



Can mast history be inferred from radial growth? A test using five species of California oaks



Walter D. Koenig^{a,b,*}, Johannes M.H. Knops^c, William J. Carmen^d

^a Hastings Reservation, Museum of Vertebrate Zoology, University of California Berkeley, Carmel Valley, CA 93924, USA

^b Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA

^c Department of Health and Environmental Sciences, Xi'an Jiaotong Liverpool University, Suzhou, Jiangsu Province 215123, China

^d Carmen Ecological Consulting, 145 Eldridge Ave., Mill Valley, CA 94941, USA

ARTICLE INFO

Keywords:

Masting behavior
Dendrochronology
Oaks
Quercus
Radial growth
Tree-rings

ABSTRACT

Quantifying masting behavior—the highly variable, yet synchronized, production of seeds by forest trees and other plants—is of considerable importance to ecosystem function and forest management, yet typically requires years of study to acquire. In contrast, measuring radial growth by mean of tree-ring cores potentially yields decades or more of data relatively quickly. Given the widespread existence of a negative correlation between growth and reproduction, can radial growth be used to infer historical masting behavior and detect long-term changes in reproductive behavior? Here we test this hypothesis in five species of California oaks (genus *Quercus*) for which we have long-term weather and 40 years of acorn production data at Hastings Reservation in central coastal California. Radial growth was measured for the three deciduous species using tree-ring analysis between 1980 and 1994 and for all five species using dendrometers between 1996 and 2019. Success was judged based on four criteria focused on the proportion of variance in annual acorn production explained, whether values using radial growth predicted very large and very small crop years, and whether five basic metrics of radial growth quantifying variance, autocorrelation, and synchrony matched values based on acorn production. Of the criteria, none was met using tree-rings with the exception of one of the metrics (mean pairwise synchrony). Dendrometers performed better but still failed two of the four criteria entirely and only met the other two for at most three of the five species. We conclude that radial growth does a generally poor job of estimating historical acorn production in these oaks. Although future advances may help resolve these shortcomings, demonstration that the relationship between radial growth and masting meet appropriate criteria based on years of overlapping data is currently necessary prior to any use of tree-ring growth to infer masting patterns.

1. Introduction

Masting behavior—the synchronized production of seeds by a population of plants—is a topic of considerable current controversy and interest (Kelly and Sork, 2002; Pearse et al., 2016; Bogdziewicz et al., 2019). Key ecological and evolutionary questions about this phenomenon include: what are the evolutionary benefits and ecological consequences of masting? What mechanisms drive variable seed production? What synchronizes reproduction within and between populations? And how will climate change alter the frequency or magnitude of mast-seeding patterns in the future?

Although highly variable, in certain cases masting takes place every other year (“alternate bearing”) and is thus predictable; this is the case in many fruit and nut crops but also in at least a few natural populations (Monselise and Goldschmidt, 1982; Crawley and Long, 1995). This is

not true for most wild populations, however, where masting typically occurs irregularly at multi-year intervals (Herrera et al., 1998; Koenig and Knops, 2000).

Given such irregularity and unpredictability, it is generally necessary to collect many years of data in order to quantify the degree of variability and to understand the ecological consequences of both years of heavy mast (“mast” years), and, conversely, poor mast years (“mast-failure” years). Such ecological effects have been shown to be important in a range of communities and taxa, including eastern deciduous forests, where the pulsed resource of acorn crops produced by oaks (*Quercus* spp.) have dramatic effects on everything from white-tailed deer (*Odocoileus virginianus*) to the incidence of lyme disease (Jones et al., 1998; Ostfeld and Keesing, 2000); Indonesia, where masting by dipterocarps (Dipterocarpaceae) drive population increases and regional movements of vertebrate seed predators (Curran and Leighton,

* Corresponding author at: Hastings Reservation, Museum of Vertebrate Zoology, University of California Berkeley, Carmel Valley, CA 93924, USA.
E-mail address: wicker@berkeley.edu (W.D. Koenig).

<https://doi.org/10.1016/j.foreco.2020.118233>

Received 30 March 2020; Received in revised form 9 May 2020; Accepted 10 May 2020

Table 1
Key characteristics of the species used in this study. Phylogeny from [Hipp et al. \(2014, 2020\)](#).

Species	Common name	Section	Winter deciduous?	Seasons required to mature acorns	Sample size
<i>Q. lobata</i>	Valley oak	<i>Quercus</i> ("white")	Yes	1	86
<i>Q. douglasii</i>	Blue oak	<i>Quercus</i> ("white")	Yes	1	56
<i>Q. chrysolepis</i>	Canyon live oak	<i>Protobalanus</i> ("intermediate")	No	2	21
<i>Q. agrifolia</i>	Coast live oak	<i>Lobatae</i> ("black")	No	1	63
<i>Q. kelloggii</i>	California black oak	<i>Lobatae</i> ("black")	Yes	2	20

2000); and across North America, where the variable seed production of conifer trees are an important instigator of boreal bird eruptions ([Bock and Lephthien, 1976](#); [Koenig and Knops, 2001](#); [Strong et al., 2015](#)).

Acquiring the data needed to understand such ecological effects generally entails many years of effort. Understanding historical masting patterns are, however, critical to gaining the insight necessary to test for long-term changes in masting linked to climate or other environmental change as well as an understanding of long-term forest ecology ([Szabó, 2012](#)). Given the time and effort required to gather mast crop size data, it would clearly be valuable if there were a quicker way to gather such data other than painstakingly measuring seed production over the course of many years.

A potential candidate for such a method is to measure radial growth, which often correlates inversely with seed production in many tree species. There are at least two factors that potentially drive this relationship. First, there may be a direct trade-off between growth and reproduction such that individuals investing more in one invest less in the other ([Holmsgaard, 1958](#); [Barringer et al., 2013](#)); that is, the relationship may be causal. Indeed, a growth-reproduction trade-off is one of the cornerstones of life-history theory ([Stearns, 1989](#); [1992](#)). Second, both growth and reproduction may be correlated or obscured by a third variable. In the case of masting trees this is likely to be local weather ([Knops et al., 2007](#)), but it could also be spatial variation in resources or other conditions that affect growth and reproduction in opposite ways ([Fox and Stevens, 1991](#)). In either of these latter situations the relationship is indirect; nonetheless, if the correlation is sufficiently strong, it would open the door for measures of radial growth both reconstructing masting histories dating back decades or even centuries and extending existing records into the future to predict long-term changes.

