

# Testing the environmental prediction hypothesis for mast-seeding in California oaks

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**Abstract:** We analyzed 29 years of acorn production by five species of California oaks (genus *Quercus*) to test the hypothesis that trees produce large seed crops prior to wet years, conditions facilitating seedling germination and survival. The mean crop of three of the species correlated positively and nontrivially with the following year's rainfall, but none was statistically significant. Including the acorn crop 1 and 2 years earlier yielded several significant relationships between the acorn crop and future rainfall, but none held up when applied to a second, independent site. Across individuals, acorn production by 7% of trees correlated significantly with subsequent rainfall. Although these trees differed from other trees in several characters, differences were not sufficient to discriminate between trees that correlated significantly with subsequent rainfall from those that did not. We conclude that acorn production by California oaks does not forecast wet years and does not support the environmental prediction hypothesis.

**Résumé :** Nous avons analysé la production de glands durant 29 années chez cinq espèces de chêne de la Californie (genre *Quercus*) pour tester l'hypothèse selon laquelle les arbres produisent de grandes quantités de glands en prévision des années de forte pluviosité qui favorise la germination et la survie des semis. La production moyenne de trois des espèces était positivement et sans équivoque corrélée avec la pluviosité de l'année suivante mais aucune corrélation n'était statistiquement significative. Le fait d'inclure la production de glands durant les 2 années précédentes a produit plusieurs relations significatives entre la production de glands et la pluviosité future mais aucune de ces relations ne tenait lorsqu'elles étaient appliquées à un deuxième site indépendant. Sur une base individuelle, la production de glands de 7% des arbres était significativement corrélée avec la pluviosité subséquente. Bien que ces arbres fussent différents des autres sur la base de plusieurs caractères, ces différences n'étaient pas suffisantes pour distinguer les arbres dont la production de glands était significativement corrélée avec la pluviosité subséquente de ceux dont la production de glands ne l'était pas. Nous concluons que la production de glands des chênes de la Californie ne permet pas de prévoir les années de forte pluviosité et ne supporte donc pas l'hypothèse de la prévision environnementale.

[Traduit par la Rédaction]

## Introduction

Masting or mast-fruiting — the intermittent, synchronous production of seeds by a population of plants — is a well-documented phenomenon among a variety of plant taxa, although it appears to be particularly prevalent among wind-pollinated Northern Hemisphere trees (Kelly 1994; Koenig and Knops 2000; Kelly and Sork 2002). There are at least three reasons why this phenomenon is of ecological and evolutionary interest. First, masting can produce large resource pulses of great significance to terrestrial ecosystems, acting “bottom-up” to initiate cascades of ecosystem effects (Ostfeld and Keesing 2000). Second, the mechanisms producing reproductive synchronization, which may be evident over large geographic areas of thousands of square kilometres (Koenig and Knops 1998; Koenig et al. 1999a, 1999b), remain controversial, the two main hypotheses

being that spatial synchrony is driven by (i) environmental synchrony (the Moran effect: Ranta et al. 1997; Koenig 2002) and (ii) reproductive efficiencies related to the dependence of trees on the availability of outcrossed pollen, or pollen coupling (Satake and Iwasa 2000, 2002). Third, the selective factors favoring the evolution of masting behavior are unresolved. Currently, the two most commonly considered hypotheses are predator satiation (Janzen 1971) and enhanced pollination efficiency (Smith et al. 1990; Kelly et al. 2001). However, several other hypotheses have been proposed, most of which are rarely tested because they are thought to be applicable only to specific systems (Kelly 1994).

Here, we consider one of these frequently overlooked explanations for mast-fruiting, the environmental prediction hypothesis. This hypothesis, which proposes that weather cues are used to predict optimum future conditions for seed germination, is well established in some Australian monots where fire is a trigger for high seed production and si-

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**Table 1.** Pearson correlations between the acorn crop at Hastings Reservation and annual rainfall and the multivariate ENSO index.

