

Acorn production by oaks in central coastal California: influence of weather at three levels

Walter D. Koenig, Johannes M.H. Knops, William J. Carmen,
Mark T. Stanback, and Ronald L. Mumme

Abstract: Mean annual acorn crop size of oaks in central coastal California correlated with weather for four of five species. For the deciduous *Quercus lobata* and *Quercus douglasii*, larger crops were produced in years when April temperatures were warmest, while for the evergreen *Quercus agrifolia* and *Quercus chrysolepis*, crops were larger when there was more rain one and two years prior to the year when acorns were produced. No correlations were found between weather and mean annual acorn production by *Quercus kelloggii*. Within years, individual *Q. douglasii* that flowered during periods of greater solar radiation produced more acorns, and during 1 of 5 years individual *Q. lobata* and *Q. agrifolia* produced larger crops when they flowered during warm, dry periods. These results indicate that conditions favorable for pollination and fertilization strongly enhance mean annual acorn production in *Q. lobata* and *Q. douglasii* and may have an effect on differences in acorn crop size among individual *Q. lobata*, *Q. douglasii*, and *Q. agrifolia*. Mean annual acorn crops of these three species were significantly concordant among three sites in central coastal California 300 km apart. Weather conditions were also significantly correlated, especially annual rainfall and mean April temperatures. Thus, the environmental factors that have the strongest influence on mean annual acorn production within a site are also those that are the most geographically concordant. However, we found no relationship between environmental factors and differences in mean annual acorn production by these same three species at the three sites.

Résumé : Le volume moyen annuel de la récolte des glands de chênes dans la région côtière centrale de la Californie a présenté une corrélation avec le climat pour quatre des cinq espèces étudiées. En ce qui concerne les chênes décidus *Quercus lobata* et *Quercus douglasii*, les récoltes les plus importantes ont eu lieu au cours des années où les températures d'avril étaient les plus chaudes, alors que pour les *Quercus agrifolia* et *Quercus chrysolepis* sempervirents, les récoltes étaient plus considérables lorsque les précipitations étaient plus abondantes au cours de l'année ou des deux années précédant celle où les glands ont été produits. Aucune corrélation n'a été trouvée entre le climat et la production moyenne annuelle de glands de *Q. kelloggii*. Au cours des années, des individus de *Q. douglasii* qui ont fleuri pendant des périodes de plus grande radiation solaire ont produit plus de glands, et durant l'une des 5 années, des individus de *Q. lobata* et *Q. agrifolia* ont produit des récoltes plus abondantes quand ils fleurissaient lors des périodes chaudes et sèches. Ces résultats indiquent que des conditions favorables à la pollinisation et à la fécondation augmentent fortement la production moyenne annuelle de glands chez *Q. lobata* et *Q. douglasii*, et peuvent avoir un effet sur les différences dans le volume de la récolte de glands entre *Q. lobata*, *Q. douglasii* et *Q. agrifolia*. Les récoltes moyennes annuelles des glands de ces trois espèces ont été significativement concordantes entre trois sites de la région côtière centrale de la Californie distants, entre eux, de 300 km. Les conditions climatiques, particulièrement la précipitation annuelle et les températures moyennes d'avril, ont aussi été corrélées de façon significative. Ainsi, les facteurs environnementaux ayant la plus forte influence sur la production annuelle de glands à l'intérieur d'un site sont aussi les plus concordants au point de vue géographique. Cependant, aucune relation n'a été trouvée entre les facteurs environnementaux et les différences dans la production annuelle de glands de ces trois mêmes espèces dans les trois sites.

[Traduit par la Rédaction]

Received June 29, 1995. Accepted February 16, 1996.

W.D. Koenig.¹ Hastings Reservation, University of California, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924, U.S.A.

J.M.H. Knops. Cedar Creek Natural History Area, University of Minnesota, 2660 Fawn Lake Drive NE, Bethel, MN 55005, U.S.A.

W.J. Carmen. Wetlands Research Associates, San Rafael, CA 94901, U.S.A.

M.T. Stanback. Department of Biology, Davidson College, Davidson, NC 28036, U.S.A.

R.L. Mumme. Department of Biology, Allegheny College, Meadville, PA 16335, U.S.A.

¹ Author to whom all correspondence should be addressed.