Numerous prior studies have investigated the relationship between growth and reproduction in masting trees, with variable results. Strong inverse correlations between these traits—sometimes lagged and sometimes not—have, for example, been reported in various conifers ([Holmsgaard, 1958](#); [Eis et al., 1965](#); [Patterson and Knapp, 2016](#)), various species of beech (*Fagus* spp.) ([Holmsgaard, 1958](#); [Drobyshev et al., 2010](#); [Kabeya et al., 2017](#)), several oak species ([Knops et al., 2007](#); [Martín et al., 2015](#)), and New Zealand rimu *Dacrydium cupressinum* ([Norton and Kelly, 1988](#)). Conversely, weak or no correlation has been reported in whitebark pine *Pinus albicaulis* ([Sala et al., 2012](#)), Aleppo pine *Pinus halepensis* ([Santos-del-Blanco and Climent, 2014](#)), mature individuals of the tropical tree *Bertholletia excelsa* ([Staudhammer et al., 2013](#)), mountain hemlock *Tsuga mertensiana* ([Woodward et al., 1994](#)), and rowan *Sorbus aucuparia* ([Żywiec and Zielonka, 2013](#)). There have, nonetheless, been several attempts to use or advocate radial growth as a means to infer historical masting events ([Speer, 2001](#); [Drobyshev et al., 2014](#); [Hacket-Pain et al., 2019](#); [Rodríguez-Ramírez et al., 2019](#)). How do we know whether such attempts are well-founded?

Here we test whether the relationship between radial growth and reproduction is sufficiently close as to allow inference regarding his-

investigated are those previously studied by [Knops et al. \(2007\)](#), who provided evidence that the negative correlation observed between radial growth and reproduction was the consequence not of a trade-off, but of the mutual, inverse relationship of both life-history variables with rainfall. Thus, the correlation between growth and reproduction in these species, and quite possibly many other masting species, is not causal. Nonetheless, it is still possible that they are linked closely enough that historical masting events can be inferred from measures of radial growth.

2. Methods

2.1. General

2.1.1. Study site and species

Work was conducted at Hastings Natural History Reservation, a field station run by the Museum of Vertebrate Zoology, University of California, Berkeley, located in central coastal California (36°23'N, 121°33'W). Habitat consisted of a mixture of oak savanna, oak woodland, and mixed forest ([Griffin, 1974](#)). The climate is Mediterranean, with cool, wet winters (mean annual precipitation [1939 – 2018] 524 mm, range 135 – 1131 mm) and hot, dry summers.

We studied five species representing a diverse set of North American oaks ([Table 1](#)). Particularly relevant to the analyses here is the difference in flower maturation rate; three species (*Q. lobata*, *Q. douglasii*, and *Q. agrifolia*) are “1-year” species that mature acorns from flowers produced the same year (that is, acorns maturing in the autumn of year *x* come from flowers produced in the spring of year *x*), whereas *Q. chrysolepis* and *Q. kelloggii* are “2-year” species that mature acorns from flowers produced the prior year (that is, acorns maturing in the autumn of year *x* come from flowers produced in the spring of year *x* – 1). All are common at the study site, although they differ ecologically in various ways, including their water use strategies, site preferences, and elevational distributions ([Griffin and Critchfield, 1972](#); [Knops and Koenig, 1994, 1997](#)).

2.1.2. Data

We tagged 246 trees of the five species in autumn 1980; subsequent sample sizes decreased somewhat due to mortality. Starting in 1980 and continuing each year through 2019, we estimated the acorn crop on each tree by means of visual surveys during which two workers counted as many acorns as possible, usually using binoculars, for 15 s; for analysis, counts were added together and then *ln*-transformed in order to reduce non-normality ([Koenig et al., 1994a, 1994b](#)). Values across all conspecific individuals were averaged within years to estimate the mean annual acorn crop for each species.

To test the relationship between reproduction and radial growth, we used both dendrochronological measurements (tree-rings) from cores and annual growth estimates from dendrometers ([Cattellino et al.,](#)

plywood, sanded and polished. Measurements were made on a tree-ring measuring table to the nearest 0.01 mm dating back to 1965. The two cores from each tree were matched by year. Non-matching cores were checked against two consecutive drought years in 1976 and 1977; cores not showing these years were dropped from the analysis. All cores were standardized by dividing years by the 30 year average growth to eliminate inherent growth differences between and within trees.

Cores were made on all individuals of the three deciduous species; annual growth rings were poorly defined in the evergreen species and were not analyzed. *Q. kelloggii* showed a significant decrease in growth over the 30 year period (linear regression, $F_{1,28} = 11.1$, $P = 0.002$). However, detrending the tree-ring widths (Fritts, 1972; Swetnam et al., 1985) did not change the significance of any cross-correlations with acorn production. Consequently the standardized (but not detrended) tree-ring widths were used in all analyses. No significant temporal trend was detected for *Q. douglasii* or *Q. lobata*. There were 15 years of overlap between the acorn surveys and the tree-rings (1980–1994).

Dendrometers were established in 1994 and have been measured each year through 2019. After letting bands settle on the trees during their first year, this yielded 24 years of overlap (1995–1996 to 2018–2019). Annual dendrometer growth values were standardized within trees to a mean of 0 and standard deviation of 1.

As a contrast to the radial growth data, we also compared our estimates of acorn crop size with annual rainfall. Rainfall was measured at Hastings Reservation headquarters and summed over the fiscal year from 1 September of the prior year (year $x - 1$) through 31 August of year x .

2.2. Analyses

Previous studies have found negative correlations between radial growth and reproduction either in the same or subsequent years (Knops et al., 2007; Hackett-Pain et al., 2015; Patterson and Knapp, 2016). Alternatively, the effect might go the other way around, with reproduction in year x significantly reducing radial growth the following year (Fox and Stevens, 1991). Thus, for both tree-ring and dendrometer analyses, we included as predictors values for year $x - 2$, year $x - 1$, year x , and year $x + 1$. Since reproduction in year x cannot affect future rainfall, we did not include year $x + 1$ in analyses of reproduction on annual rainfall. All analyses were conducted in R 3.5.3 (R Development Core Team, 2019). Statistical significance was set at $P < 0.05$.

For each species, we first performed multiple regressions of the mean $\ln$ -transformed acorn crop on mean standardized values of tree-ring growth, dendrometer increase, and annual rainfall. We present effect sizes $\pm$ standard errors for fixed factors and the adjusted R^2 values for the multiple regression. For a second set of analyses, we calculated mixed models in which each tree was considered individually and included in the models as a random factor. R^2 values, representing the proportion of variance accounted for by the fixed effects (marginal R^2), and the fixed effects plus the random effect (conditional R^2) are presented.

To further quantify the ability of radial growth to estimate mast production, we used the *predict* function in R to estimate the mean acorn crop for each year of overlap based on the multiple regressions using values for year $x - 2$, year $x - 1$, year x , and, except for annual rainfall, year $x + 1$ as explanatory fixed factors. Predicted values were plotted along with the observed values and compared in three ways: (1) the percent of observed values within the 95% confidence intervals of the predicted values; (2) the percent of observed mast years (defined, arbitrarily, as years where the mean $\ln$ -transformed number of acorns counted per tree was ≥ 3) that were successfully identified by the predicted values; and (3) the percent of observed mast-failure years (defined, arbitrarily, as years where the mean $\ln$ -transformed number of acorns counted per tree was ≤ 0.5) that were successfully identified by

standardized radial growth values on current year rainfall, and then regressed the residuals on the mean acorn crop. The rationale for this follows from the widespread and well-known relationship between rainfall and radial growth (Fritts, 1974; Cook, 1987; Le Quesne et al., 2006): once this correlation is removed, is there still an effect of radial growth on the size of the acorn crop?

