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Is the relationship between mast-seeding and weather in oaks related to their life-history or phylogeny?

WALTER D. KOENIG,[1,2,9] REYES ALEJANO,[3] MARIA DOLORES CARBONERO,[4] PILAR FERNÁNDEZ-REBOLLO,[5]
JOHANNES M. H. KNOPS,[6] TEODORO MARAÑÓN,[7] CARMEN M. PADILLA-DÍAZ,[7] IAN S. PEARSE,[8]
IGNACIO M. PÉREZ-RAMOS,[7] JAVIER VÁZQUEZ-PIQUÉ,[3] AND MARIO B. PESENDORFER[1]

[1]*Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850 USA*
[2]*Department of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853 USA*
[3]*Agroforestry Department, University of Huelva, Escuela Politécnica Superior, Campus de La Rábida,*
Palos de la Frontera, Huelva, 21819 Spain
[4]*Department of Agricultural Production, Institute of Agricultural and Fishing Research and Education (IFAPA),*
Hinojosa del Duque, Córdoba, 14270 Spain
[5]*Forestry Department, University of Córdoba, Campus de Rabanales, Leonardo Da Vinci, Apdo. 3048, Córdoba, 14071 Spain*
[6]*School of Biological Sciences, University of Nebraska, 348 Manter Hall, Lincoln, Nebraska 68588 USA*
[7]*Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), Avenida Reina Mercedes, 10, Sevilla, 41012 Spain*
[8]*Illinois Natural History Survey, 1816 S. Oak Street, Champaign, Illinois 61820 USA*

Abstract. Although the functional basis of variable and synchronous seed production (masting behavior) has been extensively investigated, only recently has attention been focused on the proximate mechanisms driving this phenomenon. We analyzed the relationship between weather and acorn production in 15 species of oaks (genus *Quercus*) from three geographic regions on two continents, with the goals of determining the extent to which similar sets of weather factors affect masting behavior across species and to explore the ecological basis for the similarities detected. Lag-1 temporal autocorrelations were predominantly negative, supporting the hypothesis that stored resources play a role in masting behavior across this genus, and we were able to determine environmental variables correlating with acorn production in all but one of the species. Standard weather variables outperformed "differential-cue" variables based on the difference between successive years in a majority of species, which is consistent with the hypothesis that weather is linked directly to the proximate mechanism driving seed production and that masting in these species is likely to be sensitive to climate change. Based on the correlations between weather variables and acorn production, cluster analysis failed to generate any obvious groups of species corresponding to phylogeny or life-history. Discriminant function analyses, however, were able to identify the phylogenetic section to which the species belonged and, controlling for phylogeny, the length of time species required to mature acorns, whether they were evergreen or deciduous, and, to a lesser extent, the geographic region to which they are endemic. These results indicate that similar proximate mechanisms are driving acorn production in these species of oaks, that the environmental factors driving seed production in oaks are to some extent phylogenetically conserved, and that the shared mechanisms driving acorn production result in some degree of synchrony among coexisting species in a way that potentially enhances predator satiation, at least when they have acorns requiring the same length of time to mature.

Key words: acorn production; climate change; environmental drivers; leaf-habit; mast-seeding; Quercus.

INTRODUCTION

Masting (or mast-fruiting) is a population-level phenomenon relatively common among temperate trees, including many conifers and oaks (genus *Quercus*). At the ultimate level, masting is generally thought to be an adaptive behavior selected for by one or more "economies of scale" (Kelly 1994), such as predator satiation (Janzen 1971), greater pollination efficiency (Kelly and Sork 2002), or enhanced dispersal efficiency. These adaptive hypotheses are consistent with the observation that many masting species devote so much of their resources to reproduction during "mast" years that trees apparently require more than a year to recover (Sork et al. 1993, Koenig et al. 1994*b*), resulting in highly variable or, in the case of some horticultural fruit trees, alternate bearing (Monselise and Goldschmidt 1982, Smith and Samach 2013). Such observations constitute the main empirical basis for the assumption that stored resources play an important role in masting behavior.

Beyond resource dynamics, however, the proximate drivers of masting behavior remain more poorly understood (Crone and Rapp 2014). It has long been recognized that masting is frequently correlated with

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[9]E-mail: wdk4@cornell.edu

weather—either temperature, water availability, or a combination of both—often, but not always, during the spring, when flowers are being produced and fertilized, or summer, when acorns are developing (Koenig and Knops 2014, Pérez-Ramos et al. 2015). Only recently, however, has attention been focused on the mechanisms potentially linking weather and seed production, or on the implications of those mechanisms for issues such as how masting behavior may be affected by climate change (Kelly et al. 2013, Pearse et al. 2014).

There are several ways by which environmental factors may interact with plant resources to influence seed set and result in the variable, synchronized, seed production defining masting behavior. These include resource matching (Kelly 1994), resource switching (Norton and Kelly 1988), and various kinds of "veto" mechanisms that may limit resource use and seed production in some years but not in others. Prominent among mechanisms in this category is pollen limitation, driven functionally by the economy of scale benefits of pollen coupling or more proximally, by weather factors (the pollination Moran effect) (Pearse et al. 2016). Among the fundamental questions to be answered is the degree to which a similar set of environmental factors play a role in masting among species with similar (or different; Pérez-Ramos et al. 2015) growth forms, modes of seed maturation, geographic range, or evolutionary histories.

Here we address this question using data from 15 species of oaks that encompass a range of attributes, including leaf habit (deciduous or evergreen) and length of time needed for seed maturation (1 or 2 yr). The species represent most of the major intrageneric subgroups within the genus and are endemic to three geographic regions on two continents.

We address two main questions. First, are similar sets of environmental factors important to annual variability in seed production by these species, and if so, to what life-history or other characteristics are they related? The answer to this question has the potential to provide insight as to the proximate mechanisms driving masting behavior as well as the consequences of variable seed production. For example, if there are consistent differences between species depending on the length of time they require to mature acorns, this would support the hypothesis that the same general mechanism is involved in both sets of species, offset, perhaps, by a year lag in the species requiring 2 yr to mature acorns. If differences are concordant with geographic location, it would suggest that sympatric species have evolved similar mechanisms that differ according to the kinds of weather regimes to which they are subject and that, reacting similarly to weather, the species may facilitate predator satiation of acorn generalists at the community level. Alternatively, if response to weather differs among species within a site, this would suggest that environmental factors affecting endogenous processes within the species drive asynchronous seed production in a way that potentially facilitates species coexistence (Mohler 1990). If differences are related to leaf habit, it would suggest that the mechanism driving the relationship between weather and seed production is determined in part by the different abiotic requirements and resource use strategies of the two kinds of species. Finally, if differences are concordant with phylogeny, it would suggest that the cues being used by the trees to synchronize seed production are phylogenetically-conserved and that they have changed relatively little as species diverged and colonized different geographic regions.

