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Does nutrient scarcity lead to greater variability in seed production? The case of the California valley oak *Quercus lobata*

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Based on an interspecific comparison, Fernández-Martinez *et al.* (Fernández-Martinez *et al.* 2019 *Nat. Plants* **5**, 1222–1228 (doi:10.1038/s41477-019-0549-y)) found that masting is stronger in populations growing under conditions of nutrient scarcity, a relationship potentially providing a mechanistic link to resource-budget models of mast fruiting. Using comparisons among individual *Quercus lobata*, a common California masting oak species, we tested whether access to groundwater, foliar nitrogen (N) and foliar phosphorus (P) correlate with greater interannual acorn crop variability, increased synchrony of acorn production with other trees in the population and more negative lag-1 autocorrelations with acorn production the prior year—metrics indicative of masting-like behaviour. Our analyses failed to support the nutrient scarcity hypothesis. Three of the significant correlations between masting metrics and resources were in the opposite direction predicted by the hypothesis—trees with greater foliar N showed greater variability and synchrony in acorn production—while the other two (more water-stressed trees exhibited larger coefficient of variation (CV) in interannual acorn production) were apparently due to the inverse relationship between CV and mean overall productivity. More studies at different geographic and taxonomic scales and of other potentially important nutrients are needed to understand the relationship between masting and resources.

1. Introduction

Masting, or mast-seeding, refers to the synchronized and highly variable production of seeds by a population of plants [1–3]. Although masting behaviour is a well-described phenomenon, particularly among temperate and boreal tree species, it remains unclear exactly what drives either the variability in seed production or how trees can synchronize reproduction over what in some cases are subcontinental scales of >1000 kms [4,5].

The most successful models of mast-seeding are based on the idea that the accumulation of stored resources, commonly thought to be carbon or nitrogen, is central to driving the annual variability found in masting species [6–8]. In combination with an additional factor promoting synchrony—typically pollination efficiency—such ‘resource-budget’ models have been used to approximate and even predict the future seed production behaviour of masting species [8–13]. Yet, although resources are clearly required

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for masting to occur, there are few data testing the mechanisms by which resources modulate seed production [14–17].

Here, we examine a recently proposed relationship potentially providing insight into the relationship between resources and masting. Based on an interspecific comparison of 219 species, Fernández-Martinez *et al.* [1] found that masting behaviour was stronger in populations growing under conditions of nutrient scarcity, specifically low foliar nitrogen (N), low foliar phosphorus (P) and imbalanced N : P ratios. Although unlikely to be an ultimate factor selecting for masting behaviour [18], the correlation between nutrient scarcity and masting offers a potential mechanistic link to resource-budget models. It predicts that populations with access to lower or imbalanced nutrients will have a harder time acquiring the necessary resources for seed production. Such trees should consequently exhibit greater masting intensity expressed as high interannual variability, strong negative temporal autocorrelation and greater synchrony of seed production with other individuals in the population [1].

Differences among species potentially confound the interpretation of Fernández-Martinez *et al.*'s [1] results. Different species are likely to be limited by different nutrients, as indicated by the variable findings of studies investigating the role of carbon and nitrogen in seed production [8,19–22]. Thus, although the interspecific relationship reported by Fernández-Martinez *et al.* suggests that selection across species for masting behaviour may be positively associated with nutrient scarcity, whether such a relationship exists within a species is unknown and has not been previously tested. More importantly, only an intraspecific study investigating the relationship between nutrients and seed production can distinguish whether the effects of nutrients select for masting behaviour, as suggested by Fernández-Martinez *et al.* [1,23], or are an unavoidable constraint on masting behaviour, as argued by Kelly [18].

Here, we perform such an analysis, focusing on the valley oak *Quercus lobata*. Our goal is to better understand how variable seed production interacts with nutrient availability within a population, thereby providing insight into the mechanisms driving masting behaviour.

2. Methods

Quercus lobata is a widespread California endemic common in foothill regions north of Los Angeles [24]. It is a winter deciduous, a member of the section Quercus ('white oaks'), and a '1 year' species whose acorns mature in the autumn from flowers that were fertilized in the spring a few months earlier. The study site was Hastings Reservation, Monterey County, central coastal California, USA (36º23′ N, 121º33′ W). Trees used were part of a long-term study of reproduction and growth initiated in 1980. For the analyses performed here, 80 individuals examined each year between 1980 and 2024 (45 years) growing over a 900 ha area, ranging in elevation from 475 to 875 m, were used.