Lastly, we present data on basic metrics, including the population coefficient of variation (CVp), mean individual coefficient of variation (xCVi), the consecutive disparity index (D), lag-1 autocorrelation, and mean pairwise synchrony of mean annual acorn production, tree-ring measurements, dendrometer measurements, and annual rainfall. These metrics are the most frequently used to quantify masting behavior (Koenig et al., 2003), but include the recently proposed consecutive disparity index, which is an alternative estimate of temporal variability that exhibits several advantages over the coefficient of variation (Fernández-Martínez et al., 2018). Mean individual coefficient of variation and pairwise synchrony could not be calculated for annual rainfall, since rainfall was only measured at a single site within the study area.

2.3. Growth vs. reproduction: Is the relationship good enough?

Many previous studies found negative correlations between growth and reproduction. Is the relationship sufficiently strong that tree-rings can be used to infer historical mast production?

Deciding whether the relationship between growth and reproduction is “sufficiently strong” is obviously arbitrary. Thus, if growth is to be used to infer historical mast behavior, it is critical to specify the criteria used to decide that the relationship between these life-history characters allows such an analysis to be worthwhile.

Here we propose the following criteria:

- 1) The proportion of variance in the mast crop explained by annual growth (lagged or unlagged) must be at least 40%.
- 2) The predicted mast crop values should fall within the 95% confidence intervals of the actual mast crop in at least 90% of years.
- 3) Very large mast years and very small mast-failure years predicted by radial growth should identify the majority ($\geq 50\%$) of observed mast and mast-failure years.
- 4) Basic masting metrics measured using radial growth should be within 20% of values based on observed annual seed production data.

All four criteria require a minimum of several years of overlap where both growth and reproduction are measured. Given the current status of mast reconstruction, we know of no way to avoid starting an attempt to reconstruct masting behavior from radial growth in the absence of such preliminary data.

3. Results

Results of multiple regressions of the mean annual acorn crop on mean annual tree-ring growth, mean annual dendrometer growth, and annual rainfall are summarized in Table 2. Regressions were not significant for any of the three species for which tree-ring growth was measured, nor were any of the individual lagged growth variables significant. The mean adjusted R^2 value (proportion of variance explained) for the three species was less than zero (-0.073).

Results were better using dendrometer measurements. Regressions were significant for four of the five species, and R^2 values were greater than 0.40 for three of the species. Regressions were also significant for four of the five species using annual rainfall, but none of the R^2 values was greater than 0.40.

Analyses using mixed models in which data for individual trees

Table 2

Effect sizes $\pm$ standard errors (*p*-value) from multiple regressions of mean annual values of the acorn crop (*ln*-transformed) on mean annual tree-ring growth, mean annual dendrometer growth, or annual rainfall, each measured in year $x - 2$, year $x - 1$, year x , and, except for analyses with annual rainfall, year $x + 1$. R^2 values above the 40% cutoff are in boldface.

	Year $x - 2$	Year $x - 1$	Year x	Year $x + 1$	Adjusted R^2
Tree-ring growth					
<i>Q. lobata</i>	-0.28 ± 1.64 (0.87)	-1.09 ± 2.01 (0.60)	-1.13 ± 1.88 (0.56)	1.10 ± 1.72 (0.54)	-0.20 (0.76)
<i>Q. douglasii</i>	0.75 ± 1.24 (0.56)	-0.49 ± 1.65 (0.77)	-1.38 ± 1.42 (0.36)	1.20 ± 1.30 (0.38)	-0.18 (0.74)
<i>Q. kelloggii</i>	1.99 ± 1.19 (0.13)	0.01 ± 1.37 (0.99)	0.85 ± 1.43 (0.57)	-2.71 ± 1.54 (0.11)	0.16 (0.25)
Dendrometer growth					
<i>Q. lobata</i>	0.11 ± 0.32 (0.75)	0.49 ± 0.35 (0.18)	-0.83 ± 0.32 (0.02)	0.41 ± 0.30 (0.19)	0.18 (0.11)
<i>Q. douglasii</i>	0.04 ± 0.26 (0.89)	0.95 ± 0.27 (0.002)	-0.57 ± 0.26 (0.04)	0.61 ± 0.25 (0.03)	0.41 (0.008)
<i>Q. agrifolia</i>	-0.23 ± 0.29 (0.26)	1.02 ± 0.21 (< 0.001)	0.16 ± 0.20 (0.43)	0.06 ± 0.20 (0.78)	0.56 (< 0.001)
<i>Q. chrysolepis</i>	0.43 ± 0.20 (0.04)	-0.83 ± 0.21 (< 0.001)	0.84 ± 0.21 (< 0.001)	-0.02 ± 0.22 (0.92)	0.58 (< 0.001)
<i>Q. kelloggii</i>	0.53 ± 0.23 (0.03)	0.07 ± 0.24 (0.76)	0.67 ± 0.24 (0.01)	-0.20 ± 0.24 (0.41)	0.31 (0.03)
Annual rainfall					
<i>Q. lobata</i>	0.91 ± 0.62 (0.15)	-0.10 ± 0.63 (0.88)	-2.29 ± 0.61 (< 0.001)	—	0.27 (0.002)
<i>Q. douglasii</i>	1.04 ± 0.64 (0.11)	1.14 ± 0.66 (0.09)	-1.82 ± 0.63 (0.007)	—	0.24 (0.005)
<i>Q. agrifolia</i>	0.60 ± 0.65 (0.36)	2.37 ± 0.66 (0.001)	-0.21 ± 0.64 (0.75)	—	0.22 (0.007)
<i>Q. chrysolepis</i>	2.20 ± 0.58 (< 0.001)	-0.37 ± 0.59 (0.54)	2.01 ± 0.57 (0.001)	—	0.35 (< 0.001)
<i>Q. kelloggii</i>	0.58 ± 0.87 (0.51)	-0.64 ± 0.89 (0.48)	0.45 ± 0.86 (0.61)	—	-0.05 (0.77)

variation in this manner reduced the differences among the three data sets (tree-rings, dendrometers, and rainfall) and resulted in a high proportion of the fixed factors being statistically significant in all analyses (tree-rings: 7/12 [58%]; dendrometers: 16/20 [80%]; annual rainfall: 10/15 [67%]). However, marginal R^2 values (considering only the fixed factors) were still small (range 0.02–0.19), and only three of the conditional R^2 values (including the random factor of individual ID) were (barely) above the 0.40 cutoff (all three $R^2 = 0.41$), including *Q. agrifolia* and *Q. chrysolepis* in the dendrometer analyses and *Q. douglasii* using annual rainfall.