Species	Subsequent rainfall			Multivariate ENSO index		
	<i>r</i>	<i>t</i>	<i>P</i>	<i>r</i>	<i>t</i>	<i>P</i>
<i>Quercus lobata</i>	0.24	1.27	0.21	-0.23	-1.24	0.23
<i>Quercus douglasii</i>	0.26	1.39	0.18	-0.26	-1.44	0.16
<i>Quercus chrysolepis</i>	0.01	0.03	0.97	0.15	0.82	0.42
<i>Quercus agrifolia</i>	0.35	1.93	0.06	-0.01	-0.05	0.97
<i>Quercus kelloggii</i>	-0.31	-1.68	0.10	0.08	0.45	0.66

Note: *N* = 28 years (1980–2007).

**Table 2.** Best models predicting rainfall for each species of oak at Hastings Reservation.

Species	Years (mean acorn crop) included in the model	Variable estimate ( $\pm$ SE)	Variable <i>P</i>	Overall <i>F</i> (df)	Overall <i>P</i>	Adjusted <i>R</i> <sup>2</sup>
<i>Quercus lobata</i>	Year <i>x</i> – 1	-0.190 $\pm$ 0.070	0.012	4.74 (2,24)	0.018	0.22
	Year <i>x</i> – 2	-0.196 $\pm$ 0.073	0.013			
<i>Quercus douglasii</i>	Year <i>x</i> – 1	-0.167 $\pm$ 0.069	0.023	6.20 (2,24)	0.007	0.29
	Year <i>x</i> – 2	-0.236 $\pm$ 0.069	0.002			
<i>Quercus chrysolepis</i>	Year <i>x</i> – 2	0.087 $\pm$ 0.075	0.26	1.35 (1,25)	0.26	0.01
<i>Quercus agrifolia</i>	Year <i>x</i>	0.146 $\pm$ 0.069	0.046	3.38 (2,24)	0.051	0.15
	Year <i>x</i> – 2	-0.129 $\pm$ 0.070	0.08			
<i>Quercus kelloggii</i>	Year <i>x</i>	-0.098 $\pm$ 0.058	0.10	2.84 (1,27)	0.10	0.06

Note: Presented are the best (based on bias-adjusted AIC<sub>c</sub> values) out of seven candidate models for each species that included all combinations of three independent variables: (i) the mean acorn crop in year *x*, (ii) the mean acorn crop in year *x* – 1, and (iii) the mean acorn crop in year *x* – 2. Thus, for *Q. lobata* and *Q. douglasii*, the best candidate models included the acorn crop in years *x* – 1 and *x* – 2, while for *Q. kelloggii*, it included only the acorn crop in year *x*.

multaneously can be used to predict conditions of enhanced nutrient availability and reduced competition favoring seedling establishment (Kelly 1994). The environmental prediction hypothesis has also been proposed to be potentially important in mesic forests where seed production following a period of water stress may take advantage of favorable understory conditions for regeneration (Williamson and Ickes 2002; Piovesan and Adams 2005). However, environmental cues such as rainfall could potentially play a similarly beneficial role, especially in cases where recruitment is limited by drought or interspecific competition.

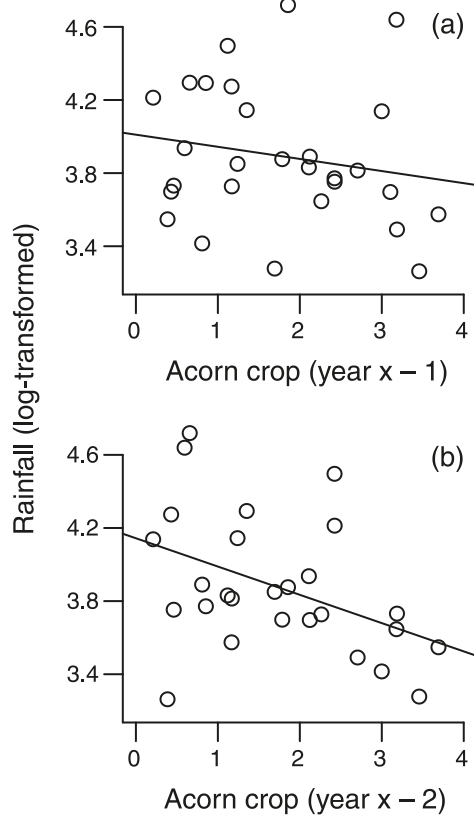
One system where these conditions are met is that of California oak woodlands where several common tree species, including the widespread valley oak (*Quercus lobata* Née) and blue oak (*Quercus douglasii* Hook. & Arn.), appear to have experienced low recruitment throughout much of their range for the past century or longer (Tyler et al. 2006). Although several factors most likely contribute to low recruitment (Tyler et al. 2008), water availability, primarily determined by winter rainfall, is highly variable in the Mediterranean climate of this region and a key limiting factor is clearly water availability affecting subsequent emergence and survival of seedlings (Welker and Menke 1990; Swiecki et al. 1997; Tyler et al. 2002), the latter of which is mediated in part by competition with annual plants (Gordon et al. 1989; Momen et al. 1994).

