of the studies were from the United States, but others were located for England, Sweden, Finland, and Japan.

For each study, we standardized the data in the following manner. If the data presented were categorical, we ranked the categories in order of increasing crop size, giving the highest category a "10," the lowest category a "0," and making the difference between all intermediate categories equal. Thus, if only three categories were used (i.e., good, fair, and poor), years when the crop was rated as "good" were given a 10; those in which the crop was "poor" were given a 0; and those in which it was rated as "fair" were given a 5. Categories were divided more finely, but still equally, if more than three categories were used.

If values presented were interval or ratio-level data, such as actual counts or number of acorns falling in traps, then values were log-transformed and standardized such that the best year received a 10, the worst year received a 0, and intermediate years received values between 0 and 10.

These data were analyzed as follows: Pearson correlation coefficients (r) were calculated for all pairwise combinations of sites for which data from at least 4 years were in common. For example, if data set A presented data between 1980 and 1989 while data set B went from 1984 to 1992, the correlation between the acorn production values of the two data sets for the 6 years 1984 through 1989 was calculated along with the distance between the two sites.

Correlation coefficients were divided into seven categories depending on whether the distance between the sites being compared was <10 km, 10-99 km, 100-499 km, 500-999 km, 1,000-2,499 km, 2,500-4,999 km, or $\geq$5,000 km. Within each category, we tested whether r values were significantly greater than 0 by performing trials in which sets of correlation coefficients were chosen at random from the entire pool such that individual sites were used only once. For example, if the correlation between sites A and B was chosen, all other pairwise combinations involving either site A or site B (i.e., not only the correlation between A and B but also that between sites A and C, A and D, B and C, etc.) were eliminated from the pool. This procedure was continued until no sites remained. Once a complete set of correlations was chosen, we calculated the mean r value and counted the number of positive and negative correlation coefficients present in the set.

A total of 100 trials was performed for each distance category. Means ($\pm$ SD) were calculated from the set of mean r values generated by the randomization trials. Statistical significance of individual analyses was based on the number of trials for which positive *r* values outnumbered negative *r* values. Analyses for which at least 95 (or 99) trials resulted in more positive than negative *r* values were considered significantly ($P < 0.05$) or highly significantly ($P < 0.01$) synchronous.

This procedure reduces pseudoreplication and provides a statistical test that measures whether among-years acorn production at sites a given distance apart tends to be synchronous, defined as having mean *r* values greater than zero. However, this definition of synchrony is much less strict than usually envisioned, because sites may be statistically synchronous according to the test even though mean *r* values are small.

Geographic Patterns of Tree Growth

The third data set we used was a series of tree-ring chronologies from the International Tree-Ring Data Bank, obtained through the internet from the National Geophysical Data Center. More than 1,200 tree-ring chronologies from throughout the world are in this data bank, of which 174 are for oaks. Most of these (103, or 59 percent) are North American, but unfortunately none is from California. Virtually all the data sets are on species that require 1 year to mature acorns; the few requiring more than 1 year were excluded from the analysis. A total of 44,338 years' worth of data were represented by these chronologies. All California data were from conifers, including various species of *Pinus, Abies, Pseudotsuga,* and *Juniperus*. Data from 66 sites summed to 50,867 years.

Raw data from each site had been standardized by the compilers by fitting a curve to each series of ring widths and then calculating the residuals, thereby allowing samples to be compared that had large differences in absolute growth rates or that varied systematically in growth rate during their life spans. Values used were the residuals from this procedure. Chronologies were tested for synchrony as described above for the acorn production data, except that sites had to share at least 10 years in common for a correlation coefficient to be calculated.

Results

Statewide Acorn Survey

Kendall rank correlations between the three central coastal California sites were significant for all three species (*lobata*: $\chi^2_6 = 13.0$, $P = 0.043$; *douglasii*: $\chi^2_6 = 12.7$, $P = 0.048$; *agrifolia*: $\chi^2_6 = 14.9$, $P = 0.021$). As an example, results for *Q. agrifolia* are graphed in *figure 2*.

Statewide, data comparing mean acorn crops in 1994 and 1995 are presented in *table 2*. For the four species that require 1 year to mature acorns (*Q. lobata, Q. douglasii, Q. engelmanii,* and *Q. agrifolia*), mean crops for all sites were worse in 1995 than in 1994 with the exception of the single *Q. engelmanii* site. These differences are significant for *Q. lobata, Q. douglasii, Q. agrifolia,* and for all comparisons of 1-year species combined. There was no consistent trend for the two species of oaks (*Q. kelloggii* and *Q. chrysolepis*) that require 2 years to mature acorns.