The second question we address is whether the environmental variables that better correlate with annual acorn production by these species are standard weather variables, such as rainfall or temperature (Koenig et al. 1996, Schauber et al. 2002), or differences in conditions between years ("differential-cue" variables; Kelly et al. 2013). The answer to this has implications for the future effects of climate change on masting behavior. In particular, if differential-cue variables are driving masting behavior, this phenomenon is likely to be insensitive to climate change, whereas the effects of a changing climate on masting behavior being driven by standard weather variables may be considerable (Koenig et al. 2015).

Materials and Methods

Oak species

We compiled data on 15 species of oaks, including species from California (eight species), Minnesota (four species), and Spain (three species). The number of individuals within each population ranged from 12 to 86 (total of 570), whereas the number of years of data for each population ranged from 10 to 35 (total of 327 population-years) (Table 1). Only a single population of each species was included in the analysis with the exception of *Q. ilex*, for which two populations in southern Spain measured over non-overlapping years were combined into a single, 14-yr composite sample.

Species were categorized according to whether they required one ("1-yr") or two ("2-yr") years to mature acorns and their leaf habit (evergreen or deciduous). *Q. canariensis* was assumed to require 1 yr to mature acorns, but conclusions were not significantly altered if it was considered a 2-yr species, as hypothesized by Pérez-Ramos et al. (2015). We divided species into the clades recognized by Pearse and Hipp (2009); thus, the 15 species represented four clades, including sections *Quercus, Protobalanus, Lobatae*, and *Cerris* (Table 1).

Acorn production data

Within each population, acorn crop data for individual trees were estimated in one of three ways, depending on the study. Data for all 12 North American species were acquired by visual surveys involving two researchers counting as many acorns as possible in 15 s and combining their counts for an estimate of relative annual

TABLE 1. Species of oaks used in the analysis and their main characteristics (Suzuki and Shimodaira 2014).

Species	Section	Acorn type	Leaf type†	Location‡	Specific locality and years	*N* trees§	*N* years
Q. lobata	*Quercus*	1-yr	Decid	CA	Hastings Reservation, Monterey County, California, USA (1980–2014)	86	35
Q. douglasii	*Quercus*	1-yr	Decid	CA	Hastings Reservation, Monterey County, California, USA (1980–2014)	56	35
Q. engelmannii	*Quercus*	1-yr	Decid	CA	Santa Rosa Plateau, Riverside County, California, USA (1994–2014)	19	21
Q. garryana	*Quercus*	1-yr	Decid	CA	Trinity County, California, USA (2002–2014)	12	13
Q. macrocarpa	*Quercus*	1-yr	Decid	MN	Cedar Creek Reserve, Anoka County, Minnesota, USA (1995–2011)	58	17
Q. alba	*Quercus*	1-yr	Decid	MN	Cedar Creek Reserve, Anoka County, Minnesota, USA (1995–2011)	11	17
Q. canariensis	*Quercus*	1-yr	Decid	Spain	Aljibe Mountains, Straits of Gibraltar, southern Spain (2002–2011)	20 [3]	10
Q. suber	*Cerris*	1-yr	Ever	Spain	Aljibe Mountains, Straits of Gibraltar, southern Spain (2002–2011)	30 [6]	10
Q. ilex	*Cerris*	1-yr	Ever	Spain	Villanueva de Córdoba, Córdoba, southern Spain (2001–2006); San Bartolomé de la Torre, Huelva, SW Spain (2007–2014)	49 34	6 8
Q. chrysolepis	*Protobalanus*	2-yr	Ever	CA	Hastings Reservation, Monterey County, California, USA (1980–2014)	21	35
Q. agrifolia	*Lobatae*	1-yr	Ever	CA	Hastings Reservation, Monterey County, California, USA (1980–2014)	63	35
Q. wislizeni	*Lobatae*	2-yr	Ever	CA	Sierra Foothills Research and Extension Center, Yuba County, California (1999–2014)	12	16
Q. kelloggii	*Lobatae*	2-yr	Decid	CA	Hastings Reservation, Monterey County, California, USA (1980–2014)	21	35
Q. ellipsoidalis	*Lobatae*	2-yr	Decid	MN	Cedar Creek Reserve, Anoka County, Minnesota, USA (1995–2011)	59	17
Q. rubra	*Lobatae*	2-yr	Decid	MN	Cedar Creek Reserve, Anoka County, Minnesota, USA (1995–2011)	19	17

† "Decid" = deciduous; "Ever" = evergreen.
‡ "CA" = California, USA; MN = Minnesota, USA.
§ Number in brackets is the number of individual trees with complete data for all years when it differs from the total number of trees.

acorn production (Koenig et al. 1994*a*, *b*). Five of the California species (*Q. lobata, Q. douglasii, Q. chrysolepis, Q. agrifolia,* and *Q. kelloggii*) were from Hastings Reservation in central coastal California; the other three California species were from other sites around the state (Table 1; W. Koenig and J. Knops, *unpublished data*). The Minnesota species (*Q. macrocarpa, Q. alba, Q. ellipsoidalis*, and *Q. rubra*) were studied at Cedar Creek Ecosystem Science Reserve (Koenig and Knops 2014).

The Spanish *Q. suber* and *Q. canariensis* were studied in the Aljibe Mountains, southern Spain (Pérez-Ramos et al. 2015). Acorn production for these two species was estimated using four 0.5 m diameter seed traps placed under the crown of each tree; only mature acorns attaining complete seed size were used in the analyses. Finally, data for *Q. ilex* were combined from two studies in southern Spain. The first, from a study near Cardeña (Córdoba province) between 2001 and 2006, quantified total fresh mass of acorns m^{-2} of the orthogonal projection of the crown based on four 0.40 m diameter containers placed under the crown of each tree (M. Carbonero, *unpublished data*). The second, from a study near San Bartolomé de la Torre (Huelva province) between 2007 to 2014, involved visual surveys similar to those used for the North American sites (R. Alejano, *unpublished data*). Sites were ~200 km apart, well within the range of highly significant spatial synchrony observed in other *Quercus* species (Koenig and Knops 2013).