As a result of the advantages sprouts gain by having access to more water, there would be a considerable selective advantage for trees to produce large crops of acorns in advance of wet years. Although no mechanism by which this might be accomplished is currently known, there are reasons

to believe it is a possibility. The phenomenon most likely to provide an appropriate cue is that of the El Niño–Southern Oscillation (ENSO). First, ENSO events are known to have strong effects on masting behavior in other, mostly tropical systems (Curran et al. 1999; Wright et al. 1999; Wich and Van Schaik 2000; Schaubert et al. 2002). Second, ENSO events are highly correlated with rainfall in California (Schonher and Nicholson 1989; Mo and Higgins 1998) and the western United States in general (Cayan et al. 1999). Third, cycles in ENSO variability have been detected that are 2–5 years in length (Rasmusson et al. 1990; Tomita et al. 2004; Lau and Yang 2006), a temporal scale that approximates the (variable) length of masting cycles observed in California oaks (Koenig et al. 1994b). If oaks are able to track these cycles, even imperfectly, it would potentially allow them to produce large acorn crops in anticipation of wet years favorable for subsequent seedling survival, as postulated by the environmental prediction hypothesis.

Here, we examine this hypothesis using data on acorn production by five species of California oaks over a 29-year period at Hastings Reservation in Monterey County, California. First, we test whether the mean acorn crop of any of the species correlates positively with subsequent rainfall or whether trees produce larger crops prior to particularly wet El Niño years. We subject the significant relationships that emerge to a test by applying them to a second site where the acorn crop is not highly correlated with that at Hastings Reservation. As a second approach, we screened all trees surveyed at Hastings Reservation and examined the characteristics of those whose acorn production patterns were correlated with subsequent rainfall to see if any of the

**Fig. 1.** Mean acorn crop of *Quercus douglasii* at Hastings Reservation versus annual rainfall (cm) (a) 1 year later ( $r = -0.18$ ,  $df = 26$ ,  $P = 0.35$ ) and (b) 2 years later ( $r = -0.42$ ,  $df = 25$ ,  $P = 0.03$ ).



characters could potentially be used to identify such trees a priori.

The goal of these analyses is to subject the environmental prediction hypothesis to a test in a system where trees would gain a significant fitness advantage by forecasting future rainfall and where environmental conditions vary in a way that could potentially be anticipated by the trees. Such anticipatory effects have been detected on the part of seed predators of mast-fruiting conifers (Boutin et al. 2006), making it more cogent to explore parallel possibilities on the part of the trees themselves.

## Methods

The acorn production data that we analyzed consisted of visual acorn surveys at two sites. The primary site was Hastings Reservation, a field station located 42 km southeast of Monterey, California, run by the Museum of Vertebrate Zoology, University of California at Berkeley. Included in the analyses were data on 246 marked individuals including 87 *Q. lobata*, 56 *Q. douglasii*, 63 coast live oak (*Quercus agrifolia* Née), 21 canyon live oak (*Quercus chrysolepis* Liebm.), and 19 California black oak (*Quercus kelloggii* Newberry). The secondary site was the American Canyon campground near Pozo in San Luis Obispo County located 36 km inland from San Luis Obispo and approximately 160 km south of Hastings where we surveyed 75 trees including 25 *Q. lobata*, 25 *Q. douglasii*, and 25 *Q. agrifolia*.

Starting in 1980 (at Hastings) and 1989 (for Pozo) and continuing each year through 2008 (29 years total for Hastings and 20 years for Pozo), we visited each tree in September and conducted a visual survey of the acorn crop during which two observers, scanning different parts of the tree's canopy, counted as many acorns as they could in 15 s (Koenig et al. 1994a, 1994b). These counts were added to yield the number of acorns per 30 s, or N30. For statistical analyses, values were log-transformed ( $\ln[N30 + 1] = LN30$ ) so as to reduce the correlation between the mean and the variance. The size of the acorn crop in year  $x$  was estimated as the mean of the LN30 counts for all individuals surveyed of that species in year  $x$ .

