# ACORN YIELDS IN THREE COASTAL-CENTRAL CALIFORNIA COUNTIES DURING 1988-1997

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*ABSTRACT*: Acorns are the ultimate source of regeneration for oaks (*Quercus* spp.) and are an important food source for many species of vertebrate and invertebrate wildlife. We conducted visual counts as an index of blue oak (*Q. douglasii*), coast live oak (*Q. agrifolia*), and valley oak (*Q. lobata*) acorn production in San Benito, San Luis Obispo, and Santa Barbara Counties, California, during 1988-1997. Mean mast score of all species combined was highest in Santa Barbara County and lowest in San Luis Obispo County ($P = 0.004$). Mean mast scores did not differ among species ($P = 0.064$), but scores were highest for valley oak and lowest for blue oak. Mean mast scores differed widely among years ($P \leq 0.001$), but did not correlate well among counties or oak species. Open canopy trees had higher ($P$ 0.001) mean mast scores than trees suppressed by other canopy trees. Mast scores were weakly and inconsistently correlated with total annual precipitation and average March-April temperature. Differences in acorn abundance among years and counties likely can be attributed to climatological differences (temperature, wind speed, precipitation) among counties and at micro-site locations.

*Key Words*: acorns, blue oak, coast live oak, masting, mast, California, oak woodlands, *Quercus*, valley oak

*1999 TRANSACTIONS OF THE WESTERN SECTION OF THE WILDLIFE SOCIETY 35:41-49*

Nine species of tree-sized oaks are native to California. Of these species, 3 (blue oak, coast live oak, valley oak) dominate within the central coast region. Acorns have long been considered an important food for vertebrate wildlife (Christisen and Korschgen 1955, Reid and Goodrum 1957, Goodrum et al. 1971, Barrett 1980). The California Wildlife Habitat Relationship System (Airola 1988) predicts that acorns are necessary for the maintenance of normal population levels of 33 species of oak woodland birds and mammals. Mast production has been correlated with population fluctuations in small mammals (Wolff 1996), and annual population levels in deer (*Odocoileus* spp.; Dasmann 1971), feral hogs (*Sus scrofa*; Barrett 1978) and acorn woodpeckers (*Melanerpes formicivorus*; Stacey and Koenig 1984). A relationship between acorn production and population dynamics of many species of vertebrate wildlife is suspected, although research is needed to verify such relationships.

Acorn production studies in Pennsylvania (Sharp and Sprague 1967) and Missouri (Sork et al. 1993) have concluded that year-to-year variation in size of the acorn crop is the result of an intrinsic physiological response modified by annual variation in weather events. Weather events responsible for variability in acorn production include winter cold; spring frost, temperature, and humidity; wind at time of pollination; and drought and high temperatures. Research in California has been conducted on temporal variation in acorn production for individual blue oak trees (McKibben and Graves 1987) and effects of spring weather on acorn production (Koenig et al. 1996). Also in California, Koenig and Knops (1997) addressed long-term acorn synchrony over large geographic areas.

Over a 10-year period (1987 - 1997), we assessed acorn production in 3 counties of coastal-central California: San Benito (SBE), San Luis Obispo (SLO), and Santa Barbara (SBA) (Fig. 1). These counties comprise approximately 11% (314,000 ha) of the 3.1 million ha of oak woodlands of California (Mayer et al. 1986). Our objectives were to document acorn production over this period for the 3 dominant tree-sized species of the region: blue, valley, and coast live oak within and among counties; and how tree canopy position affects production.

METHODS

During summer and fall 1988, in Santa Barbara, San Luis Obispo, and San Benito Counties, 19 blue oak, coast live oak, and valley oak stands were located, mostly on private livestock ranches, and on a variety of slopes and aspects. Within these stands, 32 0.04-ha plots were established (7, 12, and 13 plots in SLO, SBA, and SBE Counties, respectively) a minimum of 1 km apart along access roads. From each point we located along the road, we paced approximately 60.1 m from the road in the cardinal direction nearest to perpendicular with the road. Plots had 10 percent oak canopy cover and ≥3 oak trees ≥10.2 cm dbh (diameter at breast height, 1.4 m from the ground). Any plot not meeting these criteria was excluded and another located.