Literature Survey of Acorn Crop Synchrony

Results of the analysis of acorn crop synchrony based on the literature compilation are presented in *table 3*. Considering only species that require 1 year to mature acorns, crops are highly synchronous ($0.73 < r < 0.93$) between sites up to 500 km apart. Similar results were obtained for species that require 2 years to mature acorns, although mean correlation coefficients were lower ($0.28 < r < 0.59$). Unfortunately, the number of sites available for comparison were, in general, small. However, they at least support the findings of the statewide survey that acorn crops within species of oaks requiring the same number of years to mature acorns are reasonably synchronous at geographic scales on the order of at least 500 km.

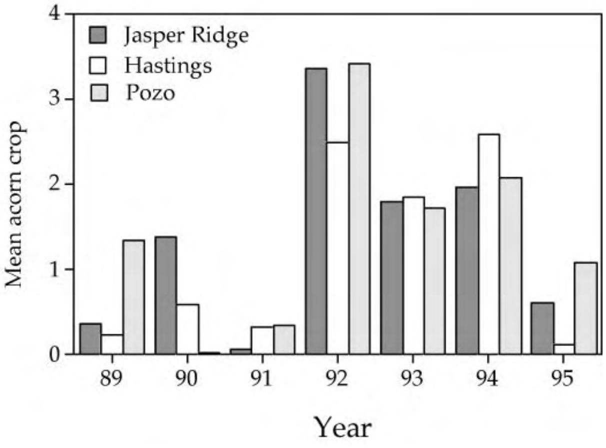

Figure 2—The mean annual acorn crop (log-transformed) of coast live oak Q. agrifolia as measured by visual surveys at Jasper Ridge (San Mateo County), Hastings Reservation (Montery County), and Pozo (San Luis Obispo County) in central coastal California between 1989 and 1995. Values are significantly concordant among years (Kendall coefficient of concordance, $\chi^2_6 = 14.8$, $P = 0.021$).

Table 2—Comparison of the 1994 and 1995 acorn crops based on surveys of 34 populations at 14 different sites throughout California[1]

Species	Number of sites for which		
	1995 better	1995 worse	*P* -value
1-year species			
Q. lobata	0	6	<0.05
Q. douglasii	0	9	<0.01
Q. engelmannii	1	0	—
Q. agrifolia	0	6	<0.05
2-year species			
Q. kelloggii	2	4	ns
Q. chrysolepis	2	4	ns
All 1-year species combined	1	21	<0.001
Both 2-year species combined	4	8	ns

[1] Listed are the numbers of sites for which a particular species or group of species produced a larger or smaller crop in 1995 compared to 1994. *P*-value from 2-tailed binomial tests; ns = $P > 0.05$.

Table 3—Mean correlation coefficients of annual acorn crops over seven geographic scales for species that require 1 and 2 years to mature acorns[1]

Statistics	Distance category (km/1000)						
	<0.01	0.01-.1	0.1-.5	0.5-1	1-2.5	2.5-5	>5.0
1-year species only							
Mean	0.82**	0.93**	0.73**	-0.13	-0.05	0.03	0.20
SD	0.02	0.04	0.07	0.09	0.10	0.13	0.13
N pairs	31	11	82	6	52	37	115
N independent pairs	15	3	11	2	6	5	11
2-year species only							
Mean	0.59**	0.46*	0.28*	0.10	0.02	0.01	—
SD	0.06	0.22	0.06	0.22	0.17	0.19	—
N pairs	54	23	155	19	38	29	—
N independent pairs	18	3	15	4	4	3	

[1] Total pairwise combinations available was 334 for 1-year species (mean number of years per correlation = 5.8) and 318 for 2-year species (mean number of years per correlation = 5.0). For details of analysis, see text. (** = $P < 0.01$; * = $P < 0.05$; other $P > 0.05$)

Tree-Ring Analyses

Results from analyses involving the 1-year species of oaks worldwide and the California conifers are presented in *table 4*. Among 1-year species of oaks, there is statistically significant synchrony in tree-ring growth between sites up to 2,500 km apart. Among California conifers, synchrony as defined here is evident among sites up to 1,000 km apart.