For Hastings, rainfall was obtained from reservation headquarters located within 3.2 km of all trees in the survey. For Pozo, rainfall was taken primarily from the US Forest Service Station located 8 km west of the site. However, data from several years were missing and when this was the case, we used data from Goodwin Ranch 36 km east-southeast of the site. (Data from both sites were missing for 1989–1990 and thus, this year was not included in the analyses.) Pozo was chosen as the secondary site because acorn production there is much less strongly correlated with the crop at Hastings Reservation than at other sites for which we have data. For example, the Pearson correlation between the mean acorn crop of *Q. douglasii* at Hastings and Pozo between 1989 and 2009 was  $r = 0.45$  ( $df = 19$ ,  $P = 0.04$ ) compared with  $r = 0.79$  ( $df = 19$ ,  $P < 0.001$ ) for the correlation between the mean acorn crop of the same species over the same 21 years at Hastings and Jasper Ridge Biological Station 130 km north of Hastings (unpublished data).

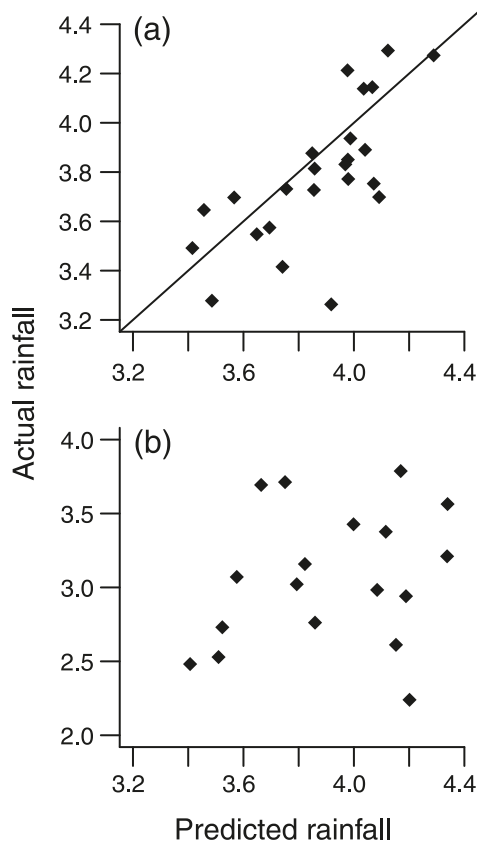
Rainfall in this region, which is subject to a Mediterranean climate, is highly seasonal, with 88% of precipitation falling between 1 October and 31 March. It is also highly variable: in the 70 years between 1939–1940 and 2008–2009, mean ( $\pm$ SD) annual rainfall at Hastings Reservation (measured from 1 July to 30 June) was  $52.7 \pm 19.7$  cm, with a high of 112.1 cm (in the El Niño winter of 1982–1983) and a low of 26.1 cm (in 1988–1989). Annual rainfall was not normally distributed (Shapiro–Wilk test,  $W = 0.904$ ,  $P < 0.001$ ), even after removing the 2 El Niño years when annual rainfall exceeded 1 m (Shapiro–Wilk test,  $W = 0.928$ ,  $P < 0.001$ ). However, log-transformation achieved normality ( $W = 0.973$ ,  $P = 0.14$ ) and thus was used in all analyses. Since the acorn crop matures in September, annual rainfall was measured from 1 September to 31 August and the fiscal year  $x$  is considered to start on 1 September of year  $x$ .

To compare the acorn crop with ENSO events directly, we used the multivariate ENSO index of Wolter and Timlin (1993), combining monthly values from September to August of the fiscal year (Wolter 2010). Rainfall at Hastings was strongly correlated with the multivariate ENSO index ( $r = 0.56$ ,  $df = 28$ ,  $P = 0.001$ ).

Rainfall was also highly correlated between the two sites (considering the years 1990–1991 to 2008–2009, the correlation between the log-transformed annual rainfall at Hastings and Pozo was  $r = 0.88$ ,  $df = 17$ ,  $P < 0.001$ ). Such a strong correlation between sites 160 km apart is expected given the high spatial synchrony in annual rainfall found globally (Koenig 2002).