Estimation of the acorn crop of each tree was done using visual surveys conducted by two observers each autumn, 1980 through 2024 [25,26]. Surveys involved both observers counting as many acorns as they could in different parts of the tree for a timed period (15 s) using binoculars. Values were added and ln-transformed (ln(N30 + 1) = LN30), a common procedure with count data that reduces the dependence of the variance on the mean [27] and avoids overemphasizing the contributions of hyper seed producers [28]. All analyses conducted here are based on ln-transformed (LN30) values; the mean overall productivity of each tree (xLN30) was calculated as the mean of LN30 values over the 45 years of the study.

Masting is a population-level phenomenon [3] and is not directly applicable to individual plants. However, it involves phenomena that are measurable on individual trees, including annual variability and synchrony of seed production with other individuals. In addition, masting is closely associated with negative temporal autocorrelation, usually with a 1-year time lag (lag-1 autocorrelation (AR1)), believed to reflect the dependence of seed production on resources whose depletion requires a variable number of years to recover [2].

Our goal was to test the nutrient scarcity hypothesis among individuals of a single masting species using indices related to masting behaviour. The first index was the coefficient of variation (s.d./mean = coefficient of variation (CV)), the standard index of temporal variability. The standard CV, however, is overly sensitive to the proportion of zeros in the data, making alternatives desirable. Three such alternatives were calculated. The first is Kvålseth's CV (CV_k), a variance-stabilized modification of the standard CV [29]. CV_k in our dataset is highly correlated with the standard CV (Pearson correlation $r = 0.93$, $p < 0.0001$). Nonetheless, we present results using both to illustrate their differences and contribute to a potential consensus regarding their use. We sometimes refer to them together as 'the CVs.'

The second alternative to the standard CV, proportional variability (PV), is more robust to non-Gaussian behaviour [30]. The third, volatility, measures variation in frequency of seed production events, focusing on biologically significant long intervals between seed production [28]. All four variability indices are correlated with the mean, but in ways that potentially reveal biologically important differences [31,32].

Two additional indices of masting-like behaviour by individual trees calculated here were the AR1 value for each tree and synchrony (S) of tree i calculated as the mean pairwise Pearson correlation between acorn production by tree i and acorn production of all other trees in the population. As an index of how synchronized a tree is with other individuals, a reasonable assumption is that larger S values indicate enhanced masting-like behaviour. AR1 is an index of potential resource depletion, the assumption being that the extent to which stored resources are important to acorn production will be reflected in a stronger negative effect of year i's crop on crops in the subsequent year [1,12].

More intense masting behaviour is indicated by larger CV, CV_k, PV, volatility and S values, but more negative (i.e. decreased) AR1 values. Volatility was calculated using the *mastSpectralDensity* function in the R package *mastif* [33].

To test the nutrient limitation hypothesis, we used four measures of the resource status of individual trees. Following Fernández-Martinez *et al.* [1] and previous studies demonstrating the importance of the relative concentrations of foliar nutrients to plant reproduction [19,34,35], we tested foliar N, foliar P and the foliar N : P ratio. In addition, we tested access to groundwater, a key limiting factor for *Q. lobata* in this habitat [36].

Table 1. Summary of variables used in the analyses and their relationship, predicted by the nutrient scarcity hypothesis, with masting metrics. ACV = indices of acorn crop variability; *S* = pairwise synchrony of seed production with other trees in the population; AR1 = lag-1 autocorrelation.

variable	predicted relationship with			rationale
	acorn crop variability (ACV)	*S*	AR1	
predawn XWP	negative	negative	positive	more negative (more water stress) → increased ACV, more *S* and more negative AR1
foliar N	negative	negative	positive	fewer nutrients → increased ACV, more *S* and more negative AR1
foliar P	negative	negative	positive	fewer nutrients → increased ACV, more *S* and more negative AR1
foliar N : P ratio	positive	positive	negative	larger N : P ratio (less favourable conditions) → increased ACV, more *S* and more negative AR1

Access to groundwater was measured with xylem water potential (XWP) using the pressure chamber technique [37], measured at predawn, 20 September–5 October 1991 [38]. Repeated measurements in subsequent years indicated that XWP values for individual trees are concordant across years despite differences in water potential from year to year [39], thus indicating that the values used provide a good index of relative water availability across individual trees.