Within the plots, 416 oak trees (each stem of a tree that bifurcated <1.4 m was counted as a tree) were marked with numbered aluminum tags for permanent identification. We measured the height and dbh of each tree and noted its condition (live, dead) and canopy position (open, suppressed). We also counted the number of seedlings (030 cm tall), saplings (30152 cm), and pole-sized trees (1.53.1 m), and ocularly estimated cover of shrubs and ground vegetation in each plot.

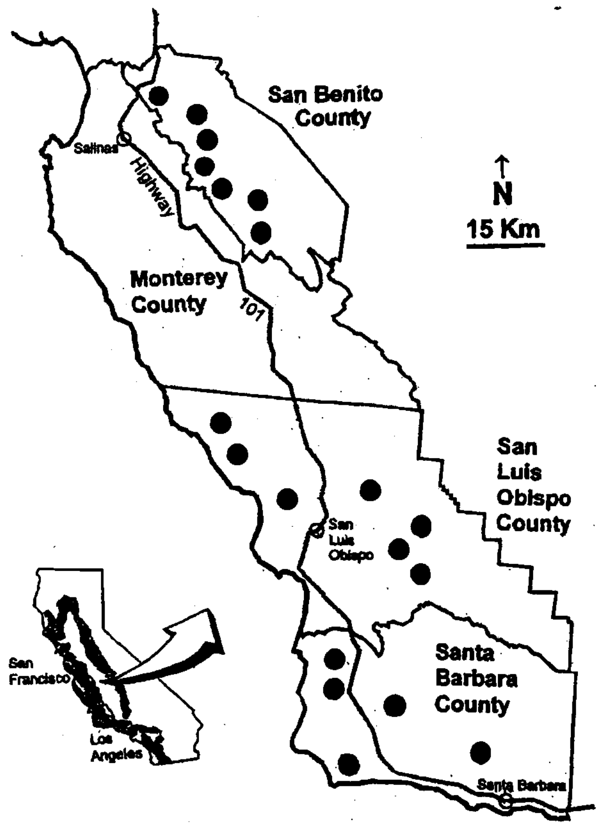


Figure 1. Locations of the 19 ranch and public oak woodlands (solid circles) in coastal-central California where 32 0.04-ha plots were established to sample acorn production of blue oaks, coast live oaks, and valley oaks during 1988-1997. The inset map shows the composite distribution of blue, coast live, and valley oaks in California (after Griffin and Critchfield 1976).

During fall (23 August - 20 October) of each year (19881997), plots were visited and acorn production was assessed. Plots generally were visited in the same order each year within counties, but acorn maturation times and logistical complications prevented our visiting each county in the same order each year. We used the method described by Graves (1980) to assess mast yields by nominal categories. Four classes of acorn production were possible: 1 - no visible acorns; 2 - acorns visible after close examination, but few (<5) observed; 3 - acorns readily visible, but they do not cover limbs and limbs do not appear to bend under their weight; 4 - acorns readily visible and cover the entire tree, limbs sag from weight of acorns. Acorn yield (hereafter mean mast score, MMS) was assessed for each tree. Those trees that died during the study were no longer given a mast score. Scores were averaged for species within plots. County-level MMS are averages of plots within counties.

Weather Data

To correlate acorn production with basic weather variables, we derived total annual precipitation and average MarchApril temperature for each of the 3 counties. Data were garnered from the western regional climate center world-wide web site (http://www.wrcc.dri.edu). On this site, data are reported from individual weather reporting stations. For each county, data were used from all weather recording stations having records for July, 1987 - June, 1998. Using these criteria, 7, 5, and 5 stations had usable data for SBA, SLO, and SBE counties, respectively (Appendix). Although these weather stations were not distributed systematically throughout counties, nor generally near the plots on which we assessed acorn production, we believe the data they provide is sufficiently representative to be able to assess acorn production relative to weather conditions for our purposes.