All values were ln-transformed (ln[x+1]) to reduce the correlation between the mean and the variance. In order to combine the two *Q. ilex* datasets, ln-transformed data from the two studies were independently standardized to a mean of 0 and a standard deviation of 1. The temporal dynamics of mean acorn crop values are graphed for all 15 species in Fig. 1.

Weather data

Weather data was obtained from nearby weather stations, or, in the case of the three species of California oaks studied at sites other than Hastings Reservation, from the PRISM dataset (Oregon State University, Corvallis,

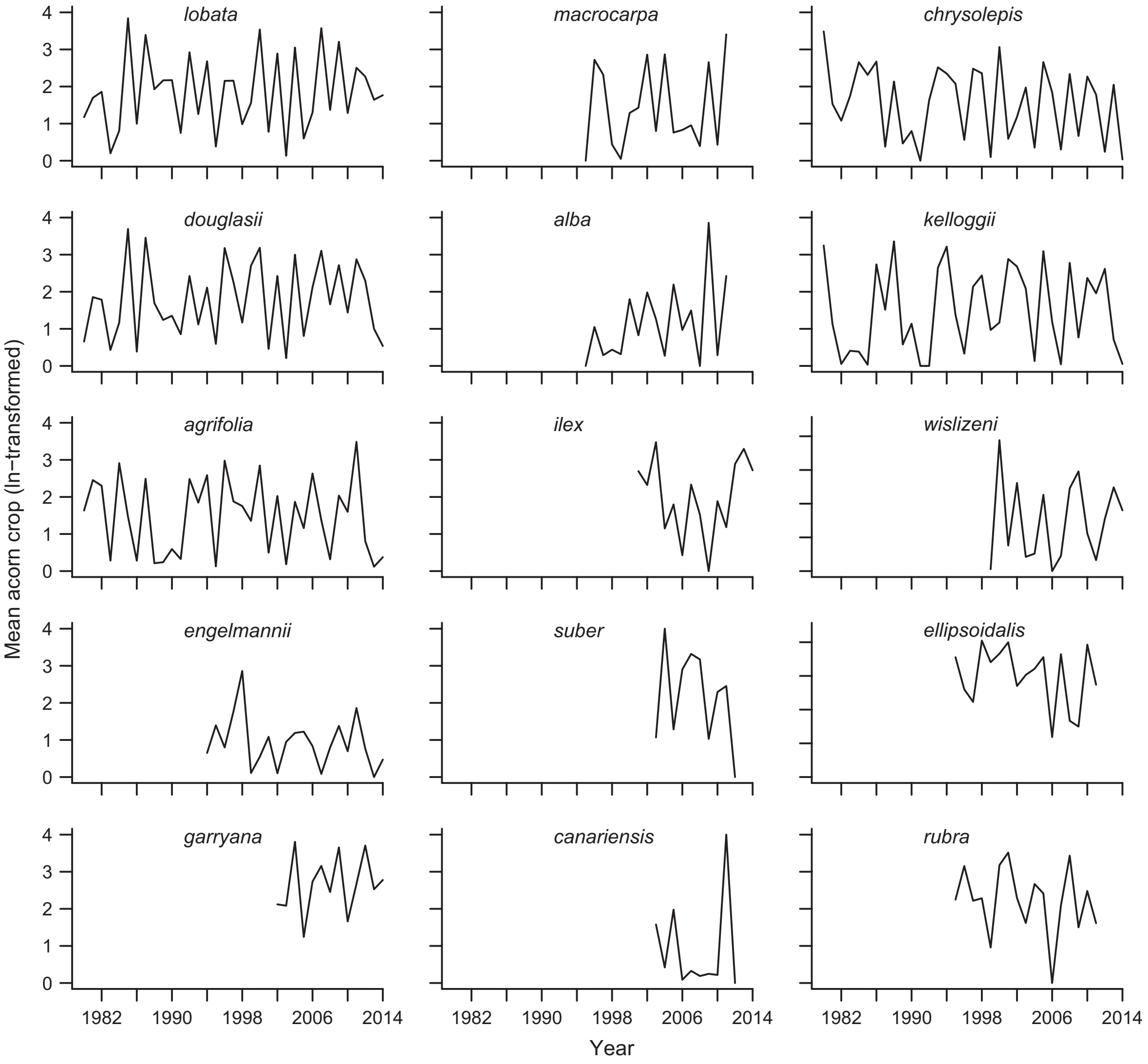

FIG. 1. Temporal dynamics of the (ln-transformed) mean acorn values data for all 15 species. Species whose acorns mature in 1 yr are in the first two columns; those requiring 2 yr to mature acorns are in the third column. Values for the Spanish species (*Q. ilex, Q. suber,* and *Q. canariensis*) were scaled between 0 and 4 to match the other species.

Oregon, USA; http://prism.oregonstate.edu). Based on prior analyses (Koenig et al. 1994*b*, Carevic et al. 2010, Carbonero and Fernández-Rebollo 2014, Koenig and Knops 2014, Pérez-Ramos et al. 2015), we restricted our analysis to eight weather variables that were most frequently found to be associated with acorn production, modifying the timing to accommodate phenological differences between the study sites (Table 2). All variables were calculated for the current year (year 0), the prior year (year −1), and 2 yr previously (year −2), since several of the species flower the year prior to acorn development and initiate bud formation 2 yr previously (Sork et al. 1993). In addition, we calculated the differences between the years for all variables (i.e., [year 0] - [year −1] and [year −1] - [year −2]); these latter are referred to as differential-cue (Kelly et al. 2013) or "Δ" variables. Summaries of the weather variables included in the analyses for each of the study sites are provided in Appendix S1: Table S1.

Analyses

In order to compare acorn production patterns across species, we first calculated standard masting metrics, including annual variability (measured as the coefficient of variation [CV]) both at the mean population ($\mathrm{CV_p}$) and mean across individuals ($\overline{\mathrm{CV}_i}$) level, the mean pairwise correlation between acorn production of individuals in the population (mean r_p), and the temporal autocorrelations between acorn production lagged both 1 (lag-1) and 2 (partial lag-2, controlling for lag-1 values) years, calculated using both mean annual acorn production of the population and the mean of the individual

TABLE 2. Weather variables used in the analyses.