Introduction

Synchronous seed production at irregular intervals, or mast fruiting, is a widespread and conspicuous phenomenon among perennial plants (Silvertown 1980). Among the questions raised by this phenomenon is, What factors synchronize reproductive patterns among individuals? Synchrony with some environmental cue is predicted by virtually all hypotheses for the functional significance of mast fruiting (Norton and Kelly 1988) and thus yields little insight into the factors ultimately leading to mast fruiting. However, the particular weather variables correlating with seed production are likely to indicate phenological stages critical to crop size. For example, seed crops correlating with summer temperature or rainfall would suggest that conditions during acorn development are important to crop size, while temperature or humidity in early spring would indicate that conditions associated with pollination or fertilization are important.

Previously, we examined five species of oaks at Hastings Reservation in central coastal California and demonstrated that acorn production is relatively variable among years and synchronous within years (Koenig et al. 1994a), exhibiting what Kelly (1994) defines as "normal masting." Here we analyze these and additional data for effects of weather at three levels. First, we test for relationships between seasonal and annual weather values and mean annual acorn production using 16 years of data on 249 individually marked oaks of five species at Hastings Reservation in central coastal California. These analyses test for correlations with weather at the among-year level. Second, using data from a 5-year period, we look for correlations between the seed crop sizes of individual trees of three species and weather conditions during the period that the individuals were flowering. This tests for effects of weather at the within-year level. Third, we examine the concordance between weather and between acorn production patterns at Hastings Reservation and two additional sites located north and south of Hastings Reservation for which we have data on acorn production by three species over a 7-year period. This looks at the geographic scale on which crops are concordant and examines the extent to which differences in weather conditions among sites may influence differences in mean acorn crop size.

Study site and methods

Study areas

The study was conducted at three sites located in the Coast Ranges of central California (Fig. 1). The first is Hastings Reservation, located 42 km southeast of the Monterey Peninsula in the northern Santa Lucia Mountains. Acorn censuses on 249 individually marked oaks, including 87 *Quercus lobata* (valley oak), 57 *Quercus douglasii* (blue oak), 63 *Quercus agrifolia* (coast live oak), 21 *Quercus kelloggii* (California black oak), and 21 *Quercus chrysolepis* (canyon live oak) were conducted each autumn between mid-September and early October, just prior to acorn fall, from 1980 through 1995, for a total of 16 years of data. Starting in 1989, thus yielding 7 years of data through 1995, two additional sites were surveyed: Jasper Ridge, located on the San Francisco Peninsula in the Santa Cruz Mountains (99 trees, including 39 *Q. lobata*, 29 *Q. douglasii*, and 31 *Q. agrifolia*), and Pozo, located at the

American Canyon campground area of the Los Padres National Forest, 36 km inland from San Luis Obispo in the southern Santa Lucia Mountains (75 trees, including 25 *Q. lobata*, 25 *Q. douglasii*, and 25 *Q. agrifolia*). Hastings is centrally located between the other two, Jasper Ridge being 130 km north and Pozo about 160 km south.

For Hastings Reservation and Jasper Ridge, weather records were taken from reserve headquarters. The Hastings weather station was operated manually through 1988, with only temperature and rainfall regularly recorded. Subsequently, an automated weather station recording relative humidity and solar radiation in addition to temperature and rainfall was installed, allowing for more detailed analysis of the phenological data set. For Pozo, rainfall data were taken from the U.S. Forest Service Station, located 8 km west of the site, and temperature from Paso Robles (the nearest inland site for which temperature records were available), 53 km northwest of the site. All sites experience a Mediterranean climate with hot, dry summers and cool, wet winters. At Hastings Reservation, for example, 91% of the annual rainfall occurs between 1 November and 30 April (mean of 54 years between 1940 and 1993).

The three species of oaks studied at each of the three sites (*Q. lobata*, *Q. douglasii*, and *Q. agrifolia*) are "1-year species," in which acorns maturing in the autumn of year x are initiated in the autumn of year $x - 1$, both pollinated and fertilized in early spring of year x , and develop during the following spring and summer. *Quercus kelloggii* and *Q. chrysolepis*, studied only at Hastings, are "2-year species," in which acorns maturing in the autumn of year x are initiated in the autumn of year $x - 2$ and pollinated in the spring of year $x - 1$, but then fertilization is delayed until the spring of year x and develop during the following spring and summer (Sork et al. 1993). *Quercus lobata*, *Q. douglasii*, and *Q. kelloggii* are deciduous species, while *Q. agrifolia* and *Q. chrysolepis* (both commonly known as "live oaks") are evergreen.