Because data from the web site are reported by station and by month, we calculated total annual precipitation at each station by summing monthly precipitation from July of the year previous to acorn surveys through June of the current year of surveys. These station-level totals were averaged to derive a county-wide average for total annual precipitation. Even if data was missing from a station for certain years, we did not discard data from other years for that station. The web site also reports the number of days during which data were not collected for each variable at each station. When ≥26 days of data were missing from a month for a station, and if the precipitation value for this month was zero, the datum from this cell was not used in calculation (Appendix). Of 2,040 total months of precipitation data ([7 + 5 + 5] weather stations x 12 months/year x 10 years = 2,040 months) potentially available during the period July, 1987June 1997, 113 (5.5%) were unavailable because 1 or more stations reported no data for several months or years or because ≥26 days of data were not reported for a month. Three months had ≥26 missing days but had non-zero precipitation totals and were used in calculations (Appendix). We could have used total annual precipitation provided on the web site; however, those totals included no data from months during which more than 10 days of data were not gathered, which could have led to significantly lower precipitation totals. Further, we were interested in total precipitation for the period prior to acorn surveys; total annual precipitation reported by the web site would have included precipitation that fell after surveys were conducted. Only 17 (5%) of 340 total months of temperature data were missing (Appendix).

*Analyses*

We used the log-likelihood ratio, *G*, to test for differences in proportions of open canopy and suppressed trees among counties and species. Analyses of variance (ANOVA) were used to test for differences in MMS among counties, species, and years, and between open canopy and suppressed trees. Because the number of observations in classes and levels was unbalanced, we used type III sums-of-squares (Milliken and Johnson 1992:184 - 185, SAS Inst. Inc. 1988:572) in the PROC GLM module of SAS (SAS Inst. Inc. 1988:547 - 640). Data were non-normally distributed; therefore, ANOVA were conducted on ranks (Conover and Iman 1981). When a main effect was significant, we used least-square means to differentiate among levels (SAS Inst. Inc. 1988:564565). We used Spearman rank correlation in PROC CORR (SAS Inst. Inc. 1990:209 - 235) to elucidate temporal patterns of MMS among species (species synchrony) and among counties (geographic synchrony); to associate plot condition (number of pole-sized trees, seedlings, shrub cover, etc.) with MMS; and to associate tree vigor (height and dbh) with MMS. We used the convention of $\alpha = 0.05$ for statistical significance.

Because sample sizes were small ($n \leq 30$) and data were non-normally distributed, we used Spearman rank correlation (Zar 1984:318 - 320, SAS Institute Inc., 1988:209-235) to correlate MMS with total annual precipitation and average March - April temperature for all counties combined. We also performed these analyses for counties to determine if relationships were stronger at smaller spatial scales.

## RESULTS

In SLO, SBA, and SBE counties, we monitored 96, 123, and 197 trees, respectively. The total of 416 trees included 254 coast live oaks, 118 blue oaks, and 44 valley oaks. The proportions of each species that we monitored were reasonably consistent among counties (Table 1). Twenty-two of the trees we monitored died during the study: 4, 9, and 9 in SLO, SBA, and SBE counties, respectively.

Table 1. Number of plots and oak trees (coast live oak [CLO], blue oak [BLO], and valley oak [VAO]) visited in San Luis Obispo (SLO), Santa Barbara (SBA), and San Benito (SBE) counties to assess mast production, 1988-1997. Within-county plot totals are not sum of row totals because more than 1 species was tallied in several plots.

| County | Coast Live Oak | Blue Oak | Valley Oak | Total |
|---|---|---|---|---|
| San Luis Obispo | | | | |
| Plots | 5 | 3 | 2 | 7 |
| Trees | 45 | 44 | 7 | 96 |
| Santa Barbara | | | | |
| Plots | 10 | 2 | 2 | 12 |
| Trees | 99 | 20 | 4 | 123 |
| San Benito | | | | |
| Plots | 6 | 4 | 6 | 13 |
| Trees | 110 | 54 | 33 | 197 |
| Total | | | | |
| Plots | 21 | 9 | 10 | 32 |
| Trees | 254 | 118 | 44 | 416 |