Variable	Description
Annual mean temperature (XTEMP)	1 September–31 August
Mean spring temperature (XTSPR)	CA and Spain: March–May MN: April–May
Mean winter temperature (XTWIN)	CA and Spain: December–February MN: December–March
Mean maximum early spring temperature (XTMAXSPR)	CA: April MN and Spain: May
Mean maximum summer temperature (XTMAXSUM)	June–August
Annual precipitation (RAINANN)	1 September–31 August
Spring precipitation (RAINSPR)	CA and Spain: March–May MN: April–May
Summer precipitation (RAINSUM)	June–August

Notes: All variables were quantified for the current year *x*, the prior year *x*-1 (e.g., RAINANN1), two years previously (e.g., RAINANN2), for the difference between the current and prior year (year *x* - year *x*-1) (e.g., ΔRAINANN), and for the difference between the prior year and two years previously (year *x*-1 - year *x*-2) (e.g., ΔRAINANN1).

temporal autocorrelation values across all individuals in the population (Herrera 1998, Koenig et al. 2003). All analyses were performed in R 3.2.0 (R Development Core Team 2014).

Next we calculated correlations between population mean acorn production and each of the weather variables. In contrast to prior analyses, however, we followed the procedure recommended by Royama (1992; equ. 3.41) for the analysis of a density-independent perturbation such as weather on a stationary time series such as acorn production. Specifically, we calculated the correlation between the second-order differences in the variable of interest (acorn production) and the weather variable being tested. This procedure has been shown to detect the population-wide influence of a perturbation (in this case weather) more effectively than alternative coefficients, and takes into account the autoregressive effects of temporal autocorrelation in acorn production. An example of the calculations involved is provided in Appendix S1: Table S2. In the example, the Pearson correlation between the mean (ln-transformed) acorn crop and the weather variable (mean maximum spring temperature) is 0.30 ($P = 0.08$), whereas the correlation between second differences is 0.72 ($P < 0.001$) (Appendix S1: Fig. S1). Thus, this illustrates how this procedure can yield results very different from simple correlations.

In order to visualize similarities among the correlations between acorn production by the oak species, we performed a cluster analysis of the standard weather variables using Ward's minimum variance method in the *pvclust* procedure of package *pvclust* in R (Suzuki and Shimodaira 2014, R Development Core Team 2014). The analysis produced both a dendrogram and an estimate the strength of association of different groups using bootstrap procedures. We also tested for a phylogenetic signal in the weather variables with Pagel's lambda (Pagel 1999) calculated using the *phylosig* procedure in package *phytools* (Revell 2012).

We analyzed for relationships between acorn production and the weather variables identified as statistically significant ($P \leq 0.05$) in the aforementioned analyses for each of the 15 species using generalized least squares regression (*gls* in package *nlme*; Pinheiro 2015) with a lag-1 autoregressive structure, as suggested by Post et al. (2001), so as to control for temporal autocorrelation. We limited these analyses to variables initially identified as being statistically significant because the limited number of years of some datasets precluded including all variables simultaneously.

Analyses were conducted as follows: First, we performed two *gls* regressions, one using all standard weather variables identified as being statistically significant in the correlation analyses, and the other using all differential-cue variables identified as being statistically significant. When multiple variables were significantly associated with acorn production, we used model selection to identify the model with the strongest support based on ΔAIC values. We did this twice for each species, once including only the standard weather variables and once including only the differential-cue variables, with the caveat that we discarded models with uninformative parameters that were more complex versions of a competitive model with fewer parameters whose ΔAIC_c was < 2 (Arnold 2010).

Next we compared the AIC values of the top models in each category (those involving the standard and the differential-cue variables), again excluding models with uninformative parameters, using the *AICctab* procedure of package *bbmle* (Bolker 2012), and present the ΔAIC_c values of the top models and their model weights. These analyses thus test the hypothesis that differential-cue variables are better predictors of seed production than standard weather variables (Kelly et al. 2013).

In order to determine whether similar suites of weather variables were important for acorn production of oak species sharing life-history characteristics, we first conducted discriminant function analyses in which we identified the environmental variables whose correlation with acorn production best discriminated among the species' phylogenetic section. Explanatory environmental variables were divided into those related to the current year (year 0 variables), the prior year (year −1 variables), and 2 yr previously (year −2 variables), along with the two sets of differential-cue variables. A priori expectations were set at the known proportion of species in each category.

TABLE 3. Masting metrics for the 15 *Quercus* species analyzed.

					Lag-1 autocorrelation		Lag-2 partial autocorrelation	
Species	Location†	CV_p	$\overline{CV}_i$	Mean r_p	Population	Individual mean	Population	Individual mean
Q. lobata	CA	55.0	103.2	0.49	−0.53	−0.25	−0.01	0.03
Q. douglasii	CA	56.9	113.0	0.50	−0.39	−0.20	−0.02	0.01
Q. engelmannii	CA	73.5	153.8	0.33	0.01	−0.08	−0.24	−0.16
Q. garryana	CA	29.4	59.6	0.29	−0.48	−0.20	−0.41	−0.13
Q. macrocarpa	MN	79.4	122.3	0.48	−0.30	−0.16	−0.01	−0.03
Q. alba	MN	91.5	137.8	0.35	−0.44	−0.30	0.30	0.17
Q. canariensis	Spain	140.1	148.9	0.55	−0.18	−0.15	−0.01	−0.13
Q. suber	Spain	42.0	82.4	0.13	−0.54	−0.06	−0.22	−0.14
Q. ilex	Spain	25.7	49.8	0.33	0.13	−0.10	0.19	−0.07
Q. chrysolepis	CA	63.5	111.7	0.44	−0.26	−0.19	0.01	−0.02
Q. agrifolia	CA	69.1	124.5	0.49	−0.19	−0.12	0.06	0.02
Q. wislizeni	CA	80.4	123.4	0.68	−0.28	−0.27	−0.24	−0.21
Q. kelloggii	CA	77.2	118.6	0.57	0.01	0.02	−0.17	−0.15
Q. ellipsoidalis	MN	30.1	50.0	0.36	−0.17	−0.01	−0.01	−0.09
Q. rubra	MN	40.8	70.4	0.60	−0.13	−0.04	−0.42	−0.32

†CA = California, USA; MN = Minnesota, USA.

We then tested for the variables whose correlation with acorn production were significantly able to predict acorn type (1-yr vs. 2-yr species), leaf habit (deciduous vs. evergreen), and geographic region (Mediterranean vs. Minnesota and California vs. Spain). These analyses were performed using phylogenetic least-squares analyses (the *pgls* procedure in package *caper*; Orme et al. 2013), the phylogeny of Pearse and Hipp (2009), and dividing correlations between acorn production and the environmental variables into the five categories detailed above. The phylogeny is based on 1230 AFLP markers using a Bayesian two-state model and is broadly concordant with the most recent *Quercus* phylogeny using RAd-tag markers (Hipp et al. 2014). Taxa used here but not in the original work were grafted onto the phylogeny using the criteria described in Pearse and Hipp (2014). To investigate the effects of phylogenetic uncertainty, three alternative phylogenies were also analyzed. These assumed (1) a different placement of the old world oaks, since this node had little support; (2) that the relationships among closely related oaks was unknown, and thus that all oaks within a section were placed on polytomies; and (3) the same as the prior phylogeny, but also assuming that all branch lengths on the tree were the same.