Table 4—Mean correlation coefficients of tree-ring growth over seven geographic scales for oaks worldwide (1-year species only) and for Califoria conifers[1]

	Distance category (km/1000)						
	<0.01	0.01-.1	0.1-.5	0.5-1	1-2.5	2.5-5	>5.0
Oaks worldwide							
Mean	0.54**	0.38**	0.28**	0.14**	0.07**	0.00	0.01
SD	0.01	0.01	0.02	0.01	0.01	0.05	0.01
N pairs	18	132	1665	2120	2204	30	4869
N independent pairs	16	53	76	68	54	4	51
California conifers							
Mean	0.55**	0.33**	0.25**	0.11**	—	—	—
SD	0.01	0.03	0.02	0.01	—	—	—
N pairs	4	49	662	504	—	—	—
N independent pairs	2	8	24	21	—	—	—

[1] Total pairwise combinations 11,038 for oaks (mean number of years per correlation = 205) and 1,219 for California conifers (mean number of years per correlation = 250). For details of analysis, see text. (** = $P < 0.01$; * = $P < 0.05$; other $P > 0.05$)

Discussion

Results presented here suggest that spatial autocorrelation of both reproduction and growth of oaks within California may be significant over most, if not all, of the state. Data supporting this hypothesis come directly from our statewide acorn survey and indirectly from analysis of published acorn crop data and tree-ring chronologies from oak species worldwide and California conifer species.

Our data are currently limited but suggest that synchrony in acorn production is significant within a range of at least 300 km in the California coast between Jasper Ridge in San Mateo County and Pozo in San Luis Obispo County. Although our statewide survey has been conducted for only 2 years, these data suggest that synchrony may be present on a much larger geographic scale, possibly encompassing most, if not all, of the state for blue oaks and for 1-year species of oaks combined *(table 2)*. No clear pattern emerged for either *Q. kelloggii* or *Q. chrysolepis*, the species surveyed that require 2 years for to mature acorns. Analysis of annual acorn crop data from published sources indicates that acorn crops vary synchronously over relatively large areas on the order of at least 500 km *(table 3)*.

Stronger conclusions can be drawn from the more extensive tree-ring data. Using all 1-year species, statistically significant synchrony between annual growth rates of oaks is detectable between sites up to 2,500 km apart *(table 4)*. Within California, no long-term tree-ring data are available for oaks. However, using tree-ring chronologies from four genera of California conifers, spatial autocorrelations are significant for sites up to 1,000 km apart *(table 4)*.

Thus, all three data sets indicate that the reproduction and growth of oaks are statistically correlated, in the sense that $r > 0$, over distances of at least 500-1,000 km, and possibly up to 2,500 km, when considering only species that require the same number of years to mature acorns. Although we are aware of no attempt to address the question of geographic synchrony in life-history strategies of oaks on this scale, prior work using "signature years" by Kelly and others (1989) found evidence of synchrony among tree-ring growth patterns of a series of oaks located over a distance of approximately 1,000 km throughout the United Kingdom and western Europe.

These findings have several important implications. First, because tree-ring chronologies are considered good proxy measures of climatic variables such as rainfall or temperature (e.g., Fritts 1976, Hughes and others 1982, Mann and others 1995), the patterns of spatial autocorrelation among these variables are probably similar to those found here for tree-ring growth patterns. Some evidence supporting this are presented by the analyses of rainfall patterns in different regions of California by Goodridge (1991). More surprising is the finding that geographic synchrony of acorn production is apparently almost as extensive as that for tree-ring growth. This result is consistent with the hypothesis that weather patterns play an important role in determining acorn crops on a large geographic scale.

Second, both growth and reproduction appear to be more or less geographically synchronized (although not necessarily with each other) within California when considering species that require the same number of years to mature acorns. Consequently, the probability of experiencing a near or total acorn crop failure may be more closely correlated to the presence of both 1- and 2-year species within a site than the diversity or number of oak species present per se.

Third, sites experiencing a near or total crop failure are likely to be geographically widespread. This has potentially important implications to wildlife and even to the understanding of the economy of California's Native Americans prior to European influence. For Native Americans, extensive travel was likely to have been required in order to find good acorn-producing stands during bad years. Poor crops would also have affected wildlife populations relatively synchronously over large geographic areas, except insofar as 2-year and 1-year species of oaks were simultaneously available and asynchronous.

Numerous questions and potential analyses remain. Of particular interest is the potential for using spatial synchrony of tree-ring growth to detect long-term changes in global climate patterns. Currently the data available to perform such analyses are primarily derived from boreal forests (Koenig and Knops 1996). Comparable data from California oaks could yield considerable insights into the factors correlating with the poor regeneration and human-induced changes of California's vast oak woodlands.

Acknowledgments

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