*Ecological Correlates*

Open canopy trees (347) dominated; 58 other trees were considered suppressed and 11 were dead at time of first survey. Proportions of open canopy and suppressed trees differed among counties ($G_2 = 23.049$, $P \leq 0.001$), but not among species ($G_2 = 3.329$, $P = 0.189$). MMS was higher for open canopy trees ($P \leq 0.001$), and no interaction between canopy position and species was detected ($P = 0.057$).

Plot-level MMS was weakly correlated ($r_s = -0.369$) with the number of pole-sized oak trees that occurred on plots ($n = 31$, $P = 0.041$). Number of saplings, number of seedlings, cover of shrubs, and cover of ground vegetation all were uncorrelated with MMS at the plot level ($n = 31$ or 32, all $P \geq 0.089$). MMS of live trees ($n = 405$) was weakly, but significantly, correlated with tree dbh ($r_s = 0.408$, $P < 0.001$) and tree height ($r_s = 0.258$, $P < 0.001$). Tree height and dbh also were correlated ($r_s = 0.683$, $P < 0.001$).

*Within County and Across County MMS Patterns*

Over all years, MMS differed among counties ($P = 0.004$) and among years ($P \leq 0.001$), but not among species ($P = 0.064$). MMS was higher in SBA than in SLO ($P = 0.014$) and SBE ($P = 0.001$). MMS did not differ between SBE and SLO ($P = 0.652$).

Within-county MMS patterns for the three species (Figs. 2A-C) tracked one another well during 1988-1997 for SBA (i.e., the highs and lows in mast production for all three oak species generally occurred during the same years within a county), and to lesser degrees in SBE and SLO counties. Among-county MMS patterns (Figs. 3A-C) revealed that blue oak displayed the strongest evidence for production of similarly big or small crops of acorns among counties in the same years (geographic synchrony); there was less evidence for geographic synchrony in MMS for coast live oak and valley oak. Of 36 possible pairs in a correlation matrix of MMS of blue oak, coast live oak, and valley oak for SBA, SBE, and SLO, only 6 correlation pairs were significantly correlated (Table 2).

*Weather Influences*

With the MMS and weather data pooled across counties, 2 significant relationships were detected (Table 3): MMS of coast live oak was positively correlated with total annual precipitation ($r_s = 0.364$, $P = 0.048$) and blue oak MMS was positively correlated with average MarchApril temperature ($r_s = 0.486$, P = 0.006). When the MMS and weather data from each county were analyzed separately, no significant correlations between MMS and precipitation or temperature were found (Table 3). Moreover, with both the pooled data and the data analyzed separately within each county, the directions of the non-significant correlations were inconsistent (Table 3).

## DISCUSSION

We used visual counts to assess mast production on blue, coast live, and valley oaks for 10 years in 3 California coastal-central counties on plots that spanned approximately 306 km from Fremont Peak in San Benito County to Cachuma Lake in Santa Barbara County. The largest trees and those in the open produced the most acorns. Acorn production of the 3 oak species generally was similar for the 10 years of the study. Evidence was

Table 2. Spearman rank correlation matrix of mast scores of blue oak (BLO), coast live oak (CLO), and valley oak (VAO) among Santa Barbara (SBA), San Benito (SBE), and San Luis Obispo (SLO) counties, 1988-1997. Correlation coefficients are shown below the diagonal, *P*-values are shown above the diagonal. Significant ($P \leq 0.05$) correlations are underlined.

