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SYNCHRONY AND ASYNCHRONY OF ACORN PRODUCTION AT TWO COASTAL CALIFORNIA SITES

WALTER D. KOENIG
Hastings Reservation, University of California, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924

DALE R. MCCULLOUGH
Department of ESPM, University of California, Berkeley, CA 94720

CHARLES E. VAUGHN
Hopland Research and Extension Center, University of California, 4070 University Road, Hopland, CA 95449

JOHANNES M. H. KNOPS
School of Biological Sciences, University of Nebraska, 348 Manter Hall, Lincoln, NE 68588-0118

WILLIAM J. CARMEN
145 Eldridge, Mill Valley, CA 94941

ABSTRACT

We measured annual acorn production of oaks *Quercus* spp. at Hastings Reservation and at Hopland Research and Extension Center, located 320 km apart in the outer coast ranges of California, for 16 years between 1982 and 1997. Of the three species measured at both sites, acorn production by *Quercus lobata* Nee (valley oak) and *Quercus douglasii* Hook. & Arn. (blue oak) was significantly correlated between sites, whereas acorn production by *Quercus kelloggii* Newb. (California black oak) was not. Both *Q. lobata* and *Q. douglasii* acorn production was significantly correlated with mean April temperatures and rainfall at their respective localities, but more closely with April temperatures at Hastings and with rainfall at Hopland. Synchrony in acorn production between *Quercus* spp. requiring one year to mature acorns was significantly greater than among those requiring two years to mature acorns. The geographic extent of the populations producing acorn crops synchronously differs between species, but in some cases may extend over distances of at least several hundred kilometers.

Mast-fruiting, or masting, is a population phenomenon (Kelly 1994). That is, a single tree may produce highly variable numbers of seeds from year to year, but it is only when a population of trees produce seeds synchronously from one year to the next that masting can be considered to occur. Recent studies in New Zealand (Norton and Kelly 1988), the midwestern United States (Sork et al. 1993) and California (Koenig et al. 1994a, 1996) have begun to elucidate the patterns and causes of masting behavior in forest trees. However, work has only recently begun to address the question: what is the geographic extent of the 'population' producing seeds synchronously?

Here we analyze data relevant to this question using data on three species of *Quercus*. Specifically, we independently collected data on acorn production by *Q. lobata* (valley oak), *Q. douglasii* (blue oak), and *Q. kelloggii* (California black oak) oaks at two sites in coastal California 320 km apart: Hopland Research and Extension Center in Mendocino County (38°58.5′N, 123°07′W; hereafter "Hopland") and Hastings Natural History Reservation in Monterey County (36°23′N, 121°33′W; hereafter "Hastings"), over a 16 year period from 1982 to 1997 (Fig. 1). We ask: 1) does the population of masting oaks extend over this distance in California? and 2) is acorn production correlated with similar environmental factors at the two sites?

METHODS

At Hopland, acorn production by each species was censused using 10 traps consisting of plastic garbage bags 0.46 m in diameter, each placed at a random location under a tree of the appropriate species. Traps were checked in December at the end of the season and the total number of sound acorns trapped log-transformed ($ln[N+1]$). Species censused included *Q. lobata, Q. douglasii, Q. kelloggii,* and interior live oak *Q. wislizenii* A. DC. (interior live oak).

At Hastings, acorn censuses were done visually between mid-September and early October just prior to acorn fall (Koenig et al. 1994b). For each tree two observers scanned different areas of the tree's canopy and counted as many acorns as possible in 15 sec. Counts were added to yield the number of acorns counted in 30 sec (N30). Values for each