Acorn censuses

Relative abundance of the acorn crop was measured using visual surveys (Graves 1980; 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 s. These counts were added, yielding the number of acorns per 30 s, or N30. For all statistical analyses these values were log-transformed ($\ln[N30 + 1]$) to reduce the correlation between the mean and variance (Sokal and Rohlf 1969). Visual surveys were chosen because of their ease and efficiency compared with using traps and because they avoid the problems of arboreal acorn removal, which can be extensive in California. More information on the Hastings study site is provided in Koenig et al. (1994a), while a discussion of our visual survey technique is given in Koenig et al. (1994b).

Phenological survey

Female oak flowers are cryptic and we did not attempt to examine them directly as part of this study. However, for the 5 years between 1991 and 1995 we obtained data on phenological differences among trees by examining male flowers (catkins) on a subsample of 67 marked trees at Hastings Reservation weekly beginning in early March. The sample consisted of 25 *Q. lobata*, 23 *Q. douglasii*, and 19 *Q. agrifolia*. Trees were all located within 1 km of the Hastings weather station and were within 100 m elevation of each other. We recorded the first date on which each tree was in bloom (as indicated by the presence of pendant male catkins and expanded flower buds), the date on which each tree ended male flowering (as indicated by the absence of catkins shedding pollen), and the relative abundance of male catkins based on a scale of 1 (few catkins present)

Table 1. Weather variables used in the analyses of among-year acorn crop size.

Variable	Description
1. Overall water availability	
<i>a</i>	Annual rainfall (1 Sept. – 31 Aug.)
<i>b</i>	Variable 1 <i>a</i> lagged 1 year
<i>c</i>	Variable 1 <i>a</i> lagged 2 years
2. Conditions during pollination	
<i>a</i>	Mean April temperature (1-year species)
<i>b</i>	Variable 2 <i>a</i> lagged 1 year (2-year species)
3. Conditions during acorn development	
Mean summer temperature (1 May – 31 Aug.)	
4. Conditions affecting flower initiation	
<i>a</i>	Variable 3 lagged 1 year (1-year species)
<i>b</i>	Variable 3 lagged 2 years (2-year species)
<i>c</i>	Mean autumn temperature (1 Sept. – 30 Nov.) (1-year species)
<i>d</i>	Variable 4 <i>c</i> lagged 1 year (2-year species)
5. Conditions during the winter	
<i>a</i>	Mean winter temperature (1 Dec. – 31 Mar.)
<i>b</i>	Variable 5 <i>a</i> lagged 1 year

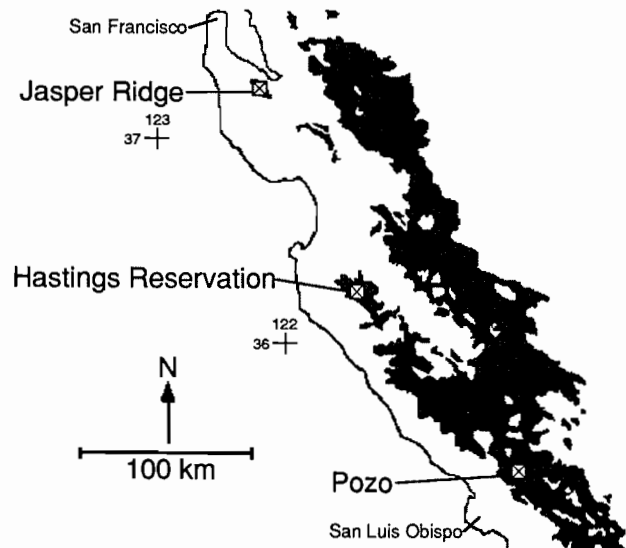
to 4 (tree loaded with catkins). Relative abundance of male catkins was averaged over all censuses during which a tree was in bloom to yield a mean catkin score for each tree.