Table 4 summarizes the success of predicted mast crop values based on the three sets of variables (tree-ring measurements, dendrometer measurements, and annual rainfall). Observed acorn crops fell within the 95% confidence intervals of both tree-ring and dendrometer values a high proportion of years (83.3% for tree-rings; 70.4% for dendrometers), whereas less than half of years fell within the estimated 95% confidence intervals using annual rainfall. None, however, fell within the 95% confidence interval 90% of the time. Mean predicted values did a particularly poor job of identifying the relatively few extreme seed production years. This was especially true for very large mast years, none of which were successfully identified in any of the analyses, whereas 2 of 9 (22.2%) mast-failure years were identified using tree-

rings and 8 of 21 (38.1%) using dendrometers. A comparison of observed vs. predicted values are graphed for *Q. lobata* in Fig. 1; graphs for all species and all three sets of predictor variables are provided in the supplemental data (Figs. S1–S3).

A clearer view of the the relationships among radial growth, the acorn crop, and annual rainfall is provided by the regressions of radial growth on annual rainfall followed by regressions of the mean annual acorn crop on the residuals (Table 5). In all cases there were strong, highly significant, positive relationships between radial growth and annual rainfall. Once the effect of annual rainfall was removed, however, the adjusted R^2 values of the regressions of the acorn crop on the residuals were all close to zero. That is, no significant relationship between radial growth and the acorn crop existed in any of the species beyond that explained by the correlation of these variables with annual rainfall.

Metrics for the predictor variables and acorn production are summarized in Table 6. Of the metrics, values derived from tree-rings matched those for acorn production fairly well (within 20% for two of the three species) for mean pairwise synchrony only; none of the other metrics based on tree-rings were within 20% of values for acorn production for any of the species. Metrics calculated from the dendrometer data performed better: values were within 20% of those for acorn

Table 3

Effect sizes $\pm$ standard errors (*p*-value) of mixed models where the acorn crop (*ln*-transformed) was the dependent variable, tree-ring growth, dendrometer growth, or annual rainfall, each for year $x - 2$, year $x - 1$, year x , and, except for annual rainfall, year $x + 1$, were fixed factors, and “tree ID” was a random effect. R^2 values above the 40% cutoff are in boldface.

	Year $x - 2$	Year $x - 1$	Year x	Year $x + 1$	Marginal/conditional R^2 values
Tree-ring growth					
<i>Q. lobata</i>	-0.12 ± 0.15 (0.43)	-0.46 ± 0.18 (0.009)	-0.05 ± 0.17 (0.76)	0.59 ± 0.16 (< 0.001)	0.02/0.25
<i>Q. douglasii</i>	0.32 ± 0.14 (0.03)	-0.52 ± 0.18 (0.004)	-0.20 ± 0.15 (0.18)	0.26 ± 0.14 (0.06)	0.02/0.31
<i>Q. kelloggii</i>	1.09 ± 0.24 (< 0.001)	-0.36 ± 0.27 (0.19)	0.83 ± 0.27 (0.003)	-1.17 ± 0.28 (< 0.001)	0.14/0.19
Dendrometer growth					
<i>Q. lobata</i>	0.14 ± 0.03 (< 0.001)	0.12 ± 0.04 (0.002)	-0.18 ± 0.04 (< 0.001)	0.06 ± 0.04 (0.09)	0.02/0.30
<i>Q. douglasii</i>	0.05 ± 0.04 (0.22)	0.37 ± 0.04 (< 0.001)	-0.15 ± 0.04 (< 0.001)	0.14 ± 0.04 (< 0.001)	0.05/0.37
<i>Q. agrifolia</i>	-0.15 ± 0.04 (< 0.001)	0.63 ± 0.04 (< 0.001)	0.12 ± 0.04 (< 0.001)	0.09 ± 0.04 (0.01)	0.17/0.41
<i>Q. chrysolepis</i>	0.33 ± 0.06 (< 0.001)	-0.47 ± 0.06 (< 0.001)	0.49 ± 0.06 (< 0.001)	-0.03 ± 0.06 (0.61)	0.19/0.41
<i>Q. kelloggii</i>	0.33 ± 0.08 (< 0.001)	-0.08 ± 0.08 (0.29)	0.43 ± 0.08 (< 0.001)	-0.19 ± 0.08 (0.01)	0.13/0.26
Annual rainfall					
<i>Q. lobata</i>	0.93 ± 0.11 (< 0.001)	-0.09 ± 0.11 (0.40)	-2.29 ± 0.11 (< 0.001)	—	0.11/0.38
<i>Q. douglasii</i>	1.02 ± 0.13 (< 0.001)	1.13 ± 0.13 (< 0.001)	-1.82 ± 0.13 (< 0.001)	—	0.10/0.41
<i>Q. agrifolia</i>	0.61 ± 0.12 (< 0.001)	2.35 ± 0.13 (< 0.001)	-0.22 ± 0.12 (0.07)	—	0.10/0.33
<i>Q. chrysolepis</i>	2.21 ± 0.21 (< 0.001)	-0.37 ± 0.22 (0.09)	2.02 ± 0.21 (< 0.001)	—	0.14/0.37

Table 4
Summary of the success of tree-rings measurements ($n = 14$ years), dendrometer measurements ($n = 23$ years), and annual rainfall ($n = 40$ years) to predict (a) the mean acorn crop within the 95% confidence interval of the model, (b) mast years (mean $\ln$ -transformed acorn crop ≥ 3), and (c) crop failures (mean $\ln$ -transformed acorn crop ≤ 0.5). Predictions based on multiple regressions of the acorn crop ($\ln$ -transformed) on values for year $x - 2$, year $x - 1$, year x , and, except for annual rainfall, year $x + 1$.

Species	Percent of years the acorn crop was within the 95% confidence interval			Number of actual mast years predicted/observed			Number of actual failure years predicted/observed		
	Tree-rings	Dendrometers	Annual rainfall	Tree-rings	Dendrometers	Annual rainfall	Tree-rings	Dendrometers	Annual rainfall
<i>Q. lobata</i>	78.6	60.9	52.5	0/2	0/4	0/6	0/1	0/1	1/3
<i>Q. douglasii</i>	85.7	65.2	40.0	0/2	0/3	0/5	0/2	0/3	0/5
<i>Q. agrifolia</i>	—	73.9	35.0	—	0/1	0/1	—	3/6	0/12
<i>Q. chrysolepis</i>	—	82.6	42.5	—	0/1	0/2	—	3/6	0/9
<i>Q. kelloggii</i>	85.7	69.6	40.0	0/2	0/1	0/4	2/6	2/5	0/12
Species mean (%)	83.3	70.4	42.5	0/6 (0%)	0/10 (0%)	0/18 (0%)	2/9 (22.2%)	8/21 (38.1%)	1/41 (2.4%)