Foliar nitrogen (N*)* and foliar phosphorus (P) were measured from leaves collected on 7–8 July 1992 and again on 10–15 June 2024 on the outer canopy of each tree. Leaves collected in 1992 were analysed for total nitrogen and total phosphorus on a continuous flow autoanalyser using standard procedures [40]. Leaves collected in 2024 were analysed for total nitrogen by means of flash combustion [41] and for total phosphorus by nitric acid/hydrogen peroxide microwave digestion [42,43] at the University of California, Davis, Analytical Laboratory.

There were strong, highly significant correlations between both foliar N and foliar P sampled in 1992 and 2024 (foliar N: $r = 0.42$, $t = 4.08$, d.f. = 78, $p = 0.0001$; foliar P: $r = 0.57$, $t = 6.05$, d.f. = 78, $p < 0.0001$). There were also no significant differences in their means (Wilcoxon two-sample tests, foliar N: $W = 9$, $p = 0.89$; foliar P: $W = 6.5$, $p = 0.77$). Because the study spanned this timeframe, we used the mean of the two values in all analyses.

The nutrient limitation hypothesis predicts that trees with poorer access to nutrients should exhibit more intense masting characteristics. Thus, there should be a negative relationship between resources and both interannual variability and pairwise synchrony, but a positive relationship between resources and AR1 (table 1). How nutrients are predicted to vary with the N : P ratio is less clear, but following Fernández-Martinez *et al.* [1], we assumed that a higher N : P ratio is indicative of unfavourable conditions and nutrient scarcity, and thus predicted a positive relationship between the foliar N : P ratio and interannual variability and synchrony, and a negative relationship between the foliar N : P ratio and AR1.

We first calculated Pearson correlations between each of the five masting metrics and the four resource variables (XWP, foliar N, foliar P and the foliar N : P ratio). For the significant correlations revealed by the correlations, we conducted linear models of the resource variable on the masting metric with which the former was correlated, in which we included mean overall acorn productivity (xLN30) as a second explanatory variable. This was done to help distinguish effects due to the relationship of interest—nutrient limitation—from those that were more likely a consequence of a relationship between the masting metric and mean productivity. In the two cases where the relationship controlling for mean overall acorn productivity warranted visualization (CV and CV_k), we plotted the resource of interest (XWP) vs. the component + residuals of the CVs controlling for acorn productivity. The component + residuals, also known as partial residuals, illustrate the relationship between the variables of interest controlling for mean overall productivity of the trees and were based on the procedure *crPlots* in R package *car* [44].

Only the 80 trees that reproduced at least once, with complete acorn production data for all 45 years, were included in the analysis. Analyses were performed using R 4.4.2 [45].

3. Results

Pearson correlations between the masting metrics and nutrient variables yielded five significant relationships: a strong negative correlation between both CVs and predawn XWP, and positive correlations between foliar N and volatility, PV and *S* (table 2). The negative relationships between the CVs and predawn XWP were consistent with predictions of the nutrient limitation hypothesis: trees with greater (less negative) XWP values and greater access to groundwater exhibited smaller CVs (figure 1a,b*)*. In contrast, the three significant correlations between foliar N and masting metrics were in the opposite direction predicted by the nutrient limitation hypothesis: trees with more foliar N exhibited greater acorn crop variability and their acorn crops were more synchronized with other trees in the study area.

All five masting metrics yielding significant correlations with predawn XWP or foliar N were significantly related to mean overall acorn production of individual trees (xLN30; table 3). In linear regressions of the masting metrics on the resource values with which they were significantly correlated, in which xLN30 was included as an explanatory factor, only the effects of foliar N on PV remained significant, controlling for mean overall productivity (table 3). In particular, the significant inverse relationship