**Table 3.** Results of the three significant (and near-significant) models summarized in Table 2 applied to the Pozo site.

Species	Years (mean acorn crop) included in the model	Variable estimate ( $\pm$ SE)	Variable $P$	Overall $F$ (df)	Overall $P$	Adjusted $R^2$
<i>Quercus lobata</i>	Year $x - 1$	$-0.086 \pm 0.104$	0.42	0.65 (2,15)	0.54	-0.04
	Year $x - 2$	$-0.103 \pm 0.098$	0.31			
<i>Quercus douglasii</i>	Year $x - 1$	$-0.028 \pm 0.103$	0.79	0.52 (2,15)	0.60	-0.06
	Year $x - 2$	$-0.103 \pm 0.101$	0.32			
<i>Quercus agrifolia</i>	Year $x$	$-0.020 \pm 0.118$	0.87	0.03 (2,15)	0.98	-0.13
	Year $x - 2$	$-0.023 \pm 0.124$	0.86			

**Fig. 2.** Predicted versus actual annual rainfall (cm) (log-transformed) where predicted values are based on the regression of the mean (log-transformed) acorn crop of *Quercus douglasii* 1 and 2 years earlier at (a) Hastings Reservation ( $r = 0.58$ ,  $df = 25$ ,  $P = 0.001$ ) and (b) Pozo ( $r = 0.24$ ,  $df = 16$ ,  $P = 0.35$ ).

To explore the relationship between the acorn crop and subsequent environmental conditions, we first performed Pearson correlations between the mean LN30 values for each species and both log-transformed rainfall and the multivariate ENSO index for the following year. We then conducted regression analyses to examine the possibility that the size of the acorn crop during any of the prior 3 years might predict winter rainfall, the rationale being that a seedling bank formed from an earlier acorn crop may be able to take advantage of rainfall in any of several subsequent seasons. For each species, we tested candidate models in which we attempted to predict rainfall in year  $x$  based on all combinations (singly, in pairs, and all three combined) of three variables: the acorn crop in year  $x$  (at the start of the fiscal year), the acorn crop in year  $x - 1$ , and the acorn crop in

year  $x - 2$ . Results were compared using bias-adjusted  $AIC_c$  values; thus, we compared seven models for each species. We assessed the success of the best-performing model for each species based on the overall  $P$  values and adjusted  $R^2$  values. We then applied the best model as determined from this procedure to the Pozo data to test whether the results were specific to the Hastings site or whether they were sufficiently general that they could successfully predict rainfall at this second site. All analyses were conducted in R 2.10.0 (R Development Core Team 2009), and results were considered to be statistically significant when  $P < 0.05$ .

For the individual tree analyses, we calculated Pearson correlations and their associated  $P$  values between the LN30 values for each of the 244 trees at Hastings Reservation and subsequent rainfall. We then compared those trees whose acorn production patterns correlated significantly with subsequent rainfall (the correlations for all such trees were  $>0$ , and thus, we refer to them as “responder” trees) with the remaining trees of the same species whose acorn production patterns did not correlate significantly with rainfall (“non-responder” trees) with Wilcoxon tests based on a series of variables including diameter at breast height, elevation, mean acorn production (averaged LN30 values between 1980 and 2009), xylem water potential (both daytime and predawn), and total N and P (in milligrams per litre of effluent) as determined from resin bags buried beneath each tree between October 1992 and April 1993 (Knops and Koenig 1997). The latter two soil variables were chosen because they, in conjunction with xylem water potential, explain a high proportion of the differences in net primary productivity among trees and thus provide a good index of relative site quality (J.M.H. Knops and W.D. Koenig, unpublished data). In total, we analyzed seven variables for each of the species for which we detected at least one responder tree.

For variables that differed significantly between responder and nonresponder trees, we tested whether the difference was sufficient to provide information that could unambiguously identify trees whose acorn production patterns correlated significantly with subsequent rainfall. This was done by choosing all trees of the given species whose value for the variable was greater than (less than) or equal to the mean value of the responder trees, depending on whether responder trees were larger (or smaller) than nonresponder trees. As an example, consider total N, which was significantly less among the seven responder *Q. lobata* than among the 80 nonresponder trees. The mean total N of the eight responder trees was  $12.95 \text{ mg}\cdot\text{L}^{-1}$  and there were 12 *Q. lobata* (out of 86) whose total N was less than or equal to this value. Consequently, we calculated the correlation between the mean LN30 values for these 12 trees and

**Table 4.** Testing for differences between trees whose acorn production patterns correlated significantly with subsequent rainfall versus those that did not.