Weather variables

We extracted five weather variables in our attempt to explain variation in the annual mean acorn crop (Table 1). Fiscal years were chosen to end with acorn fall; thus, the year of acorn fall (year x) begins in the autumn of the prior calendar year. Variables were then lagged 1 (year $x - 1$) and in some cases 2 ($x - 2$) years to yield a total of 12 variables. Variables were chosen so as to correspond to five potentially significant features of acorn development:

- (1) Overall water availability, as indexed by total annual rainfall starting in September of the year prior to acorn fall (variable 1*a*). We also lagged rainfall both 1 (1*b*) and 2 (1*c*) years so as to include water availability during the years prior to flower initiation for both the 1- and 2-year species.
- (2) Conditions during the period of fertilization. Mean (\pm SD) length of flowering varied significantly among years and species, but was generally 3 to 4 weeks, ranging from 19.2 ± 6.4 to 27.4 ± 7.6 days for *Q. lobata*, 20.6 ± 5.8 to 25.8 ± 5.1 days for *Q. douglasii*, and 17.5 ± 8.6 to 31.8 ± 5.1 days for *Q. agrifolia*. Flowering is concentrated in April: between 1991 and 1995, the 67 trees in the phenological survey were in bloom a total of 8227 tree-days, 72.4% of which were in April. Thus, we used mean April temperature (2*a*), available for all years from the Hastings weather station, as a proxy of conditions during the period of fertilization for the 1-year species and mean April temperature lagged 1 year (2*b*) as indicative of conditions during fertilization for the 2-year species.
- (3) Conditions during acorn development. We used mean summer temperature (1 May to 31 August) as our measure of these conditions, since acorn development for all species occurs during the late spring and summer prior to acorn fall.
- (4) Conditions affecting flower bud initiation. This occurs in the autumn at the end of the growing season 1 year before acorn fall (year x) in the 1-year species and 2 years before acorn fall (year $x - 1$) in the 2-year species. Also potentially important to this stage are mean summer temperatures

Fig. 1. Map of central California showing the location of the three study sites overlaid on a partial distribution map of *Q. douglasii* (Griffin and Critchfield 1972).



just prior to bud initiation. Thus, four variables are relevant: mean summer temperatures in years $x - 1$ (4*a*) and $x - 2$ (4*b*), mean autumn temperature of year x (4*c*; measured between 1 September and 30 November), and mean autumn temperature lagged 1 year (4*d*).

- (5) Conditions during the winter (indexed by mean temperature between 1 December and 31 March) both in year x (5*a*) and year $x - 1$ (5*b*). Winter is the period of maximum water availability and is thus potentially significant for nutrient reserves, particularly for the evergreen species (*Q. chrysolepis* and *Q. agrifolia*) that continue to photosynthesize during this season. In addition, nitrogen mineralization in the soil, a process affecting overall nutrient availability for growth and limited primarily by water, occurs mainly during the winter (Jackson et al. 1988; Hart et al. 1992).

Table 2. Results of stepwise multiple regressions of weather variables (see Table 1) on mean annual acorn production.

Species	F-value	df	R ²	Variables in final equation	P-value
<i>Q. lobata</i>	28.2***	2, 13	0.78	Mean April temp. (+) Mean fall temp. year $x - 1$ (-)	<0.001 0.04
<i>Q. douglasii</i>	15.0**	1, 14	0.48	Mean April temp. (+)	0.002
<i>Q. chrysolepis</i>	9.5**	3, 12	0.63	Rainfall year $x - 2$ (+) Mean winter temp. year $x - 1$ (-) Rainfall year $x - 1$ (+)	0.002 0.007 0.04
<i>Q. agrifolia</i>	10.4**	1, 14	0.38	Rainfall year $x - 1$ (+)	0.006

Note: No variables were significant for *Q. kelloggii*. The sign following the variables indicates the direction of the relationship.

** $P < 0.01$.

*** $P < 0.001$.

Female flowering in oaks is correlated with the period catkins are present, with the former appearing 5 to 10 days after male catkins (Sharp and Sprague 1967). Thus, to quantify conditions during the period of pollination for the individual trees for which we acquired phenological data, we determined the dates when individual trees were first recorded as being in bloom and when catkins were no longer detected to be shedding pollen (see above) and then calculated mean rainfall, mean maximum temperature, mean minimum temperature, mean solar radiation, and mean relative humidity as measured at the Hastings Reservation headquarters between the two dates, each plus 1 week (7 days). That is, if a tree was first noted with flowering catkins on 5 April and was spent by 26 April, we calculated mean weather conditions occurring between 12 April and 3 May so as to more accurately cover conditions during which female flowers were most likely present on the tree.