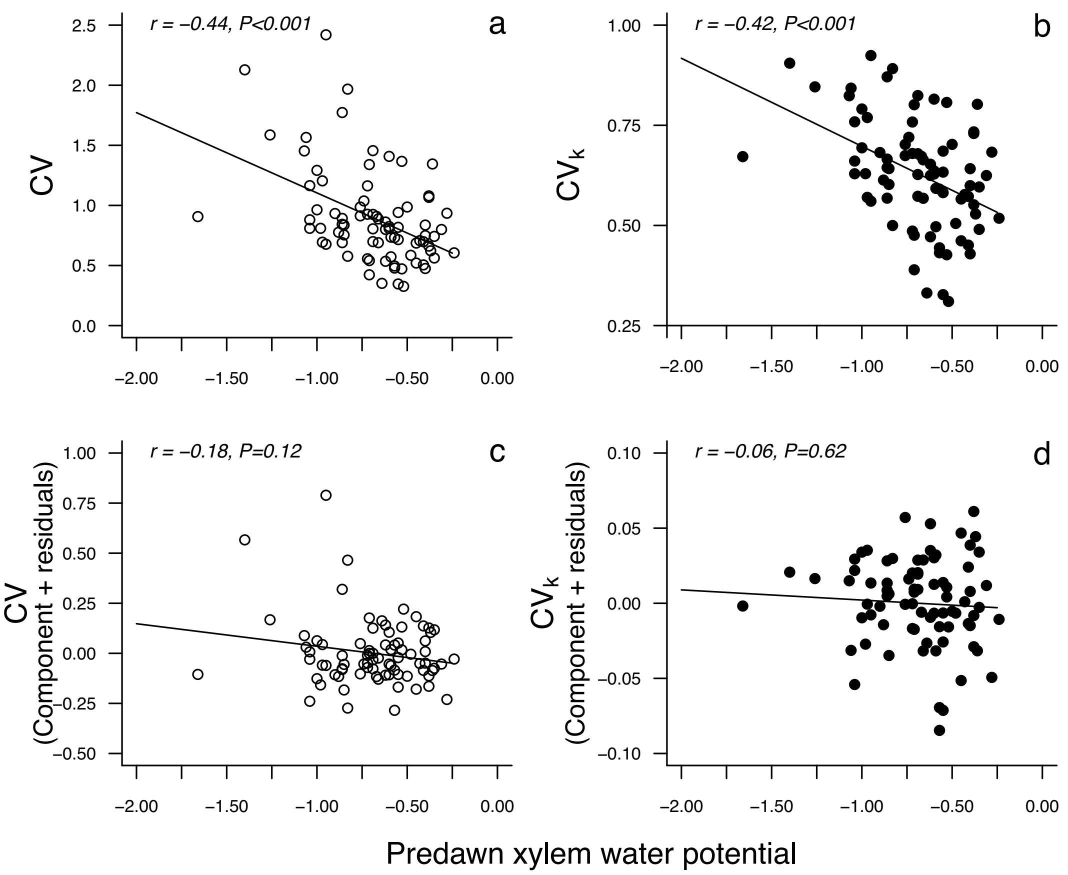

Figure 1. Scattergrams of predawn XWP versus (a) the (ln-transformed) standard CV; (b) Kvålseth's CV (CV_k); (c) the component + residuals of standard CV, thus removing the effect of mean overall acorn production; (d) the component + residuals of CV_k. Regression lines are plotted; Pearson correlation coefficients (*r*) and their *p*-values are listed.

Table 2. Pearson correlations for masting metrics versus predawn XWP, foliar N, foliar P and the foliar N : P ratio. Listed are the *r*-values (*p*-value). All d.f. = 78. Values significant at $p < 0.05$ are in bold.

masting metric	predawn XWP	foliar N	foliar P	N : P ratio
CV	**−0.444 (<0.001)**	−0.211 (0.06)	0.183 (0.10)	−0.098 (0.39)
CV_k	**−0.421 (<0.001)**	−0.099 (0.38)	0.094 (0.41)	−0.076 (0.50)
volatility	0.162 (0.15)	**0.226 (0.044)**	−0.169 (0.13)	0.112 (0.32)
PV	−0.068 (0.55)	**0.244 (0.029)**	−0.195 (0.08)	−0.020 (0.86)
S	0.152 (0.18)	**0.301 (0.007)**	−0.124 (0.27)	0.045 (0.69)
AR1	0.034 (0.76)	0.077 (0.50)	0.156 (0.17)	0.000 (1.00)

Table 3. Results (effect size ± standard error (*p*-value)) of multiple regressions for each of the five pairs of significantly correlated factors in table 2, in each case including mean acorn productivity as a second explanatory factor along with predawn XWP or foliar N. Also listed are the adjusted R^2 from the multiple regressions. Significant effect sizes ($p < 0.05$) are in bold.