| | SBABLO | SBACLO | SBAVAO | SBEBLO | SBECLO | SBEVAO | SLOBLO | SLOCLO | SLOVAO |
|---|---|---|---|---|---|---|---|---|---|
| SBABLO | | 0.001 | 0.550 | 0.258 | 0.867 | 0.038 | 0.138 | 0.013 | 0.905 |
| SBACLO | 0.927 | | 0.200 | 0.251 | 0.542 | 0.098 | 0.325 | 0.019 | 0.851 |
| SBAVAO | -0.215 | -0.443 | | 0.227 | 0.204 | 0.367 | 0.829 | 0.076 | 0.876 |
| SBEBLO | 0.395 | 0.404 | -0.420 | | 0.840 | 0.003 | 0.097 | 0.059 | .0137 |
| SBECLO | 0.061 | 0.220 | -0.440 | 0.073 | | 0.776 | 0.402 | 0.920 | 0.369 |
| SBEVAO | 0.661 | 0.552 | -0.320 | 0.833 | 0.104 | | 0.090 | 0.011 | 0.334 |
| SLOBLO | 0.503 | 0.345 | -0.074 | 0.553 | -0.299 | 0.564 | | 0.187 | 0.798 |
| SLOCLO | 0.745 | 0.721 | -0.585 | 0.614 | 0.036 | 0.758 | 0.454 | | 0.523 |
| SLOVAO | 0.044 | 0.068 | -0.057 | 0.505 | -0.312 | 0.342 | 0.093 | 0.230 | |