Statistical methods

Correlations between weather variables were generally not high; the mean (\pm SD) absolute value of the Pearson correlation coefficients between all pairs of the 12 weather variables was 0.21 ± 0.16 ($N = 66$). Only one correlation coefficient (1.5%) was significant at the $P < 0.01$ level (annual rainfall and mean April temperature, $r = -0.65$), and two (3%) were significant at the $P < 0.05$ level. The absolute values of other correlation coefficients were all < 0.5 and not significantly different from zero. This relatively low colinearity among variables allowed us to examine the relationship between weather and acorn production using a stepwise regression of the 12 weather variables on the mean annual acorn crops of each species of oak. We also performed principal components analyses, but the results were similar and are not repeated here. The advantage of multiple regression over more complex techniques is that it specifically identifies individual variables that are strongly associated with the dependent variable, in this case mean annual acorn production.

Analysis of covariance was used to test for within-year effects of weather and for a relationship between mean catkin score and subsequent acorn crop of individual trees. For both analyses, the log-transformed acorn crop of individual trees was the dependent variable, year was the main effect, and the remaining variables (rainfall, mean maximum temperature, mean minimum temperature, mean solar radiation, and mean relative humidity all measured during the presumed period of female flowering; mean catkin score for the second) were

covariates. The main effect was entered prior to the covariates so as to control for annual differences.

Similarity of weather and acorn crop data from the three sites was assessed pairwise using Spearman rank correlations and together with Kendall's coefficient of concordance. Significance tests are based on two-tailed probability distributions.

Results

Annual variation in acorn crop

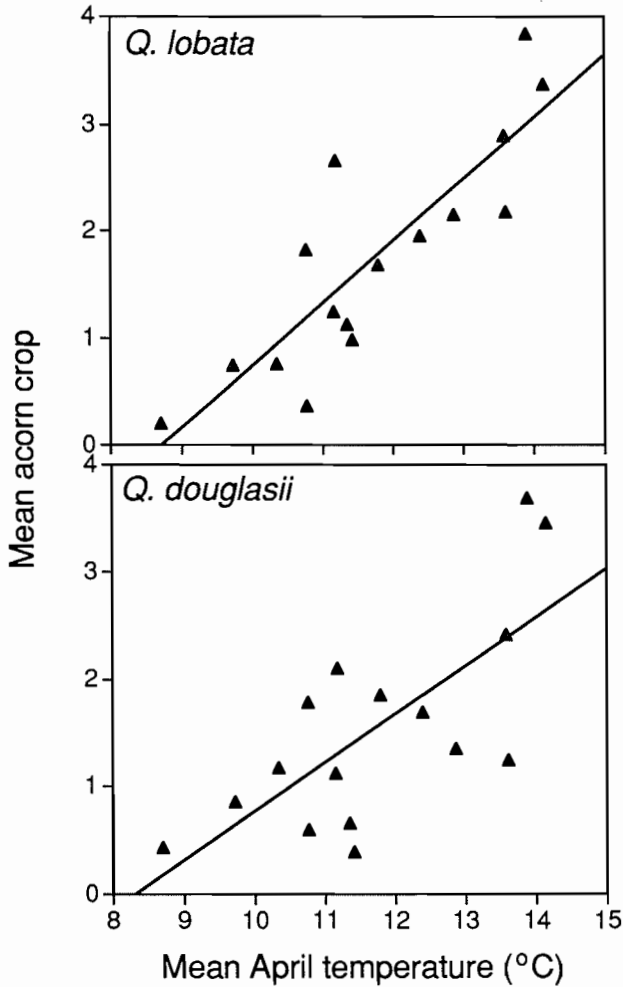
Results of the stepwise multiple regressions using the Hastings Reservation data are summarized in Table 2. None of the variables was significant for *Q. kelloggii*. However, between 38 and 78% of the variation in mean annual acorn crops was explained by the weather variables in the remaining four species. Variables associated particularly strongly with annual acorn production were mean April temperature (*Q. lobata* and *Q. douglasii*; Fig. 2), rainfall in year $x - 1$ (*Q. agrifolia*; Fig. 3) and in year $x - 2$ (*Q. chrysolepis*; Fig. 4), and mean winter temperature in year $x - 1$ (*Q. chrysolepis*).

Within-year effects during flowering

There was a significant positive relationship between mean catkin score and subsequent acorn crop, controlling for year, for *Q. agrifolia* ($F_{[1,89]} = 6.6$, $P = 0.012$) but not for either *Q. lobata* or *Q. douglasii*. Including only trees with nonzero acorn crops, mean catkin score was positively related to subsequent acorn crop for both *Q. agrifolia* ($F_{[1,57]} = 5.1$, $P = 0.024$) and *Q. lobata* ($F_{[1,84]} = 5.7$, $P = 0.019$). Annual differences in acorn crops were highly significant ($P < 0.001$) in all analyses.