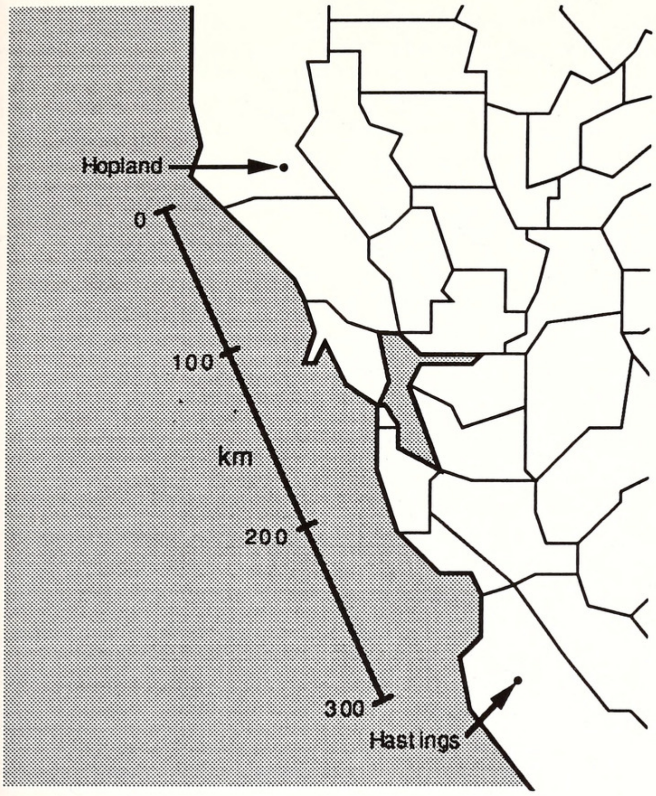

FIG. 1. A map of central coastal California showing the locations of Hopland Research and Extension Center and Hastings Natural History Reservation relative to the San Francisco Bay area (center). Lines are county boundaries; Hopland is in Mendocino County while Hastings is in Monterey County.

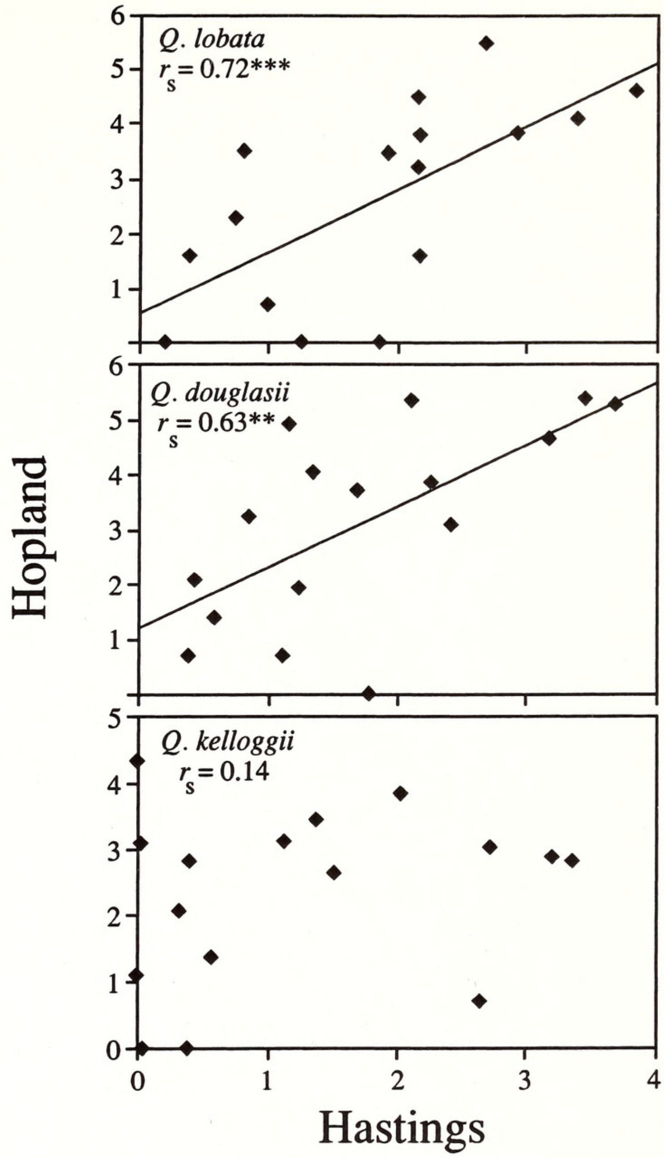

FIG. 2. Correlations between the log-transformed mean acorn crops of *Q. lobata, Q. douglasii* and *Q. kelloggii* at Hopland and Hastings between 1982 and 1997 (N = 16 years). Spearman rank correlations and their significance values (** = $P < 0.01$; *** = $P < 0.001$) are listed.

tree were log-transformed ($ln[N30+1]$) and averaged to yield the mean log-transformed number of acorns counted per tree of each species. The relative merits of visual surveys versus traps for censusing acorns in California oak woodland habitat are discussed in Koenig et al. (1994b), who also provide data demonstrating that values derived from visual counts are significantly correlated with numbers of acorns obtained by trapping for *Q. lobata* at Hastings.