We conducted rounds of model selection to identify the variables within the best-supported model (lowest ΔAIC) that discriminated among species of the different groups and report the significant variables, the direction of their effects, and the adjusted R^2 and *P*-value of the best-supported model. Thus, these analyses identified the environmental variables whose relationship with acorn production did the best job of discriminating among different life-history features of the species while controlling for phylogenetic effects.

RESULTS

Mean annual acorn production of each of the 15 species is summarized in Fig. 1. Masting metrics varied considerably; relative population variability (CV_p) ranged from 25.7 (*Q ilex*) – 140.1% (*Q. canariensis*), mean relative individual variability ($\overline{CV}_i$) ranged from 49.8 (*Q. ilex*) to 153.8% (*Q. engelmannii*), and mean pairwise correlation (r_p) ranged from 0.13 (*Q. suber*) to 0.68 (*Q. wislizeni*) (Table 3). Temporal autocorrelations of acorn production were primarily negative, with a mean (± standard error) across all 15 populations of -0.25 ± 0.05 and an individual tree mean (again averaged across the 15 species) of -0.14 ± 0.02. Lag-2 partial autocorrelations were also generally negative, but less so, with a population mean of -0.08 ± 0.05 and an individual tree mean of -0.08 ± 0.03.

Correlations of acorn production with weather factors using second differences are summarized for the standard unlagged and lagged weather variables in Appendix S1: Tables S3–S5 and for the differential-cue variables in Appendix S1: Tables S6–S7. All variables were significant for at least one species with the exception of the lag-2 mean annual temperature.

Results from the cluster dendrogram arranging the species according to their correlations with the weather variables indicated two main groups of species approximately equal in size (Fig. 2). The groups did not correspond to any obvious life-history character, however. The first consisted of four of the California species (three deciduous species in section *Quercus* and one evergreen *Lobatae*), two Minnesotan *Lobatea* species (both deciduous), and the Spanish *Q. canariensis* (section

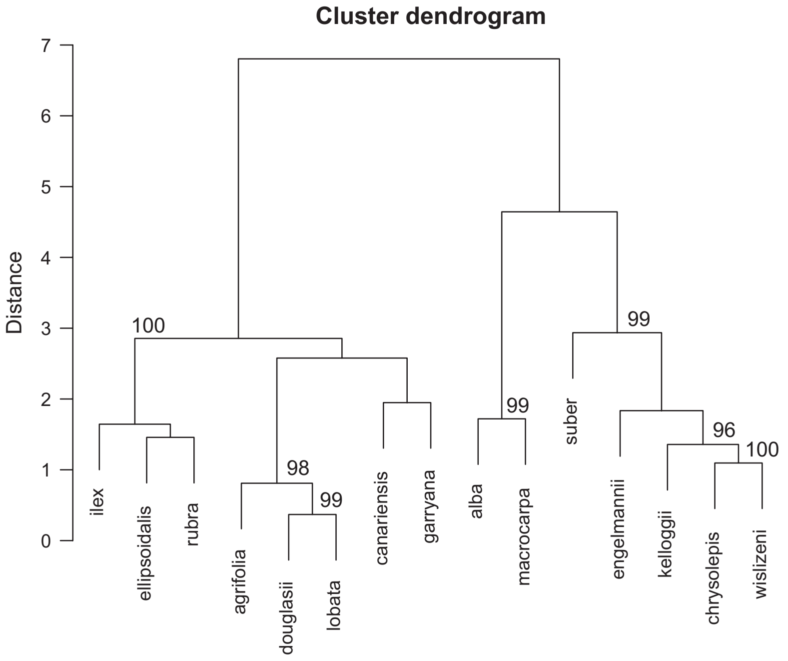

FIG. 2. A cluster dendrogram of the 15 species of oaks based on the correlations between acorn production and the weather variables (Table 2; correlations summarized in Appendix S1: Tables S3–S7). Clustering performed using Ward's minimum variance method; *P*-values, estimated by bootstrapping, are listed where statistically significant. Clusters with high *P*-values are strongly supported by the data.

Quercus, deciduous) and *Q. ilex* (section *Cerris*, evergreen). These were further subdivided into several smaller groups. The second main group consisted of the other four California species (one in section *Quercus* and three in *Lobatae*; two deciduous and two evergeen), the two Minnesotan *Quercus* species (both deciduous), and the Spanish *Q. suber* (section *Cerris*, evergreen).

Of the 40 environmental variables tested for a phylogenetic signal using Pagel's lambda (Appendix S1: Table S8), 10 yielded non-trivial lambda values (>0.01) and only one—mean winter temperature—was statistically significant ($P = 0.04$), a result that can reasonably be attributed to chance. Thus, we conclude that there is no strong phylogenetic signal in any of the environmental variables used in the analyses.

Results of the generalized least-squares regressions comparing the standard and differential-cue (Δ) weather variables whose correlations with acorn production were identified as statistically significant in the prior analyses are summarized in Table 4. None of the weather variables correlated significantly with acorn production by *Q. rubra.* Of the remaining species, models using standard weather variables outperformed Δ models in eight of 14 species (57%); in two additional species, the models using standard weather variables received competitive support ($\Delta AIC_c < 2$) even though the Δ model outperformed them. In contrast, the Δ models received greater support in six (43%) cases and had competitive support in another two. Thus, of the 14 species for which we identified weather variables correlating with acorn production, models using standard weather variables received competitive support in 10 (71%), whereas the best Δ model received competitive support in eight (57%).

The discriminant function analyses using the correlations between acorn production and the environmental variables with each of the species were in general successful at classifying the species by section, the only exception being the misclassification of *Q. agrifolia* in the analyses using the year −2 variables and the lag-1 Δ variables (Table 5). The variables loading most heavily varied among the analyses, but were the correlations with mean winter temperature and mean annual temperature among the year 0 variables; mean winter, spring, and maximum spring temperature among the year −1 variables; and mean maximum summer and summer rainfall among the year −2 variables.