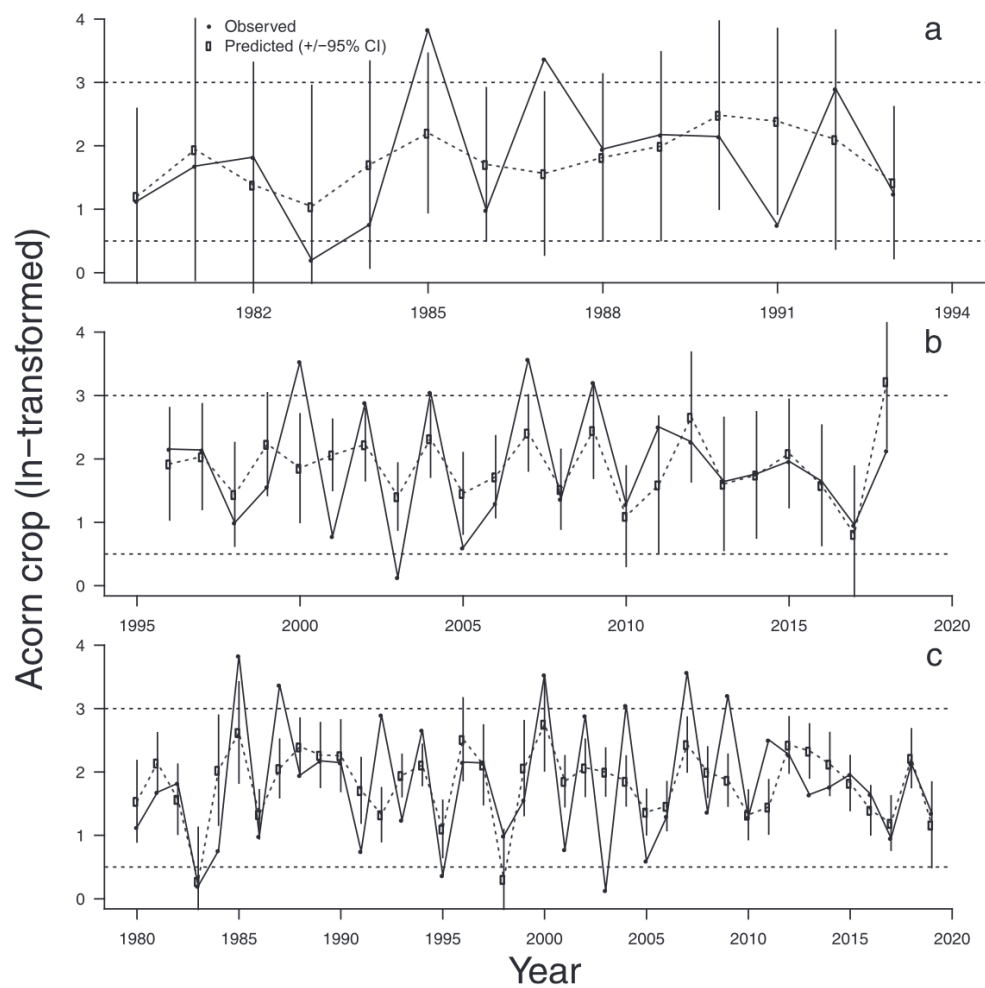


Fig. 1. Observed vs. predicted ($\pm 95\%$ confidence intervals) acorn crops ($\ln$ -transformed) for *Q. lobata* from multiple regressions on (a) tree-ring measurements from year $x - 2$, year $x - 1$, year x , and year $x + 1$; (b) dendrometer measurements from year $x - 2$, year $x - 1$, year x , and year $x + 1$; and (c) annual rainfall from year $x - 2$, year $x - 1$, and year x .

production for three of the five species for three of the metrics but were within 20% of CVp values for only *Q. chrysolepis*; estimates based on neither tree-rings nor dendrometers matched observed values of the lag-1 autocorrelation for any of the species. Values derived from annual rainfall, for which only three of the metrics could be calculated, failed to match those of acorn production for any of the species except in the case of *D*, where values were within 20% for four of the five species.

based on both tree-rings and dendrometers were of opposite sign from the mostly negative values based on the acorn crop. The only exception to this was the *Q. douglasii* dendrometer value, which was still far from within 20% of the corresponding value based on the acorn crop. Thus, whereas acorn production values tended to be strongly negatively autocorrelated from one year to the next, those based on radial growth and rainfall were not.

Table 5

Effect sizes $\pm$ standard errors (p -values) and adjusted R^2 values from linear regressions of (a) radial growth (year x) on annual rainfall (year x), and (b) the mean annual acorn crop on the residuals from regression (a).

	(a) Regression of radial growth on		(b) Regression of the mean acorn crop on	
	annual rainfall	adjusted R^2	the residuals from regression (a)	adjusted R^2
<i>Tree-ring growth</i>				
<i>Q. lobata</i>	0.62 $\pm$ 0.13 (< 0.001)	0.42	1.11 $\pm$ 1.79 (0.54)	−0.05
<i>Q. douglasii</i>	0.80 $\pm$ 0.16 (< 0.001)	0.46	0.48 $\pm$ 1.45 (0.74)	−0.07
<i>Q. kelloggii</i>	0.79 $\pm$ 0.317 (< 0.001)	0.41	3.98 $\pm$ 2.23 (0.10)	0.13
<i>Dendrometer growth</i>				
<i>Q. lobata</i>	1.94 $\pm$ 0.47 (< 0.001)	0.39	−1.89 $\pm$ 0.40 (0.64)	−0.03
<i>Q. douglasii</i>	2.58 $\pm$ 0.41 (< 0.001)	0.61	0.11 $\pm$ 0.47 (0.82)	−0.04
<i>Q. agrifolia</i>	2.35 $\pm$ 0.54 (< 0.001)	0.42	0.26 $\pm$ 0.35 (0.47)	−0.02
<i>Q. chrysolepis</i>	1.85 $\pm$ 0.359 (0.004)	0.27	0.45 $\pm$ 0.31 (0.15)	0.05
<i>Q. kelloggii</i>	2.86 $\pm$ 0.53 (< 0.001)	0.53	0.53 $\pm$ 0.39 (0.19)	0.03

4. Discussion

4.1. General

Can historical mast production be inferred from radial growth in the five species of California oaks we studied? Table 7 summarizes our results. In general, the answer was at best “partly”, but more generally, “poorly”. None of the variables met criteria 2 or 3 for any of the species. Both tree-rings and annual rainfall met only one of the criteria, and then for only some of the species, while dendrometers met two of the criteria partly for between one and three of the species. In general, the reason for this poor performance was clear: radial growth of all five species was strongly and positively related to rainfall (Table 5). Once the effect of rainfall was removed, radial growth had no remaining statistical relationship with the annual acorn crop. Thus, the correlation between radial growth and the acorn crop was entirely due to the mutual dependence of both these factors on annual rainfall.

4.2. Importance of masting to forest management

Mast crops produce pulses of resources that can have dramatic effects on ecosystems (Ostfeld and Keesing, 2000; Koenig and Knops, 2005), including many that are potentially affected by forest management practices as well as for the understanding of forest ecology (Szabó, 2012). For example, seed production often varies considerably among individuals within a population, and thus it can be important to identify and retain highly productive trees that produce many seeds in order to minimize the negative effects of harvesting on wildlife and forest regeneration (Healy, 1997; Lashley et al., 2010). Forest management can also influence specific wildlife species through interactions with resource fluctuations due to masting, as found by Zwolak et al. (2016) for yellow-necked mice (*Apodemus flavicollis*) in managed European beech (*Fagus sylvatica*) forests. Such affects highlight the importance of understanding masting patterns to forest management and thus the potential value of inferring mast events, either for historical reconstructions or to guide future practices, using techniques that are faster and more efficient than quantifying seed production over a period of many years.