Species included and the number of trees censused per species were *Q. lobata* (87), *Q. douglasii* (57), *Q. kelloggii* (21), *Q. agrifolia* Nee (coast live oak; 63), and (*Q. chrysolepis* Liebm. canyon live oak; 21). Thus, three species (*Q. lobata, Q. douglasii,* and *Q. kelloggii*) were surveyed at both localities. These species differ in that both *Q. lobata* and *Q. douglasii* are "1-year species" requiring a single year to mature acorns, whereas *Q. kelloggii* is a "2-year species" requiring two years to mature acorns. Of the three live oak species censused at one or the other site, *Q. agrifolia* (at Hastings) is a one-year species while *Q. wislizenii* (at Hopland) and *Q. chrysolepis* (at Hastings) are two-year species.

Weather data came from stations located near headquarters at both sites. Variables analyzed included seasonal rainfall (1 Sept. of year *x*-1 to 31 August of year *x*) and mean April temperature (mean of the daily averages of the maxima and minima). Statistical analyses were made using nonparametric Spearman rank correlations and Mann-Whitney *U* tests. P-values are two-tailed; values listed are means ± SD.

RESULTS

Annual acorn production at the two sites was highly correlated for *Q. lobata* and *Q. douglasii,* but not for *Q. kelloggii* (Fig. 2). Prior studies of *Q. lobata* and *Q. douglasii* at Hastings have demonstrated significant correlations between acorn production by these two species and mean April temperatures during the peak of flowering and pollination (Koenig et al. 1996), whereas no environmental variable has as yet been identified to correlate with acorn production by *Q. kelloggii.* Correlations between acorn production of these

TABLE 1. SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN ACORN PRODUCTION AT HASTINGS AND HOPLAND AND ENVIRONMENTAL VARIABLES MEASURED AT THE SAME SITES BETWEEN 1982 AND 1997 (N = 16 YEARS). * = P ≤ 0.05; ** = P < 0.01; *** = P < 0.001.

	Mean April temp.	Mean April temp. (year $x - 1$)	Seasonal rainfall	Seasonal rainfall (year $x - 1$)
Hastings				
Q. lobata	0.82***	−0.10	−0.65**	0.04
Q. douglasii	0.73***	−0.25	−0.48	0.26
Q. kelloggii	0.04	0.59*	−0.09	0.01
Hopland				
Q. lobata	0.63**	−0.32	−0.77***	0.35
Q. douglasii	0.50*	−0.35	−0.72**	0.57*
Q. kelloggii	0.12	0.42	−0.19	−0.28

three species at both Hastings and Hopland over the 16 years analyzed here and both mean April temperature and seasonal rainfall are summarized in Table 1.

Correlations between the environmental variables at the two sites over the 1982–1997 period were high (rainfall: $r_s = 0.79$, $n = 16$, $P < 0.001$; mean April temperature: $r_s = 0.94$, $n = 16$, $P < 0.001$). However, the relationships between these environmental factors and acorn production were not identical at the sites. Acorn production by *Q. lobata* and *Q. douglasii* were positively correlated with mean April temperature at both sites; however, the correlations were much higher at Hastings than at Hopland. Interestingly, the reverse pattern holds for the relationship between acorn production by these two species and seasonal rainfall: all correlations were negative, but they were considerably stronger at Hopland than at Hastings. Multiple regression analyses with these two variables yielded identical results. Acorn production by *Q. douglasii* at Hopland was also significantly positively correlated with seasonal rainfall lagged one year while *Q. kelloggii* at Hastings was positively correlated with mean April temperature lagged one year; both these correlations were low and not statistically significant at the other site.