	explanatory factors			
masting metric	predawn XWP	foliar N	*m*ean acorn productivity	adjusted R^2
CV	−0.113 ± 0.079 (0.16)	—	**−0.419 ± 0.025 (0.001)**	0.82
CV_k	−0.007 ± 0.015 (0.66)	—	**−0.161 ± 0.005 (<0.001)**	0.95
volatility	—	1.148 ± 0.631 (0.07)	**0.536 ± 0.138 (<0.001)**	0.19
PV	—	**0.142 ± 0.048 (0.004)**	**−0.048 ± 0.011 (<0.001)**	0.24
S	—	0.089 ± 0.056 (0.12)	**0.025 ± 0.012 (0.046)**	0.06

between predawn XWP and the CVs was no longer significant when controlling for mean overall productivity (table 3 and figure 1c,d), suggesting that trees with greater access to ground water exhibited reduced variability in annual acorn production because they were more productive rather than because of a direct effect of water. Similarly, the relationships between foliar N and both volatility and *S* were no longer significant, controlling for mean overall acorn productivity.

4. Discussion

Our results fail to support the hypothesis that nutrient scarcity leads to more variable masting-like behaviour in *Q. lobata*. We found five significant relationships between masting metrics and the indices of nutritional status of individual trees. Three of these were in the opposite direction predicted by the nutrient limitation hypothesis, suggesting that masting intensity decreases, rather than increases, with less foliar N. Only two correlations, those between the CVs and XWP, were in the direction predicted: trees with more negative XWP and poorer access to groundwater exhibited greater variability in annual acorn production. Additional analyses, however, indicated that these results were primarily an indirect consequence of the relationship between the CVs and mean overall productivity of individual trees. Water-stressed trees exhibited greater variability in acorn production because they were less productive and produced fewer acorns less frequently than trees with greater access to groundwater.

Fernández-Martinez *et al.* [1] provide a detailed discussion of the role of foliar nutrients as factors potentially limiting reproduction in plants. Their analyses suggest that variable and synchronized reproduction—masting—is amplified in species growing in sites with low productivity. As pointed out by Kelly [18], however, nutrient scarcity cannot, by itself, select for mast fruiting or synchrony, but must instead act in conjunction with some economy of scale, most commonly thought to be predator satiation or pollen coupling [2,15]. Our failure to detect a relationship between nutrient scarcity and masting in *Q. lobata* counters the argument that nutrient scarcity provides a selective mechanism for masting behaviour [23] and is instead consistent with the alternative that nutrient limitation constrains seed production [18].

Our failure to detect such a relationship comes with several caveats. First, masting, by definition, is the synchronous production of seeds by a population of plants [3,46]. Because our analyses were conducted on individuals, they do not test the relationship between nutrients and masting behaviour *sensu stricto*. Nonetheless, we were able to test whether variability, one of the main components of masting, varies consistently with nutrients among individuals within a closely studied population of a single masting species. The situation regarding synchrony is more complex, as synchrony depends on the fruiting dynamics of the entire population. Here, we show that synchrony does not vary consistently with resources within the population, but a thorough investigation of the relationship between nutrients and synchrony within the population would require analyses beyond the scope of this paper.

Second, Fernández-Martinez *et al.* [1] based their foliar N and foliar P values on large-scale plant trait databases in which nutrient values for different species, estimated by a combination of *in situ*-measured leaf traits, remote sensing and climatological data, were averaged within and across databases. At such a large geographic scale, it is unsurprising that correlations with patterns of plant reproduction differ from those found here, where nutrients and reproduction were determined on a tree-by-tree basis.

Caveats of both studies include the limited range of nutrients quantified and that neither was experimental. Regarding the first issue, carbon, for example, was not considered, although it has been investigated in other studies with variable results [8,20,47,48]. Regarding the second issue, experimental manipulation of resources and their effects on forest tree reproduction is difficult and has thus far also yielded inconsistent results [17,49,50]. More studies, both empirical and experimental, of potentially important resources at both the intraspecific scale reported here and at larger geographic and taxonomic scales are needed to understand the generality and applicability of the relationship between masting and resource abundance.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data are available from the Dryad Digital Repository: [51]

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. W.D.K.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, visualization, writing—original draft, writing—review and editing; W.J.C.: investigation, writing—review and editing; R.L.M.: conceptualization, investigation, writing—review and editing; R.O.: investigation, writing—review and editing; J.M.H.K.: conceptualization, formal analysis, investigation, methodology, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interests. We declare we have no competing interests.

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