The phylogenetic least-squares analyses identifying the environmental variables whose correlation with acorn production significantly discriminated species based on acorn type, leaf habit, and geography are summarized in Table 6. Distinguishing the acorn type of the species was highly successful ($P < 0.001$) using each of the five sets of variables, with the most important factors being mean maximum spring temperature, mean maximum summer temperature, and mean winter temperature. Distinguishing leaf habit was less dramatic statistically but still successfully achieved by each of the five sets of variables, with the best success being with the year 0 variables and the most significant factors being mean annual temperature and summer rainfall. Distinguishing the

Table 4. Results of the generalized least squares regressions comparing the models with the most support using weather variables from year 0, year −1, and year −2 vs. the Δ variables (year 0 – year −1 and year −1 – year −2).

	Model with the most support ($\Delta AIC_c = 0$)			Best-supported model in the other category			
Species	df	Model weight	Variables	ΔAIC_c	df	Model weight	Variables
Q. lobata	5	0.65	XTMAXSPR XTMAXSPR1	1.3	4	0.35	ΔXTMAXSPR
Q. douglasii	4	0.80	ΔXTMAXSPR	2.8	5	0.20	XTMAXSPR XTMAXSPR1
Q. engelmannii	4	0.94	RAINANN	5.1	4	0.06	ΔRAINANN
Q. garryana	5	0.92	ΔXTEMP ΔXTEMP1	4.9	5	0.08	XTMAXSPR XTEMP1
Q. macrocarpa	5	0.96	RAINANN2 RAINSUM2	6.5	5	0.04	ΔRAINANN1 ΔRAINSUM1
Q. alba	4	0.99	RAINANN2	14.3	4	<0.001	ΔRAINANN1
Q. canariensis	5	0.98	RAINSUM RAINSPR1	8.2	4	0.02	ΔRAINSPR1
Q. suber	4	0.53	ΔXTMAXSPR	0.3	4	0.47	XTMAXSPR
Q. ilex	4	0.64	ΔXTEMP	1.2	4	0.36	XTSPR2
Q. chrysolepis	5	1.00	RAINANN RAINANN2	22.9	4	<0.001	ΔRAINSPR
Q. agrifolia	4	0.98	RAINANN1	8.1	4	0.02	ΔXTMAXSPR
Q. wislizeni	5	0.88	ΔXTMAXSPR1 ΔRAINSPR1	4.0	5	0.12	RAINSPR1 RAINANN2
Q. kelloggii	4	0.8	ΔXTMAXSPR	2.8	5	0.20	XTMAXSPR XTMAXSPR1
Q. ellipsoidalis	4	0.72	XTMAXSUM1	1.9	4	0.28	ΔXTMAXSUM1

Notes: No weather variables were significant for *Q. rubra*. Models containing uninformative parameters and null models were discarded (Arnold 2010). See Table 2 for weather abbreviations.

Mediterranean species from the non-Mediterranean (Minnesota) species was the least successful overall, but was accomplished best using the year 0 variables ($P = 0.002$) with the most prominent factor being annual rainfall. Distinguishing the two sets of Mediterranean species (Californian vs. Spanish) was most significantly achieved using the year −2 variables ($P < 0.001$) with the most significant factors being mean maximum summer temperature and summer rainfall.

Results using the three alternative phylogenies differed in various, usually minor, ways, but conclusions remained unchanged. Results based on the phylogeny that assumed the least and differed the most from the phylogeny of Pearse and Hipp (2009) used here (alternative phylogeny #3, in which the relationships among closely related oaks was considered unknown and all branch lengths on the tree were assumed to be the same) are summarized in Appendix S1: Table S9.

Discussion

Seed production in oaks and other tree taxa is often correlated with temperature, water availability, or both. The mechanisms linking these environmental variables to seed production by the plants is not obvious, however. One hypothesis, proposed for *Q. ilex* by García-Mozo et al. (2007), is that rainfall during flowering washes pollen out of the atmosphere, thereby reducing subsequent acorn production. A second hypothesis, proposed by Koenig et al. (2015) for *Q. lobata*, is that annual differences in the synchrony of flowering within the population, driven by local variation in early spring temperature, determines pollen availability along with flowering synchrony and thus fertilization success in a way that drives masting behavior (the "phenological synchrony" hypothesis). There is currently little evidence, however, that either of these hypotheses are widely applicable to other taxa. Indeed, prior analyses have often identified very different environmental factors correlating with acorn production in other species (Sork et al. 1993, García-Mozo et al. 2007, Carevic et al. 2010, Pérez-Ramos et al. 2010, Koenig and Knops 2014), and there is even controversy as to whether such correlations reflect an underlying mechanism driving masting or are merely cues with no direct functional relationship to seed production (Kelly et al. 2013, Pearse et al. 2014).

In support of the existence of a general mechanism driving masting behavior in oaks, a recent meta-analysis by Pérez-Ramos et al. (2015) found considerable uniformity among Mediterranean oak species, a large fraction of which were sensitive to water resources and/or air temperature in the spring and summer, critical periods for flowering and fruit maturation. Further analyses by these authors focused on differences between the coexisting deciduous *Q. canariensis* and evergreen *Q. suber*, but failed to detect consistent differences in a meta-analysis between

TABLE 5. Classification of species into phylogenetic section by discriminant function analysis.

	Year 0 variables	Year −1 variables	Year −2 variables	Δ variables (no lag)	Δ variables (lag 1)
Percent correctly classified	100	100	93	100	93
Species misclassified	—	—	*Q. agrifolia*	—	*Q. agrifolia*
Percent of trace	87.1; 10.1	63.4; 33.2	59.7; 35.0	62.3; 35.4	48.5; 33.2
Coefficients of linear discrimination (LD1; LD2)					
XTEMP	−11.1; 3.7	5.6; 3.4	3.1; 0.5	−8.9; 12.3	−10.7; 3.7
XTSPR	4.6; 1.3	−8.8; −4.7	−5.1; −1.2	8.4; −24.7	16.9; −7.0
XTWIN	−17.3; −4.9	8.5; −8.3	2.7; −2.8	−11.2; −18.7	0.8; −2.5
XTMAXSPR	−2.6; −3.5	7.0; −2.3	1.9; −0.6	−4.9; 3.6	−5.9; 1.6
XTMAXSUM	0.5; −2.1	5.3; −8.2	6.5; −4.8	−3.8; −7.8	4.2; −2.3
RAINANN	0.4; −5.5	−1.8; −0.1	−0.7; 1.4	4.1; −2.6	−1.9; 1.6
RAINSPR	−0.9; 4.7	1.6; 1.6	−5.3; −2.1	−3.6; 4.2	1.7; −3.7
RAINSUM	6.5; −1.6	−6.4; −8.0	8.0; −2.9	6.3; −10.1	16.4; −3.0

Notes: Analyses are divided according whether the independent variables included are from year 0, year −1, year −2, or differences between years (the Δ variables). Variables were used to classify species into four sections: *Quercus, Cerris, Protobalanus,* and *Lobatae*. See Table 2 for weather abbreviations.

deciduous and evergreen species in the overall effect of water resources and temperature on mast seeding.