Table 6

Basic metrics (CVp, xCVi, D , lag-1 autocorrelation, and mean pairwise synchrony) for acorn production, tree-ring measurements, dendrometer measurements, and annual rainfall for each of the five species. Values within 20% of those for acorn production are in boldface.

Metric	Species	Acorn production	Tree-ring measurements	Dendrometer measurements	Annual rainfall
Population CV (CVp)	<i>Q. lobata</i>	0.533	0.216	0.253	0.424
	<i>Q. douglasii</i>	0.560	0.271	0.390	0.424
	<i>Q. agrifolia</i>	0.685	—	0.441	0.424
	<i>Q. chrysolepis</i>	0.607	—	0.500	0.424
	<i>Q. kelloggii</i>	0.827	0.287	0.501	0.424
Mean individual CV (xCVi)	<i>Q. lobata</i>	1.025	0.312	0.534	—
	<i>Q. douglasii</i>	1.139	0.379	0.942	—
	<i>Q. agrifolia</i>	1.251	—	1.223	—
	<i>Q. chrysolepis</i>	1.099	—	1.021	—
	<i>Q. kelloggii</i>	1.253	0.361	0.679	—
Consecutive disparity index (D)	<i>Q. lobata</i>	0.519	0.212	0.231	0.446
	<i>Q. douglasii</i>	0.548	0.238	0.398	0.446
	<i>Q. agrifolia</i>	0.526	—	0.506	0.446
	<i>Q. chrysolepis</i>	0.583	—	0.529	0.446
	<i>Q. kelloggii</i>	0.530	0.304	0.573	0.446
Lag-1 autocorrelation	<i>Q. lobata</i>	−0.513	0.350	0.219	−0.005
	<i>Q. douglasii</i>	−0.393	0.365	−0.095	−0.005
	<i>Q. agrifolia</i>	−0.135	—	0.125	−0.005
	<i>Q. chrysolepis</i>	−0.305	—	0.303	−0.005
	<i>Q. kelloggii</i>	0.091	−0.072	−0.086	−0.005
Mean pairwise synchrony (r)	<i>Q. lobata</i>	0.417	0.415	0.314	—
	<i>Q. douglasii</i>	0.460	0.429	0.358	—
	<i>Q. agrifolia</i>	0.467	—	0.466	—
	<i>Q. chrysolepis</i>	0.419	—	0.469	—
	<i>Q. kelloggii</i>	0.419	—	—	—

Table 7

Summary of how well tree-ring measurements, dendrometer measurements, and annual rainfall succeeded in predicting mastling using the proposed criteria.

Criterion	Tree-rings	Dendrometers	Annual rainfall
1 <i>Explained</i> $\geq 40\%$ of the variance in annual mast crop?	No	Partly (3 of 5 spp. using mean annual values; 2 of 5 spp. using data from individual trees)	Partly (1 of 5 spp. using data from individual trees)
2 <i>Mast crop within 95% confidence interval of predicted values</i> $\geq 90\%$ of the time?	No	No	No
3 <i>Predicted the majority of large and small mast-crop years?</i>			
a Large mast-crop years?	No	No	No
b Mast-failure years?	No	No	No
4 <i>Within 20% of mastling metrics?</i>			
a CVp	No	Partly (1 of 5 spp.)	No
b xCVi	No	Partly (3 of 5 spp.)	—
c <i>D</i>	No	Partly (3 of 5 spp.)	Mostly (4 of 5 spp.)
d Lag-1 autocorrelation	No	No	No
e Mean pairwise synchrony	Mostly (2 of 3 spp.)	Partly (3 of 5 spp.)	—

4.3. Differences related to maturation of acorns

Our results highlight differences in lag times of the variables significantly correlating with acorn production. From the multiple regression analyses, for example (Table 2), the only dendrometer variable significantly (and negatively) related to the acorn crop for *Q. lobata* was growth the same year (year x). For *Q. douglasii*, however, the acorn crop was positively related to growth the prior year (year $x - 1$), negatively related to growth in year x , and positively related to growth the following year (year $x + 1$). Meanwhile, the acorn crop for *Q. agrifolia* was positively related only to growth in year $x - 1$. All three of these are 1-year species. As for the two 2-year species, the acorn crops of both were positively related to growth in year $x - 2$ and year x , but the acorn crop of only *Q. chrysolepis* was negatively related to growth in year $x - 1$.

Although some of these differences appear to be related to whether acorns mature in one or two years (Knops et al., 2007), others are not. Clearly a careful examination of the relationship between growth and reproduction has to be made on a species by species—if not population by population—basis prior to assuming any specific relationship between life-history traits.

4.4. Measuring radial growth: tree-rings vs. dendrometers

Results differed quantitatively depending on whether tree-ring or dendrometer data were compared with mastling data; in particular, dendrometers explained a much greater proportion of variance in the acorn crop than did tree-rings (Table 2) and metrics based on dendrometers matched those based on acorn production better than those based on tree-rings (Table 6). We did not overlap years when both techniques were used, and thus are unable to critically compare them. However, there are at least two potential reasons why this may have been true. First, dendrometers measure the total annual increment in radial circumference while tree-ring analysis as conducted here estimated radial growth from two small cores. Second, dendrometers measure all trees, whereas tree-rings from some trees were excluded because they were difficult to read, had missing years, or exhibited some other kind of anomaly—problems more likely to occur among slow-growing trees in infertile sites. Both are likely to result in dendrometers providing a more complete estimate of radial growth both for individual trees and the population as a whole, and are thus more likely to yield satisfactory results when attempting to estimate mastling behavior.

4.5. What criteria are necessary?

In order to decide whether a relationship is sufficiently good to justify inferring historical mast production, we proposed a set of four criteria (Table 7). Some of these are likely to be more useful than others, and some are more relevant to a particular goal than others. For example, if the goal is to estimate past variability of the mast crop and determine whether it has changed through time (such as, for example, Pearse et al., 2017), then the only criterion that may be important is whether the CVp or xCVi of growth (or other measure of variability, such as *D*) closely matches the corresponding value of the acorn crop (Table 7, criteria 4a–4c). Alternatively, if the goal is to predict mast years and/or mast-failure years in order to identify years when food is likely to have been abundant or lacking for seed specialists, the criteria of importance would be whether growth successfully predicts very large and very small mast crops (Table 7, criteria 3a and 3b). Meeting either one of these criteria could provide important clues as to how climate change might affect mastling, and on how animals dependent on mastling events might respond in the future, even if other criteria are not met.