We also compared interspecific correlations between one-year (Table 2) and between two-year (Table 3) species of oaks, both within and between sites. For the one-year species, 9 of 10 interspecific correlations were significant, including all six of the cross-site comparisons. Overall, the mean interspecific correlation coefficient was 0.64 ± 0.16 and did not differ significantly between cross-site (mean = 0.62 ± 0.10) and within-site comparisons (mean = 0.68 ± 0.24; Mann-Whitney *U*-test, $z = 0.6$, $P = 0.52$). For the two-year species, none of the six pairwise correlation coefficients was significantly different from zero and the mean interspecific correlation coefficient was 0.11 ± 0.21, significantly less than the interspecific correlations between one-year species (Mann-Whitney *U*-test, $z = 3.2$, $P < 0.002$). Among the two-year species, only the correlation between *Q. kelloggii* and *Q. chrysolepis* at Hastings came close to being significant (P = 0.06).

DISCUSSION

These results demonstrate that for *Q. lobata* and *Q. douglasii* annual acorn crops are highly synchronous between two sites in coastal California 320 km apart. Furthermore, acorn crops of these species at the two sites are both correlated with mean April temperatures. This is consistent with the hypothesis that masting occurs over large geographic areas in these two species, and furthermore suggests that the proximate cues used by trees to synchronize reproductive effort are also similar over large distances (Koenig et al. 1996). However, patterns were not identical at the sites. At Hastings, both species were positively and strongly correlated with mean April temperature and negatively, but less strongly, correlated with seasonal rainfall, whereas at Hopland the pattern was reversed. This suggests that the precise mix of environmental fac-

TABLE 2. SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN ACORN PRODUCTION OF ONE-YEAR *QUERCUS* SPECIES, BOTH WITHIN AND BETWEEN HASTINGS AND HOPLAND, BETWEEN 1982 AND 1997 (N = 16 YEARS). * = P ≤ 0.05; ** = P < 0.01; *** = P < 0.001.

	Q. agrifolia (Hastings)	*Q. lobata* (Hastings)	*Q. douglasii* (Hastings)	*Q. lobata* (Hopland)
Q. lobata (Hastings)	0.38	—	—	—
Q. douglasii (Hastings)	0.59*	0.85***	—	—
Q. lobata (Hopland)	0.53*	0.72***	0.75***	—
Q. douglasii (Hopland)	0.53*	0.57*	0.63**	0.89***

TABLE 3. SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN ACORN PRODUCTION OF TWO-YEAR *QUERCUS* SPECIES, BOTH WITHIN AND BETWEEN HASTINGS AND HOPLAND, BETWEEN 1982 AND 1997 (N = 16 YEARS). ALL P > 0.05.

	Q. kelloggii (Hastings)	*Q. chrysolepis* (Hastings)	*Q. wislizenii* (Hopland)
Q. chrysolepis (Hastings)	0.48	—	—
Q. wislizenii (Hopland)	0.05	0.16	—
Q. kelloggii (Hopland)	0.14	−0.05	−0.10

tors influencing acorn production may differ at different localities, potentially explaining the lower correlation between acorn production at the sites (r_s = 0.82 for *Q. lobata* and 0.73 for *Q. douglasii*) compared to that for the critical environmental factor (r_s = 0.94 for mean April temperatures).

In contrast, we found no evidence of synchrony between acorn production by *Q. kelloggii* surveyed at the two sites. Because *Q. kelloggii* requires two years to mature acorns, it is possible that the environmental factors synchronizing reproduction are more complicated, and thus less likely to be geographically synchronous, than those used by the one-year species. Consistent with this hypothesis, analyses at Hastings Reservation using the 16 years of data between 1980 and 1995 found no relationship between any plausible environmental variable and acorn production in *Q. kelloggii* (Koenig et al. 1996). However, with the 1982 to 1997 data used here, there is a statistically significant correlation between mean April temperature lagged one year and acorn production by *Q. kelloggii* at Hastings. This correlation is not significant in the Hopland data over the same time period. More data will be needed before we will be able to understand what environmental factors influence acorn production in this species.

We also performed pairwise interspecific comparisons of the acorn crops of the one-year and the two-year species both within and between sites. All interspecific comparisons between one-year species were positive and 9 of 10 were statistically significant (Table 2). Mean correlations were high and there was no difference between the within-site compared to the between-site cross-correlations. In contrast, only 4 of 6 comparisons between two-year species were positive and none was statistically significant (Table 3). These results support the hypothesis that acorn production of two-year *Quercus* species is geographically less synchronous than that of one-year *Quercus* species.