Here we addressed these issues by investigating the environmental factors correlating with acorn production in 15 species of oaks across two continents and asking whether there are consistent differences among species in terms of those correlations that are concordant with their life-history. We identified significant environmental variables for all but one of the species, and although both standard and differential-cue variables (the latter calculated by subtracting the value of the variable in year *x*-1 from the value in year *x*) were generally successful at predicting acorn production, standard variables outperformed differential-cue variables in a small majority (57%) of cases, whereas differential-cue variables performed markedly better than standard variables (i.e., ΔAIC of the best-supported model using standard weather variables >2) in only four of 14 (29%) species. Thus, although differential-cue variables performed fairly well, our results do not support the hypothesis that they outperform standard environmental variables that are more directly associated with functional mechanisms potentially driving masting behavior in these species of oaks, a conclusion reached previously for *Q. lobata* (Pearse et al. 2014, Pesendorfer et al. 2016).

In order to analyze the relationships between acorn production and weather, we first conducted a cluster analysis of the 15 species. Results revealed no clear correspondence with any of the life-history features of interest, nor did we detect a strong phylogenetic signal in any of the environmental variables examined. We achieved greater success identifying the weather variables for which relationships with acorn production most clearly separated groups of species in discriminant function analyses taking advantage of the a priori knowledge of phylogeny and life history. Analyses using each of the five sets of variables (weather variables in year 0, year −1, year −2, and the two sets of differential-cue variables) were all able to successfully classify all but one species into phylogenetic sections. The exception was *Q. agrifolia* (using the year −2 and the lag-1 differential-cue variables), which was classified in these cases as a *Quercus* [white oak] species rather than a *Lobatae* [red oak]—an understandable error given that this species, unlike most other red oak species, has acorns that mature in 1 yr. Explanatory variables that loaded most heavily in these analyses were the correlations of acorn production with winter and spring temperatures in year 0 and year −1 and summer conditions in year −2.

Analyses controlling for phylogeny were generally successful in identifying explanatory variables that discriminated species based on acorn type, leaf habit, and, to a lesser extent, geography. Identifying acorn type—whether acorns mature in one or two years—was highly successful ($P < 0.001$) using each of the five sets of variables, the most significant factors being correlations between acorn production and mean maximum spring and summer temperatures among the year 0 variables and mean maximum summer and mean winter temperatures among the year −1 and year −2 variables. These correspond well to key periods in acorn production, including acorn maturation (summer of year 0 for all species), anthesis and pollination (spring of year 0 for 1-year species; spring of year −1 for 2-year species), and flower bud initiation (summer of year −1 for 1-year species, summer of year −2 for 2-year species) (Sork et al. 1993). The only variable whose significance is not apparent is that of mean winter temperature, although one possibility is that winter conditions play a critical part in determining phenological synchrony the next spring, a potentially important proximate factor driving masting in oaks (Koenig et al. 2015).

Correlations with the weather variables also discriminated whether species were evergreen or deciduous,

TABLE 6. Phylogenetic least-squares analysis contrasting acorn type, leaf habit, and locality (Mediterranean species [Spanish plus Californian] vs. Minnesotan species; Californian species vs. Spanish species) using the different sets of environmental variables.

	Significant variables in best supported model	Adjusted R^2	F-value (df)	P-value
Acorn type (− = value larger for 1-yr species; + = value larger for 2-yr species)				
Year 0 variables	XTMAXSPR (−) XTMAXSUM(+)	0.70	17.5 (2, 12)	<0.001
Year −1 variables	XTWIN1 (−) XTMAXSUM1 (−)	0.83	34.9 (2,12)	<0.001
Year −2 variables	RAINSPR2 (+) XTMAXSUM2 (+) XTWIN2 (+)	0.85	27.6 (3,11)	<0.001
Δ variables (no lag)	ΔXTMAXSUM (+) ΔXTWIN (+)	0.78	26.0 (2,12)	<0.001
Δ variables (lag 1)	ΔXTMAXSUM1 (−) ΔXTWIN1 (−)	0.81	31.0 (2,12)	<0.001
Leaf habit (− = value larger for deciduous species; + = value larger for evergreen species)				
Year 0 variables	RAINSUM (+) XTEMP (+)	0.73	20.3 (2,12)	<0.001
Year −1 variables	RAINSUM1 (−) XTEMP1 (−)	0.53	8.8 (2,12)	0.004
Year −2 variables	RAINSUM2 (+)	0.26	5.9 (1,13)	0.03
Δ variables (no lag)	ΔRAINSUM (+) ΔXTEMP (+)	0.70	17.2 (2,12)	<0.001
Δ variables (lag 1)	ΔRAINSUM1 (−) ΔXTWIN1 (+)	0.53	9.0 (2,12)	0.004
Locality (− = value larger for Mediterranean species; + = value larger for Minnesota species)				
Year 0 variables	RAINANN (−) XTSPR (−)	0.51	8.2 (2,12)	0.006
Year −1 variables	RAINANN1 (+) XTWIN1 (−)	0.21	2.9 (2,12)	0.09
Year −2 variables	RAINSUM2 (−)	0.24	5.5 (1,13)	0.04
Δ variables (no lag)	ΔRAINANN (−) ΔXTMAXSPR (−)	0.42	6.1 (2,12)	0.01
Δ variables (lag 1)	ΔRAINANN1 (+) ΔXTWIN1 (−)	0.17	2.4 (2,12)	0.13
Locality (− = value larger for California species; + = value larger for Spanish species)				
Year 0 variables	RAINSUM (−)	0.23	4.0 (1,9)	0.08
Year −1 variables	RAINSUM1 (+)	0.15	2.7 (1,9)	0.13
Year −2 variables	RAINSPR2 (−) XTWIN2 (−) XTMAXSPR2 (+)	0.47	4.0 (3,7)	0.06
Δ variables (no lag)	ΔRAINSUM (−)	0.24	4.1 (1,9)	0.07
Δ variables (lag 1)	ΔRAINSUM1 (−)	0.01	1.1 (1,9)	0.32