4.6. Potential alternative data for inferring mast behavior

At best, tree-ring analyses currently require years of preliminary overlapping data in order to demonstrate their ability to successfully infer historical mastling patterns. Are there other ways that prior seed production or mast events can be identified?

Szabó (2012) discusses this question in detail for European oaks, concluding that historical written sources, both of direct observations of acorn crops and references to monetary transactions (particularly tax records) involving acorns, are able to provide insight into mastling frequencies going back, in at least rare cases, to the Middle Ages. As an example, such transactional records were used by Curran and Webb (2000) to infer mast fruiting by dipterocarps in Indonesia. Records vary greatly in quality, however, and Szabó recommends that historical mastling information be transformed into a three-point scale consisting of: (1) no mast; (2) moderate mast; and (3) good mast. Although crude, this protocol provides the potential for testing historical hypotheses involving mast crops, particularly those dependent on the extremes of very large or poor mast-crop years, in other cases as well.

It is also possible that data, gleaned either from tree-ring cores or sampling of trees, could potentially yield information allowing better

although this remains to be demonstrated. Similarly, differences in xylem vessel frequency and diameter derived from tree-ring cores have been shown to correlate with mast events in Mexican beech (*Fagus grandifolia* subsp. *mexicana*) (Rodríguez-Ramírez et al., 2019); such characters thus exhibit promise for inferring historical mast behavior in other species as well. It is even possible that more detailed signal extraction of tree-rings may, at least under some circumstances, yield strong insight into masting events and seed production patterns (Cook, 1987), although such decomposition of tree-ring data is likely to require far longer series than we acquired here. Finally, reproduction can be dominated by a small number of individuals within a population (Hackett-Pain et al., 2019), and it is possible that identifying and restricting analysis to a subset of such “super-producers” may yield superior relationships between growth and reproduction than found here.

4.7. Proximate mechanisms driving the relationship between growth and reproduction

Although our results do not support the hypothesis that radial growth can be used to infer historical masting behavior, results comparing growth and reproduction can provide valuable insight regarding the proximate mechanisms involved in variable seed production. In the case of the oaks considered here, for example, the positive relationship between growth and reproduction the same year in the two 2-year species is consistent with the conclusion that there is no direct trade-off between growth and reproduction in these species, and that when the relationship is negative, as in *Q. lobata* and *Q. douglasii*, it is likely to be due to growth and reproduction being indirectly correlated through a third variable rather than causal, as proposed previously for these species by Knops et al. (2007) and for *Fagus sylvatica* by Hackett-Pain et al. (2015) and Mund et al. (2020).

Furthermore, the variability in the relationships between growth at various lag intervals and reproduction is inconsistent with the hypothesis of resource matching whereby varying resources are apportioned equally between the two factors (Pearse et al., 2016). Thus, of the models for the potential relationships between resources and mast production illustrated by Pearse et al. (2016), our results support prior studies in *Q. lobata* and other masting species suggesting that resources are actively stored, resulting in highly variable seed crops in part due to reproductive “vetos”—adverse weather conditions—that obviate the ability of trees to invest in reproduction in some years (Pearse et al., 2014; Pesendorfer et al., 2016; Bogdziewicz et al., 2018).

4.8. Conclusion

We conclude that radial growth, measured either using tree-rings or dendrometers, does a poor job of estimating acorn production in these oaks, and can only be used with great caution, and then only for a subset of characters and not all species. This was the case whether or not we controlled for individual variation among trees, and whether or not growth was lagged, unlagged, or considered the year following the acorn crop. These results do not eliminate the possibility that radial growth can be used to infer mast production in other populations, or that other kinds of information gleaned from tree-ring cores might potentially yield data that does a satisfactory job of indicating masting patterns. For now, however, this goal remains out of reach without careful preliminary analysis of the relationship between radial growth and reproduction based on many years of overlapping data.

CRedit authorship contribution statement

Walter D. Koenig: Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing.
Johannes M.H. Knops: Conceptualization, Investigation, Writing -

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Ron Mumme and Mark Stanback for help with the acorn counts, Clarence Lehman for developing the tree-ring increment software program, and the reviewers for their comments. This research was supported by the University of California's Integrated Hardwoods Range Management Program, the California Department of Fish and Game, and National Science Foundation grants DEB-0816691 and DEB-1256394 to WDK.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118233>.

References

- Barringer, B.C., Koenig, W.D., Knops, J.M.H., 2013. Interrelationships among life-history traits in three California oaks. *Oecologia* 171, 129–139. <https://doi.org/10.1007/s00442-00012-02386-00449>.
- Bock, C.E., Lepthien, L.W., 1976. Synchronous eruptions of boreal seed-eating birds. *Am. Nat.* 110, 559–571. <https://doi.org/10.1086/283091>.
- Bogdziewicz, M., Steele, M.A., Marino, S., Crone, E.E., 2018. Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. *New Phytol.* 219, 98–108. <https://doi.org/10.1111/nph.15108>.
- Bogdziewicz, M., Ascoli, D., Hackett-Pain, A., Koenig, W.D., Pearse, I.S., Pesendorfer, M.B., Satake, A., Thomas, P., Vacchiano, G., Wohlgemuth, T., Tanentzap, A., 2019. From theory to experiments for testing the proximate mechanisms of mast seeding: an agenda for an experimental ecology. *Ecol. Lett.* 23, 210–220. <https://doi.org/10.1111/ele.13442>.
- Cattellino, P.J., Becker, C.A., Fuller, L.G., 1986. Construction and installation of home-made dendrometer bands. *N. J. Appl. For.* 3, 73–75.
- Cook, E.R., 1987. The decomposition of tree-ring series for environmental studies. *Tree-ring Bull.* 47, 37–59.
- Crawley, M.J., Long, C.R., 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *J. Ecol.* 83, 683–696. <https://doi.org/10.2307/2261636>.
- Curran, L.M., Leighton, M., 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* 70, 101–128. [https://doi.org/10.1890/0012-9615\(2000\)1070\[0101:VRTSVI\]1892.1890.CO;1892](https://doi.org/10.1890/0012-9615(2000)1070[0101:VRTSVI]1892.1890.CO;1892).
- Curran, L.M., Webb, C.O., 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* 70, 129–148. [https://doi.org/10.1890/0012-9615\(2000\)1070\[0129:ETOTSS\]1892.1890.CO;1892](https://doi.org/10.1890/0012-9615(2000)1070[0129:ETOTSS]1892.1890.CO;1892).
- Drobyshev, I., Övergaard, R., Saygin, I., Niklasson, M., Hickler, T., Karlsson, M., Sykes, M.T., 2010. Masting behaviour and dendrochronology of European beech (*Fagus sylvatica*, L.) in southern Sweden. *For. Ecol. Manage.* 259, 2160–2171. <https://doi.org/10.1016/j.foreco.2010.01.037>.
- Drobyshev, I., Niklasson, M., Mazerolle, M.J., Bergeron, Y., 2014. Reconstruction of a 253 year-long mast record of European beech reveals its association with large scale temperature variability and no long-term trend in mast frequencies. *Agri. For. Meteorol.* 192–193, 9–17. <https://doi.org/10.1016/j.agrformet.2014.02.010>.
- Eis, S., Garman, E.H., Ebell, L.F., 1965. Relation between cone production and diameter increment of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Pinus grandis* (Dougl.) Lindl.) and western white pine (*Pinus monticola* Dougl.). *Can. J. Bot.* 43, 1553–1559.
- Fernández-Martínez, M., Vicca, S., Janssens, I.A., Carnicer, J., Martín-Vide, J., Peñuelas, J., 2018. The consecutive disparity index, D: a measure of temporal variability in ecological studies. *Ecosphere* 9 (12), e02527. <https://doi.org/10.1002/ecs2.2527>.
- Fox, J.F., Stevens, G.C., 1991. Costs of reproduction in a willow: experimental responses vs. natural variation. *Ecology* 72, 1013–1023. <https://doi.org/10.2307/1940601>.
- Fritts, H.C., 1972. Dendroclimatology and dendroecology. *Quat. Res.* 1, 419–449. [https://doi.org/10.1016/0033-5894\(71\)90057-3](https://doi.org/10.1016/0033-5894(71)90057-3).
- Fritts, H.C., 1974. Relationships of ring widths in arid-site conifers to variations in monthly temperature and precipitation. *Ecol. Monogr.* 44, 411–440. <https://doi.org/10.2307/1942448>.
- Griffin, J.R., 1974. Botanical resources of the Hastings Reservation, Monterey County, California. *Madroño* 22, 329–332.
- Griffin, J.R., Critchfield, W.B., 1972. The distribution of forest trees in California. Pacific SW Forest & Range Experiment Station, USDA Forest Service Research Paper PSW-82, Berkeley, CA.