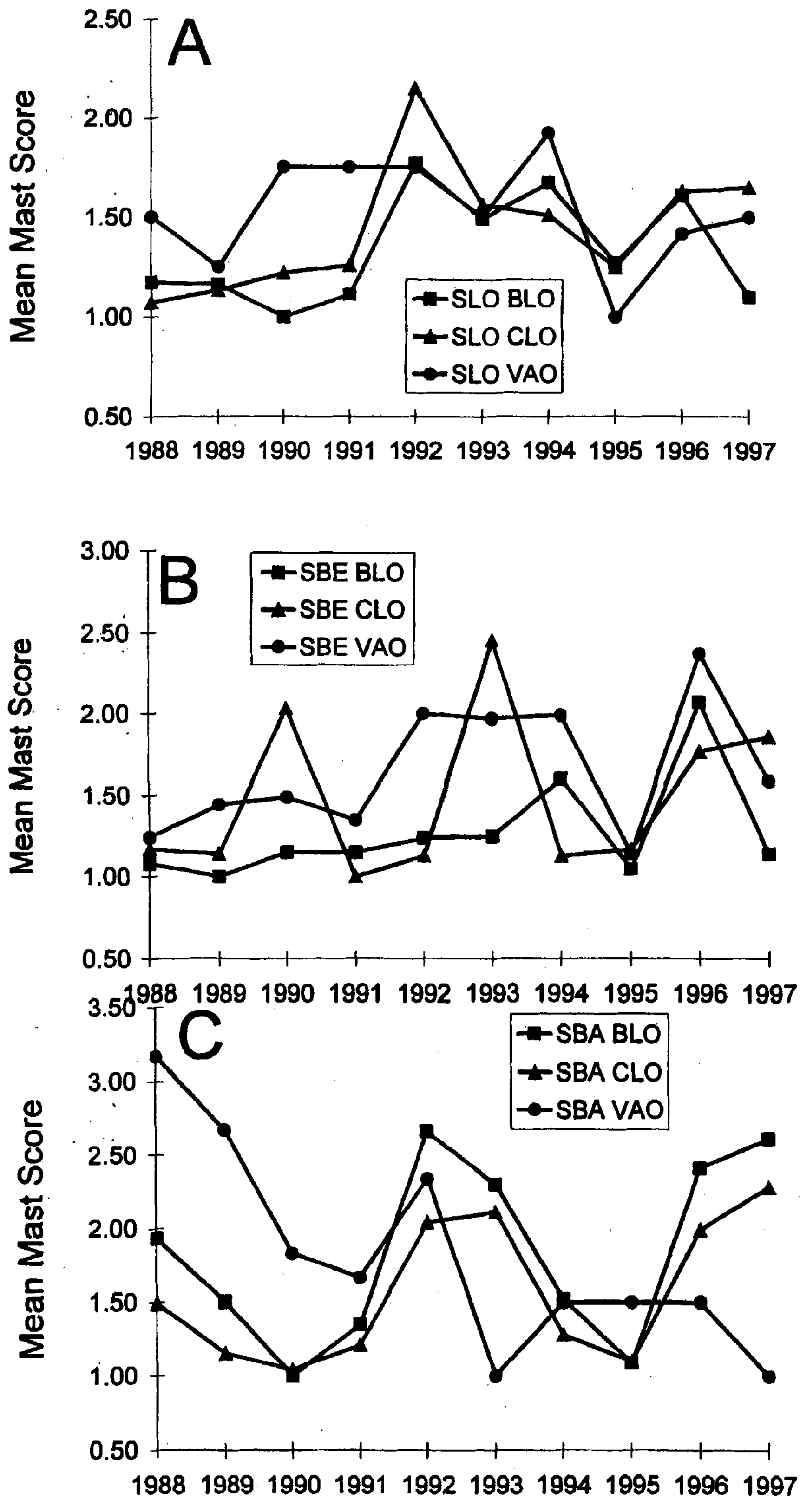


Figure 2. Mean mast scores (MMS) of blue oaks (BLO), coast live oaks (CLO), and valley oaks (VAO) in (A) San Luis Obispo (SLO), (B) San Benito (SBE), and (C) Santa Barbara (SBA) counties, California, 1988-1997. MMS is mean of mast scores for trees within plots in each county. See text for sample sizes.