Notes: Analyses are divided according to whether the variables included are from year 0, year −1, year −2, or differences between years (the Δ variables). Listed are the variables significant in the best-supported models along with the direction of the effect. See Table 2 for weather abbreviations.

although success of these analyses was greatest with the year 0 variables ($P < 0.001$) and statistical significance declined as the explanatory variables receded in time ($P = 0.004$ and $P = 0.03$ for the year −1 and year −2 variables, respectively). The most significant factors were mean annual temperature and summer rainfall, correlations between acorn production, and both variables being stronger for evergreen species. The significance of these relationships is unclear, although mean annual temperature plausibly reflects different abiotic requirements, with evergreen species being more dependent on favorable temperature conditions in order to devote more resources to reproduction (Moreira et al., unpublished data); whereas the importance of summer rainfall may reflect contrasting resource use strategies of deciduous species, whose growth is primarily during the summer, compared to evergreen species, whose growth is spread more evenly across the year.

We also tested for variables distinguishing the Mediterranean and non-Mediterranean (Minnesota) species, and those separating the California and Spanish Mediterranean species. Separation of the Mediterranean and non-Mediterranean species was marginal

($0.03 \leq P \leq 0.08$), with the exception of the analyses involving correlations with the year 0 variables ($P = 0.002$), among which annual rainfall was the most important. Separation of the California and Spanish Mediterranean species was also mostly marginally significant ($0.02 \leq P \leq 0.04$), with the exception of the year −2 variables ($P < 0.001$), among which mean maximum summer temperatures and summer rainfall—presumably indicative of water stress—were the most important, which is a distinction previously noted by Koenig et al. (2013) and emphasized as important to Spanish oak species by Pérez-Ramos et al. (2015). Thus, these results are concordant with prior studies of masting that have found correlations between seed set of disparate species of plants within similar geographic regions and weather (Schauber et al. 2002, Kelly et al. 2013).

The results presented here offer several insights into the proximate mechanisms driving masting behavior in oaks. First, the relatively strong negative lag-1 autocorrelations in seed production found for nearly all the species supports the hypothesis that resources are being devoted to fruit production that require more than 1 yr to replenish (Sork et al. 1993, Koenig et al. 1994*b*, Smith and Samach 2013, Crone and Rapp 2014, Pearse et al. 2014), as has been previously proposed by theoretical models (Isagi et al. 1997, Satake and Iwasa 2000, Rees et al. 2002, Satake and Iwasa 2002). Second, we identified weather correlates of acorn production for all but one of the 15 species, and thus our results generally support the hypothesis that weather acts as a proximate driver of masting in oaks (Pearse et al. 2014, Pérez-Ramos et al. 2015). We failed to find strong evidence for the hypothesis that these species use differential-cue variables to synchronize seed production (Kelly et al. 2013), since the latter variables did not outperform standard environmental variables in terms of their relationships to acorn production except in a minority of species. Thus, we predict that climate change is likely to affect masting behavior in oaks, the effects depending on exactly how key environmental variables affect acorn production (Koenig et al. 2015).

Additional insights are provided by our analyses investigating how acorn production of the 15 species differ in their response to the environmental variables. The ability to discriminate the phylogenetic section of the species based on the correlations between acorn production and weather indicates that the proximate mechanisms driving acorn production are to some extent phylogenetically conserved. This finding is not surprising given the general concordance between phylogeny and the length of time required for acorn maturation, with white oaks (section *Quercus*) and species in the section *Cerris* generally requiring one year to mature acorns and red oaks (*Lobatae*) and "intermediate" oaks (*Protobalanus*) requiring two years. Species such as *Q. agrifolia* (the coast live oak of California), a 1-yr red oak species, and *Q. suber* (the cork oak of the Mediterranean region), a mostly 1-yr species in which populations living in harsher climates contain individuals requiring two years to mature acorns (Pons and Pausas 2012), demonstrate that flexibility in these patterns exists, however.

Taking phylogeny into account, correlations between acorn production and weather, particularly spring and summer temperatures, consistently and significantly distinguished whether species required one or 2 yr to mature acorns. This finding is consistent with prior work indicating that acorn production is often synchronized among species with similar acorn-development phenology (Mohler 1990, Koenig et al. 1996), and supports the hypothesis that similar proximate mechanisms drive acorn production in this genus, with the key environmental factors being lagged by a year in species requiring the additional year to mature acorns. How exactly weather interacts with the physiology of the trees to affect acorn production patterns remains to be determined, although the greater importance of temperature compared to rainfall is more consistent with the hypothesis that the key factor involves phenology (Koenig et al. 2015) rather than affecting pollen "wash-out" due to precipitation (García-Mozo et al. 2007).

Our analyses were also able to distinguish between evergreen and deciduous species based on their correlations with environmental factors, most successfully when using current year variables (either standard variables or differential-cue variables involving the current year). Thus, in contrast to the meta-analysis of Pérez-Ramos et al. (2015), we are able to conclude that leaf habit does indeed matter, with acorn production by evergreen oak species exhibiting significantly greater correlations with current year summer rainfall and mean annual temperature than deciduous species.

We were also successful at distinguishing species growing in the three geographic regions after taking phylogeny into account, although differences were generally based on a small number of specific variables: annual rainfall and mean spring temperatures in the case of Mediterranean vs. non-Mediterranean species, and summer rainall and maximum summer temperatures—indicative of summer drought—in the case of California vs. Spanish species. These results suggest that species are potentially facilitating predator satiation of acorn generalists by producing acorn crops more or less synchronously when present in the same geographic location. This pattern is inevitably offset, however, by the coexistence of 1-yr and 2-yr species of oaks, which co-occur more frequently than expected by chance (Mohler 1990).

In summary, the environmental factors potentially driving acorn production by oaks are to some extent conserved phylogenetically and related to acorn maturation time, leaf habit, and, to a lesser extent, geography. This suggests that the mechanisms driving masting behavior may be qualitatively similar across many, if not all, species within this genus. Our results also support the hypothesis that weather plays an important mechanistic role in driving masting behavior in conjunction with resource dynamics. Future work is needed to broaden these results taxonomically and to better understand the mechanisms linking environmental variables and masting behavior. In addition, future long-term studies at the individual tree as opposed to the population level are likely to be important in detecting the plant traits and local abiotic factors that influence the magnitude and/or identity of the weather cues triggering masting behavior (Pérez-Ramos et al. 2014).

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