Analysis of covariance revealed that for individual *Q. douglasii*, the mean amount of solar radiation during the period of flowering was positively related to the size of the subsequent acorn crop ($P = 0.03$) after controlling for yearly differences. We found no significant effects of any of the weather variables measured during the presumed period of female flowering for individual trees and the subsequent acorn crops of the same individual *Q. lobata* or *Q. agrifolia*. Yearly differences were again highly significant for all three species.

Fig. 2. Correlations between mean April temperature and the mean annual acorn crop (log transformed) of *Q. lobata* and *Q. douglasii* at Hastings Reservation. $N = 16$ years. Spearman rank correlations are as follows: *Q. lobata*, $r_s = 0.84$, $P < 0.001$; *Q. douglasii*, $r_s = 0.64$, $P = 0.008$.



Analyzing the data separately for each year, there were no significant correlations between weather variables and acorn crop of *Q. douglasii*. For *Q. lobata*, larger acorn crops were associated with increased solar radiation and warmer temperatures in 1991 only (solar radiation: $r_s = 0.55$, $N = 25$, $P < 0.01$; mean minimum temperature: $r_s = 0.55$, $N = 25$, $P < 0.01$; mean maximum temperature: $r_s = 0.46$, $N = 25$, $P < 0.05$). For *Q. agrifolia*, larger acorn crops were associated with lower mean relative humidity, less rain, and lower mean minimum temperature in 1994 only (relative humidity: $r_s = -0.51$, $N = 19$, $P < 0.05$; rainfall: $r_s = -0.46$, $N = 19$, $P < 0.05$; mean minimum temperature: $r_s = -0.50$, $N = 19$, $P < 0.05$).

Concordance of acorn crops and weather among populations

The similarity between the mean acorn crops measured at the three central coastal California sites are presented in Table 3. The mean acorn crops of all three species were

Fig. 3. Correlation between annual rainfall (lagged 1 year) and the mean annual acorn crop (log transformed) of *Q. agrifolia*. $N = 16$ years. Spearman rank $r_s = 0.65$, $P = 0.006$.

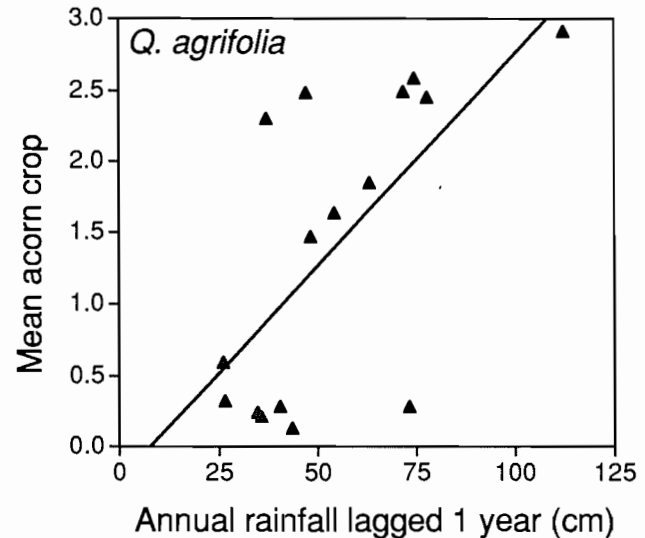
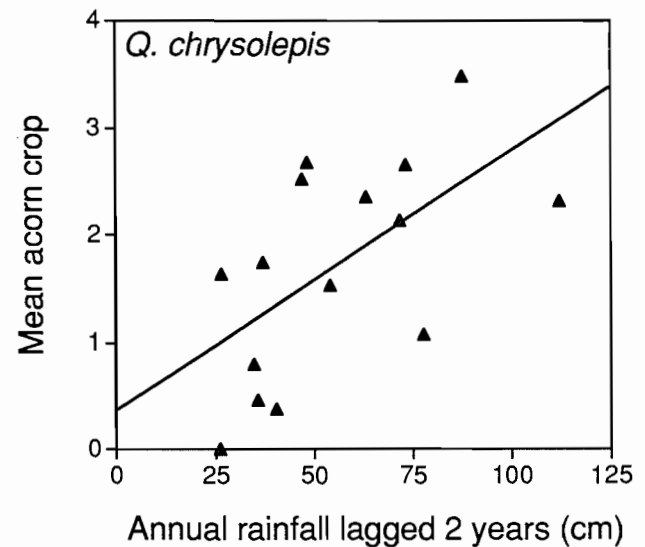


Fig. 4. Correlation between annual rainfall (lagged 2 years) and the mean annual acorn crop (log transformed) of *Q. chrysolepis*. $N = 16$ years. Spearman rank $r_s = 0.59$, $P = 0.016$.



significantly concordant when considered together. In pairwise comparisons, correlations were all positive but were strongest between Jasper Ridge and Hastings Reservation.