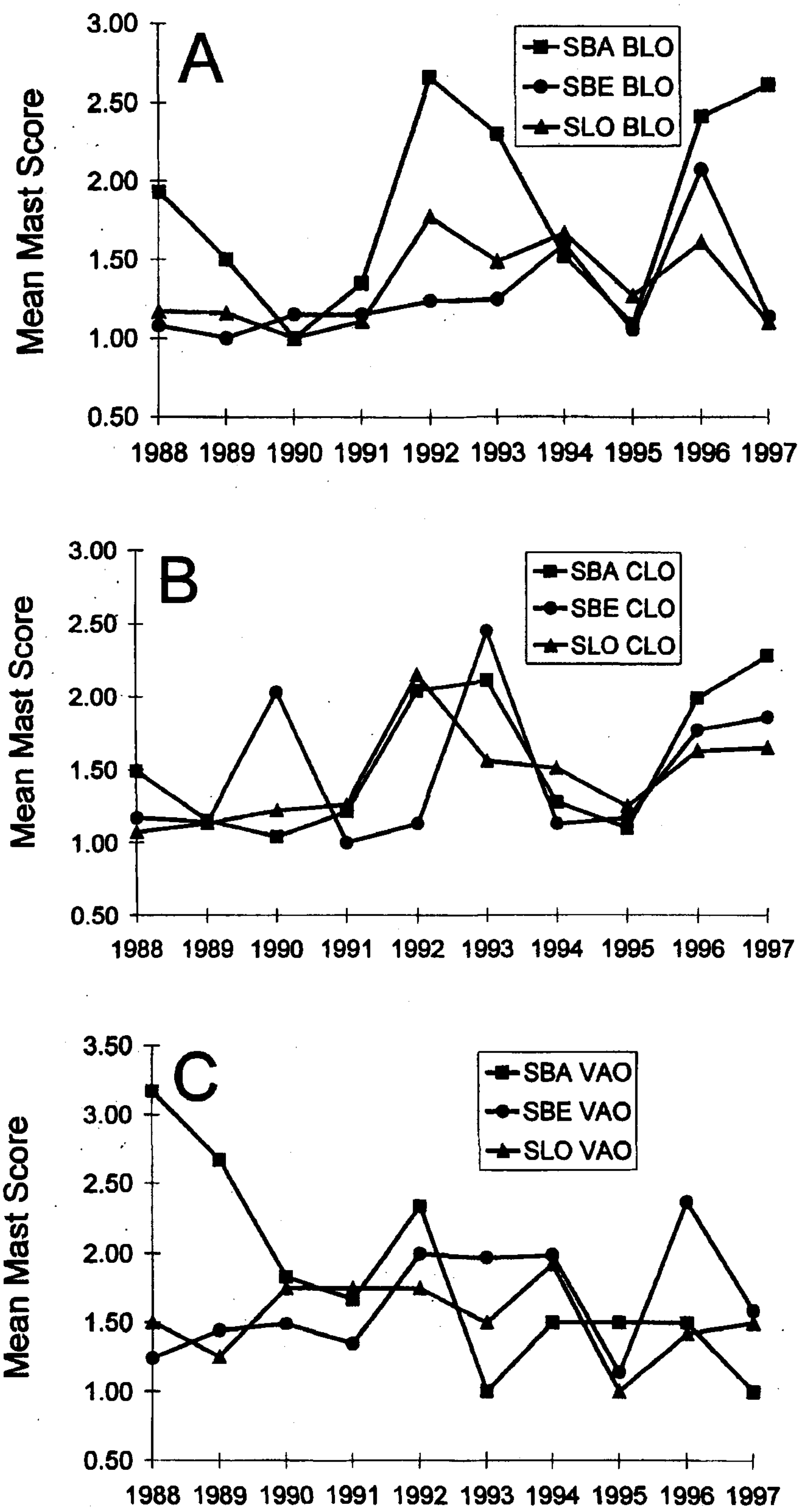


Figure 3. Mean mast scores (MMS) of (A) blue oaks (BLO), (B) coast live oaks (CLO), and (C) valley oaks (VAO) in San Luis Obispo (SLO), San Benito (SBE), and Santa Barbara (SBA) counties, California, 1988-1997. MMS is mean of mast scores for trees within plots in each county. See text for sample sizes.

limited, but the patterns of the highs and lows of acorn production were similar across the geographic area we surveyed (geographic synchrony), and most so for blue oak. Two weather variables (total annual precipitation and mean spring temperature) were inconsistent and unreliable correlates of acorn production.

That mast production was greater on open canopy trees than suppressed or closed canopy trees is not surprising. Open-canopy trees suffer less stress: trees in the open have less competition for light, water, and nutrients. Similarly, after thinning, acorn production in residual blue oaks is greater compared to the same trees before thinning (R. Standiford, Univ. of Calif., Berkeley, pers. comm.).

Our finding that production among all 3 oak species demonstrated the same annual trends within the counties generally agrees with other, more rigorous work in California oak woodlands (Koenig et al. 1994, Koenig et al. 1996). The similar production trends can be explained by two factors. First, blue oak and valley oak are closely related species in the white oak subgenus (*Lepidobalanus*). Second, the white oaks and coast live oak require one year to mature acorns. Koenig et al. (1994) demonstrated that a like acorn maturation period may account more for interspecies similarity in masting pattern than does taxonomic relationship. Although coast live oak is in the black oak group (*Erythrobalanus*), it is the only black oak species that requires 1 year to produce acorns. Of the 3 black oaks surveyed in Koenig et al. (1994), coast live oak had the closest masting pattern to blue and valley oak.

Table 3. Spearman rank correlation between mast scores of blue oak, coast live oak, and valley oak and total annual precipitation and average March-April temperature in Santa Barbara, San Benito, and San Luis Obispo counties, 1988-1997. Significant ($P \leq$ ( 0.05) correlations are underlined.

| County/Species | Precipitation | Temperature |
|---|---|---|
| Santa Barbara | | |
| Blue oak | 0.221 | 0.564 |
| Coast live oak | 0.285 | 0.479 |
| Valley oak | -0.245 | 0.080 |
| San Benito | | |
| Blue oak | 0.249 | -0.106 |
| Coast live oak | 0.335 | 0.262 |
| Valley oak | 0.151 | 0.273 |
| San Luis Obispo | | |
| Blue oak | 0.248 | 0.491 |
| Coast live oak | 0.503 | 0.454 |
| Valley oak | -0.329 | -0.118 |
| Pooled | | |
| Blue oak | 0.173 | 0.486 |
| Coast live oak | 0.364 | 0.318 |
| Valley oak | -0.175 | 0.069 |