Analyses of acorn production from data reported in the literature similarly indicate that the geographic extent of synchrony in acorn production by two-year *Quercus* species is less than that of one-year species (Koenig and Knops 1997). At the proximate level, this could be because the two-year species are sensitive to more complicated environmental factors or because they are sensitive to different sets of environmental factors in different sites, as suggested by our results for *Q. lobata* and *Q. douglasii.* At a more ultimate level, it could be because the ecological factors selecting for mast-fruiting in two-year species differ from those important to one-year species, due for example to differences in the habitats they inhabit. Hypotheses suggested to favor masting include predator satiation (Silvertown 1980), wind pollination (Smith et al. 1990), and several other lesser ways by which efficiency may be increased by devoting more resources to reproduction in some years than others (Norton and Kelly 1988; Kelly 1994).

These results add to the small but growing amount of data available concerning the geographic scale of, and the proximate factors involved in, synchronizing acorn production by *Quercus* spp. Combined with prior analyses demonstrating significant synchrony between acorn production of *Q. lobata* and *Q. douglasii* at Hastings and at Jasper Ridge in San Mateo County 130 km away, and between acorn production of *Q. agrifolia* not only at Jasper Ridge and at Hastings but also at Pozo, 290 km south of Jasper Ridge (Koenig et al. 1996), these data extend synchrony in acorn production by *Quercus* spp. to a distance of over 300 km. The proximate cue used to synchronize acorn production by *Q. lobata* and *Q. douglasii* throughout this range appears to be either spring temperature or seasonal rainfall, which are themselves correlated over large distances. Whether these patterns extend throughout the state is currently under investigation.

In contrast, we found no statistical synchrony in acorn production by *Q. kelloggii* between Hopland and Hastings. This negative finding is consistent with prior analyses indicating that the environmental factors affecting synchrony in acorn production in oaks requiring two years to mature acorns are more difficult to discern than those used by one-year species of *Quercus*.

Also supporting the contention that synchrony is lower in oaks requiring two years to mature acorns are the results of interspecific correlations, both within and between sites, between one-year and between two-year *Quercus* species. Correlations between annual acorn production of one-year species were all positive and, with a single exception, statistically significant. In contrast, correlations between annual acorn production of two-year species were not consistently positive or negative and none was significantly different from zero. Geographic synchrony in acorn production appears to be greater both within and between one-year species than within or between two-year species of *Quercus*.

These results suggest a complex pattern of spatial autocorrelation in acorn production by *Quercus* spp. Within and even between one-year species, the extent of geographic synchrony in acorn production appears to be large, possibly encompassing the entire state. However, for two-year *Quercus* species, geographic synchrony appears neither to be as extensive nor to cross species boundaries.

What this means for a particular locality depends largely on the geographic scale being considered. On a local scale of a few square kilometers, many California sites contain only one-year *Quercus* species and thus may be subject to relatively frequent community-wide acorn crop failures due to the synchrony in acorn production across one-year *Quercus* species. Such synchrony is likely to extend over large geographic areas thousands or even tens of thousands of square kilometers in size. However, once the geographic scale over which one is concerned starts to encompass such larger areas, the topographic heterogeneity and complexity of the California landscape will generally ensure that sites containing both one-year and two-year *Quercus* species will be present somewhere within the area. Thus, despite large-scale geographic synchrony in at least several of the most widespread species of California oaks, the diversity of habitats occurring over moderately large geographic areas makes it unlikely that the acorn crop of all species will fail in any particular year (Koenig and Haydock 1999).

Masting by oaks has been shown to have cascading effects on communities in the eastern United States via its affect on mouse populations (Jones et al. 1998). Consequently, large-scale geographic synchrony in acorn production such as is suggested here could plausibly have major effects on communities over similarly large geographic areas, especially to the extent that the species involved are specialized on the acorns of one-year *Quercus*. No vertebrate acorn predator of which we are aware is specialized in this way. However, at least some of the many invertebrate species that depend on acorns are restricted to the acorns of particular *Quercus* subgenera, and sometimes usually a single *Quercus* species (Russo 1979; Cornell 1985). The effects of geographic synchrony in acorn production on populations of such taxa remain to be documented.

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