Table 3 also presents comparisons of the weather variables among the three sites. Using weather records between 1980 and 1994, relationships between variables are generally positive but are strongest and consistently significant only for annual rainfall and mean April temperature.

Based on the results of the regression analyses performed on the Hastings Reservation data, the two weather variables most likely to correlate with differences among

Table 3. Similarity between weather and mean annual acorn production at three central coastal California sites assessed by Spearman rank correlations (pairwise comparisons) and Kendall's *W* (all three sites combined).

Variable	JR–HNHR	HNHR–Pozo	JR–Pozo	JR–HNHR–Pozo
Mean acorn crop (1989–1995; <i>N</i> = 7 years)				
<i>Q. lobata</i>	0.89**	0.54	0.32	0.72*
<i>Q. douglasii</i>	0.89**	0.54	0.25	0.71*
<i>Q. agrifolia</i>	0.82*	0.64	0.75*	0.83*
Weather (1980–1994; <i>N</i> = 15 years)				
Annual rainfall	0.87***	0.85***	0.81***	0.90***
Mean April temp.	0.59*	0.83***	0.78***	0.82**
Mean summer temp.	0.36	0.52*	–0.04	0.52
Mean fall temp.	0.05	0.56*	0.25	0.52
Mean winter temp.	–0.09	0.82***	0.16	0.53

Note: Sites are Jasper Ridge (JR), Hastings Reservation (HNHR), and Pozo.

**P* < 0.05.

***P* < 0.01.

****P* < 0.001.

populations were mean April temperature for *Q. lobata* and *Q. douglasii* and rainfall lagged 1 year for *Q. agrifolia*. Can differences in these weather variables explain differences in mean acorn crops between sites? To test this possibility, we performed Spearman rank correlations for each year between mean April temperatures at the three sites and the mean acorn crops of *Q. lobata* and *Q. douglasii*, and between annual rainfall lagged 1 year at the sites and mean acorn crop of *Q. agrifolia*. Results were not consistent: of the 12 correlations (1989 to 1994) between mean April temperatures and mean acorn crops of *Q. lobata* and *Q. douglasii*, 6 were positive and 6 negative. Of 7 correlations (1989 to 1995) between annual rainfall lagged 1 year and the mean acorn crop of *Q. agrifolia* at the three sites, 3 were positive and 4 negative.

Discussion

Acorn production in central coastal California varies considerably from year to year (Koenig et al. 1994a). Variation in weather was able to explain between 38 and 78% of annual variation in the mean acorn crop for four of the five species studied (Table 2). For the fifth species, *Q. kelloggii*, we failed to detect any significant correlation between mean annual acorn crop and weather.

These findings indicate that different species of oak vary considerably in the degree to which environmental variability affects annual seed crop size. Previous analyses demonstrated that individual trees of the four species for which weather variables were able to explain a significant amount of annual variation in mean acorn crop size tend to produce acorns in 2- to 3-year cycles, whereas the cycle length for individual *Q. kelloggii* appears to be much longer, possibly 7–8 years (Koenig et al. 1994a). This suggests that *Q. kelloggii* may be influenced more by endogenous factors than the other species and that determining the correlations between acorn production and weather will require additional years of data for this species.

Species also differ in the particular weather variables that are important. For both *Q. lobata* and *Q. douglasii*,

closely related deciduous species in the white oak group (subgenus *Quercus*) that require 1 year to mature acorns, the most important weather variable determining mean annual acorn production is mean April temperature, the period when trees are flowering and when pollination and fertilization occur. This relationship closely matches that documented for three species of white oaks in Pennsylvania by Sharp and Sprague (1967) and for *Quercus alba* (the eastern white oak), in Missouri by Sork et al. (1993). Taken together, these studies provide strong evidence that acorn production by many species of oaks in this subgenus is determined by favorable weather conditions during the flowering and fertilization period.