Species	Variable	Mean value		W	P	N trees whose value was $\leq x_{\text{pos}}$ ( $P_{\text{all}}$ )	$r$ ( $P$ ) between the acorn crop of $P_{\text{all}}$ trees and rainfall
		Responder trees ( $x_{\text{pos}}$ )	Nonresponder trees				
<i>Quercus lobata</i>	Total N (mg-L effluent <sup>-1</sup> )	12.95 (7)	36.22 (80)	492	<0.001	12	0.31 (0.11)
<i>Quercus lobata</i>	Total P (mg-L effluent <sup>-1</sup> )	19.72 (7)	32.40 (80)	412	0.04	23	0.31 (0.10)
<i>Quercus douglasii</i>	Predawn xylem water potential (MPa)	-2.61 (2)	-1.49 (54)	102	0.04	4	0.28 (0.15)
<i>Quercus agrifolia</i>	Elevation (m)	628 (8)	546 (55)	115	0.03	8	0.32 (0.09)

**Note:** For each of the four characters that differed significantly between responder and nonresponder trees, the table summarizes the mean values and differences between the two groups, the number of trees whose value for that variable was less than or equal to the mean value of the responder trees (greater than or equal to the mean value for *Q. agrifolia* elevation), and the correlation between the acorn crop of trees meeting this latter criterion and subsequent rainfall.

subsequent rainfall to determine whether this subset of trees, identifiable by a cutoff on the basis of total N, could be used to accurately forecast future rainfall.

## Results

### Predicting rainfall from the acorn crop

None of the correlations between the mean acorn crop and either subsequent rainfall or the multivariate ENSO index was significant (Table 1). However, the correlations between subsequent rainfall and the mean acorn crops of three species were moderately positive and one (for *Q. agrifolia*) was close to being significant ( $P = 0.06$ ).

The results of the best candidate models analyses indicate that for both *Q. lobata* and *Q. douglasii*, rainfall was significantly correlated with the mean acorn crop 1 and 2 years earlier, with these variables explaining between 22% and 29% of the variance (Table 2). In both cases, however, the correlations with both independent variables were negative; that is, good acorn crops 1 and 2 years earlier correlated with relatively dry, rather than wet, years (Fig. 1). Best candidate models for none of the other three species successfully predicted subsequent rainfall, although that for *Q. agrifolia* was close to significant.

Although these analyses provide little support for the environmental prediction hypothesis, they suggest the possibility that knowledge of prior acorn crops might in some cases have significant predictive power regarding future rainfall, albeit not in the direction expected. We test this possibility in the next section.

### Testing the model

We tested the generality of the significant (and near-significant) results reported in Table 2 by applying the models to the Pozo data set. Results indicated that none of the models was successful at forecasting rainfall at this second site: no  $P$  value approached significance and adjusted  $R^2$  values were all negative, indicating that the models had no explanatory power (Table 3). A comparison of the best of these relationships (using the mean acorn crop of *Q. douglasii* 1 and 2 years earlier) with subsequent rainfall at Hastings Reservation and at Pozo is presented in Fig. 2.

### Predicting rainfall from individual trees

For this analysis, we first calculated correlations between the LN30 values and subsequent rainfall for each of the 246 trees in the survey. This yielded 17 trees (seven *Q. lobata*, two *Q. douglasii*, and eight *Q. agrifolia*) whose correlation with subsequent rainfall was statistically significant, a number not different from what would be expected by chance ( $\chi^2$  test with continuity correction = 0). The correlation coefficients for all 17 trees were positive and ranged  $0.37 \leq r \leq 0.55$ . We refer to these trees as “responder” trees.