The difference in mast production among the 3 counties in this study is not consistent with the regional concordance of mast production documented by Koenig and Knops (1997). Differences that we documented over the 10 years of study could be ascribed to climatological differences among counties. During the study period, SLO County was warmer and wetter whereas SBA and SBE counties were cooler and drier. When selecting plots, we made no attempt to control for elevation, aspect (windward or leeward side of coast mountain range), soil type, or grazing intensity (which could affect soil compaction), all of which could affect pollination, tree stress and vigor, and therefore acorn production.

This study occurred during 5 dry (1988-1992) and 5 wet years (1993-1997). We attributed the dying of some oak trees on our study plots to the drought (Tietje et al. 1993). Many ranchers and other landowners also reported dying and dead oak trees on their lands during the drought years. Despite its severity, the drought apparently did not influence acorn production in the two white oaks we studied, blue and valley oak. In contrast, it was a significant determinant of acorn production in coast live oak, a black oak. This result is consistent with a conclusion of Koenig et al. (1996) that overall water availability alone is not a major determinant of acorn production in the white oaks, but it is in the black oaks. Koenig et al. (1996) also concluded that in blue and valley oak, mean April temperature is the most important influence on subsequent acorn production. Similarly, during the 10 years of this study, we found that the largest fall acorn crops generally followed a warm spring. This positive influence of temperature on acorn production was strong for blue oak, and it was at least apparent for valley and coast live oak. Although most studies of masting concur that dry, warm conditions in spring favor pollen transfer and fertilization, specific aspects of acorn development influenced by weather still are unclear.

We made no observation that moderate grazing adversely affects acorn production directly (pers. obs.), although we did not design this study to test effects of grazing on acorn production. In the long term, grazing may affect acorn production to the extent that it influences the natural regeneration of oaks by, for example, reducing water competition from annual grasses and reducing seedling survival. That the more open-canopy trees are the best acorn producers suggests that thinning of oaks may enhance production of residual trees. Importantly, however, whether total production of a stand before thinning equals that of the residual stand after thinning has not been evaluated. Aesthetic and wildlife habitat values of oak woodlands should be carefully weighed against any possible enhancement of acorn production due to thinning of oak trees.

## ACKNOWLEDGMENTS

We gratefully acknowledge the Santa Barbara, San Luis Obispo, and San Benito County landowners who provided access to their properties during the 10 years of this study. This study was supported by the University of California, Berkeley's Integrated Hardwood Range Management Program and the University of California Cooperative Extension Service in Santa Barbara, San Luis Obispo, and San Benito Counties.

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Appendix. Station names and number of months of data garnered from the western regional climate center web site (http://www.wrcc.dri.edu) of total annual precipitation and average minimum March-April temperature, San Luis, Santa Barbara, and San Benito counties, California, 1987-1997.

| County | Precipitation[1] | Temperature[2] |
|---|---|---|
| Santa Barbara | | |
| Santa Maria Airport | 120 | 20 |
| Twitchell Dam | 77 | 13 |
| Lompoc | 118 | 20 |
| Cachuma Lake | 119 | 20 |
| Santa Barbara Airport | 100 | 160 |
| Santa Barbara | 114 | 190 |
| New Cuyama Fire Station | 118 | 20 |
| San Luis Obispo | | |
| Paso Robles Airport | 120 | 20 |
| Paso Robles | 120 | 20 |
| Morro Bay Fire Department | 120 | 20 |
| San Luis Obispo, California Polytechnic and State University | 110 | 19 |
| Pismo Beach | 117 | 20 |
| San Benito | | |
| Salinas | 118 | 20 |
| Salinas Airport | 99 | 16 |
| Pinnacles National Monument | 118 | 20 |
| King City | 119 | 20 |
| Priest Valley | 120 | 20 |
| Total | 1,927 | 323 |

[1] Maximum number of months for a station = 120.
[2] Maximum number of months for a station = 20.