Still unclear is the precise aspect of acorn development influenced by spring temperatures. Sharp and Sprague (1967) attributed the effect to the impact of spring conditions on pollen dehiscence and pollination success, while Sork et al. (1993) suggested that the effect may instead be on fertilization per se and subsequent ovule development. This latter conclusion was based on the finding that acorn production in *Quercus rubra* and *Quercus velutina*, two species of red oaks (subgenus *Erythrobalanus*) requiring 2 years to mature acorns, was correlated with spring temperatures during year *x*, when fertilization occurs, rather than in year *x* – 1, when pollination takes place. In contrast, we found no relationship between spring conditions, in either year *x* or year *x* – 1, on acorn production of either of the 2-year species (*Q. chrysolepis* or *Q. kelloggii*) we studied at Hastings Reservation. We are thus unable to evaluate their interpretation for either of these species.

For the two live oak species *Q. agrifolia* and *Q. chrysolepis*, acorn crop size correlated most strongly with rainfall in prior years and, for *Q. chrysolepis* only, mean winter temperature in year *x* – 1. The significance of the latter correlation is unclear, although photosynthesis continues in these species during the winter and thus an effect of winter temperature on subsequent acorn production is at least plausible. The correlations between acorn production in these species with rainfall lagged by 1 and 2 years suggest that overall water availability is important to acorn

production, but that the effects are delayed. The delay is longer in *Q. chrysolepis*, a species requiring 2 years to mature acorns, than in *Q. agrifolia*, which matures acorns in a single season.

Our results were less successful at documenting effects of weather during flowering on subsequent acorn production within populations of *Q. lobata*, *Q. douglasii*, and *Q. agrifolia*. For *Q. douglasii*, the mean amount of solar radiation during the presumed period of female flowering of individual trees was positively related to their subsequent acorn crops after controlling for annual differences. This result, along with the significant correlations emerging when considering years separately in the other two species, are generally consistent with the hypothesis that warm, dry conditions favoring pollen transfer and fertilization promote larger acorn crops by individual trees in these 1-year species. However, the effect is relatively weak and may only occur in some years.

Mean annual acorn production by *Q. lobata*, *Q. douglasii*, and *Q. agrifolia* at three sites in central coastal California located nearly 300 km apart were significantly concordant (Table 3). Correlations across the three sites of the five basic weather variables tested for their effect on mean annual acorn production at Hastings Reservation (Table 1) indicate that annual rainfall and mean April temperature, the variables correlating most strongly with annual acorn production at Hastings Reservation (Table 2), are also the most strongly concordant of the variables among the sites (Table 3). Thus, the environmental variables that influence annual crop size at Hastings Reservation are also the most geographically synchronous, at least within the central California coast.

We were unsuccessful at explaining differences in the mean annual acorn crop among the three sites surveyed on the basis of differences in weather conditions at the sites: there were no consistent relationships within years between either mean April temperatures at Jasper Ridge, Hastings Reservation, and Pozo and the subsequent acorn crops of *Q. lobata* or *Q. douglasii*, nor between rainfall in year $x - 1$ and the subsequent acorn crop of *Q. agrifolia* at the three sites. These data are limited, but fail to support the hypothesis that the same weather factors influencing acorn crop size within a site can also explain differences in mean acorn production among sites.

In summary, acorn production by four of five oak species studied at Hastings Reservation is strongly correlated with either conditions favorable to pollination and fertilization in the spring or rainfall in prior years (although not the winter immediately preceding an acorn season). Apparently, even 16 years of data are insufficient to determine the environmental factors, if any, correlating with annual acorn production by *Q. kelloggii*. Differences in environmental conditions during the period of flowering by individual trees have only a small effect on differences in acorn production by trees, but what correlations emerge suggest that trees flowering during warm, dry conditions favorable for

pollination and fertilization may experience increased acorn production. However, we found no consistent relationship between either spring conditions or annual rainfall and differences in the mean annual acorn crop at three sites located nearly 300 km apart. Environmental factors generally appear to have a strong influence on annual acorn production within a site, are of lesser importance to acorn crop size within populations, and have little or no relationship to mean crop size differences among sites.

Acknowledgments

We thank the University of California's Integrated Hardwoods Range Management Program for support, Paul Neal and the reviewers for comments, Pam Muick for advice on study sites, Bill Tietje for help acquiring weather data, Nona Chiariello and Stanford University for permission to work at Jasper Ridge, and the U.S. Forest Service for access to Pozo. We also thank the Marks for logistic support and Fanny Arnold and her family for their support of Hastings Reservation.

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