The fact that the acorn crops of a small proportion of trees (6.9%) significantly correlated with subsequent rainfall is potentially useful only if those trees differ in some definable way from other trees whose acorn production patterns did not correlate with rainfall (the “nonresponder” trees). To address this possibility, we tested for differences between responder and nonresponder trees in seven characters including diameter at breast height, elevation, mean overall long-

term acorn production, xylem water potential (day and pre-dawn) measured during 1 year of the study, and two soil nutrient measures (N and P) determined from resin bags buried under each tree during one winter of the study. Of the 21 analyses ( $7 \times 3$  species), four were significant; that is, there were four variables (total N and total P for *Q. lobata*, pre-dawn xylem water potential for *Q. douglasii*, and elevation for *Q. agrifolia*) that differed significantly between responder and nonresponder trees (Table 4). For each of these variables, we calculated the correlation between rainfall and the mean acorn crop of all trees (of the appropriate species) whose value for the target variable was less than or equal to (greater than or equal to in the case of elevation) the mean value of the subset of responder trees.

For none of the four variables was the resulting correlation significant (Table 4). This indicates that despite the significant differences between responder and nonresponder trees in some variables, none defines a cutoff beyond which acorn production patterns of trees correlated significantly with subsequent rainfall. Put differently, this indicates that although there are detectable differences between responder and nonresponder trees, the differences are not enough to allow us to distinguish a group of trees whose acorn production pattern reliably correlates with subsequent rainfall.

## Discussion

Our results fail to support the environmental prediction hypothesis. We found no evidence that the mean acorn crop of any of five species of California oaks at Hastings Reservation correlated significantly with either the ENSO or subsequent rainfall, a highly variable environmental character known to influence emergence and survival of seedlings. For three of the species, a combination of prior acorn crops 0, 1, and 2 years earlier correlated significantly (or nearly so) with subsequent rainfall. However, a key test to determine whether these relationships have generality beyond this single study site is to apply them to a relatively independent site. When we did this, no significant relationship was found at a second location located 160 km away.

Although acorn production patterns of a small proportion of trees correlated significantly with subsequent rainfall and we detected significant differences between these trees and other trees for three of the species, differences were not sufficient to define a subset of trees whose acorn production patterns could be used to predict subsequent rainfall. Thus, although acorn production by some trees correlated with subsequent rainfall, the number of such trees matched the number expected by chance and we were unable to determine a character that would allow these trees to be identified a priori. Contrary to the environmental prediction hypothesis, California oaks do not produce large acorn crops in advance of conditions that would potentially facilitate their subsequent survival and fitness.

Prior analyses have found a strong correlation between prior environmental conditions and acorn production patterns of North American oaks, including several of the species considered here (Sork et al. 1993; Koenig et al. 1996). Thus, there is good evidence that trees respond to variable environmental factors. Whether they can use such factors to forecast future conditions would presumably depend on the

extent to which such conditions are cyclic and predictable. Given that short, multiyear cycles have been described for ENSO events (Rasmusson et al. 1990; Tomita et al. 2004; Lau and Yang 2006), the possibility that oaks might be able to use such cycles to their advantage in accord with the environmental prediction hypothesis is not out of the question. Clearly subtle cues are sometimes present that can be used by some populations to anticipate future conditions. For example, recent work has suggested that some seed predators are able to anticipate masting events, presumably by cueing on buds, flowers, or pollen cones, and adjusting their reproductive investment accordingly, thus increasing their population size in synchrony with the future resource pulse (Boutin et al. 2006). Although no comparable mechanism is known that could potentially allow trees to similarly adjust their reproductive investment to future, rather than past, conditions, this is not the same as knowing that no such mechanism could exist.

There is considerable popular evidence for a relationship between the acorn crop and subsequent winter weather, most prominently in the “Farmer’s Almanac” (Geiger and Duncan 2010). Our analyses fail to support the existence of any such relationship in this system. Given the various steps involved in acorn production, each of which may be influenced by environmental or other external factors, combined with the many species of oaks — there are over 60 species in North America alone — it is clearly possible that the acorn production patterns of one or more correlate with future environmental conditions. Indeed, given the large pool of potential correlations that can be made, it is likely that significant correlations will be found in any particular analysis. The challenge will be to find a relationship between the acorn crop and future environmental conditions that meets the criteria for strong ecological forecasting (Clark et al. 2001), that is, reducing uncertainty to a point where the relationship offers a useful amount of information for predicting results in other, independent systems. Until this is accomplished, we will have to conclude that acorn production does not anticipate future environmental conditions.

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