- influence of previous summers' climate on ring width. *Tree Physiol.* 35, 319–330. <https://doi.org/10.1093/treephys/tpv007>.
- Hackett-Pain, A., Ascoli, D., Berretti, R., Mencuccini, M., Motta, R., Nola, P., Piussi, P., Ruffinatto, F., Vacchiano, G., 2019. Temperature and masting control Norway spruce growth, but with high individual tree variability. *For. Ecol. Manage.* 438, 142–150. <https://doi.org/10.1016/j.foreco.2019.02.014>.
- Han, Q., Kagawa, A., Kabeya, D., Inagaki, Y., 2016. Reproduction-related variation in carbon allocation to woody tissues in *Fagus crenata* using a natural ^{13}C approach. *Tree Physiol.* 36, 1343–1352. <https://doi.org/10.1093/treephys/tpw074>.
- Healy, W.M., 1997. Thinning New England oak stands to enhance acorn production. *N. J. Appl. For.* 14, 152–156. <https://doi.org/10.1093/njaf/14.3.152>.
- Herrera, C.M., Jordano, P., Guitián, J., Traveset, A., 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *Am. Nat.* 152, 576–594. <https://doi.org/10.1086/286191>.
- Hipp, A.L., Eaton, D.A.R., Cavender-Bares, J., Fitzek, E., Nipper, R., Manos, P.S., 2014. A framework phylogeny of the American oak clade based on sequenced RAD data. *PLoS One* 9 (4), e93975. <https://doi.org/10.1371/journal.pone.0093975>.
- Holmgaard, E., 1958. Effect of seed-bearing on the increment of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst). In: Proceedings of the 12th International Union of Forestry Research Organizations Conference, Oxford, UK, pp. 158–161.
- Hipp, A.L., Manos, P.S., Hahn, M., Avishai, M., Bodénès, C., Cavender-Bares, J., Crowl, A.A., Deng, M., Denk, T., Fitz-Gibbon, S., Gailing, O., González-Elizondo, M.S., González-Rodríguez, A., Grimm, G.W., Jaing, X.-L., Kremer, A., Lesur, I., McVay, J.D., Plomion, C., Rodríguez-Correa, H., Schulze, E.-D., Simeone, M.C., Sork, V.L., Valencia-Avalos, S., 2020. Genomic landscape of the global oak phylogeny. *New Phytol.* 226, 1198–1212. <https://doi.org/10.1111/nph.16162>.
- Jones, C.G., Ostfeld, R.S., Richard, M.P., Schaubert, E.M., Wolff, J.O., 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* 279, 1023–1026. <https://doi.org/10.1126/science.279.5353.1023>.
- Kabeya, D., Inagaki, Y., Noguchi, K., Han, Q., 2017. Growth rate reduction causes a decline in the annual incremental trunk growth in masting *Fagus crenata* trees. *Tree Physiol.* 37, 1444–1452. <https://doi.org/10.1093/treephys/tpx1081>.
- Kelly, D., Sork, V.L., 2002. Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* 33, 427–447. <https://doi.org/10.1146/annurev.ecolsys.1133.020602.009543>.
- Knops, J.M.H., Koenig, W.D., 1994. Water use strategies of five sympatric species of *Quercus* in central coastal California. *Madroño* 41, 290–301.
- Knops, J.M.H., Koenig, W.D., 1997. Site fertility and leaf nutrients of sympatric evergreen and deciduous species of *Quercus* in central coastal California. *Plant Ecol.* 130, 121–131. <https://doi.org/10.1023/A:1009798327200>.
- Knops, J.M.H., Koenig, W.D., Carmen, W.J., 2007. Negative correlation does not imply a trade-off between growth and reproduction in California oaks. *Proc. Nat. Acad. Sci. (USA)* 104, 16982–16985. <https://doi.org/10.1073/pnas.0704251104>.
- Koenig, W.D., Knops, J.M.H., 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. *Am. Nat.* 155, 59–69. <https://doi.org/10.1086/303302>.
- Koenig, W.D., Knops, J.M.H., 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. *J. Anim. Ecol.* 70, 609–620. <https://doi.org/10.1046/j.1365-2656.2001.00516.x>.
- Koenig, W.D., Knops, J.M.H., 2005. The mystery of masting in trees. *Am. Sci.* 93, 340–347.
- Koenig, W.D., Knops, J.M.H., Carmen, W.J., Stanback, M.T., Mumme, R.L., 1994a. Estimating acorn crops using visual surveys. *Can. J. For. Res.* 24, 2105–2112. <https://doi.org/10.1139/x2194-2270>.
- Koenig, W.D., Mumme, R.L., Carmen, W.J., Stanback, M.T., 1994b. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75, 99–109. <https://doi.org/10.2307/1939386>.
- Koenig, W.D., Kelly, D., Sork, V.L., Duncan, R.P., Elkinton, J.S., Peltonen, M.S., Westfall, R.D., 2003. Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos* 102, 581–591. <https://doi.org/10.1034/j.1600-0706.2003.12272.x>.
- Lashley, M.A., McCord, J.M., Greenberg, C.H., Harper, C.A., 2010. Masting characteristics of white oaks: implications for management. In: *Proc. Annu. Conf. SE Assoc. Fish & Wildl. Agencies* 63, pp. 21–26.
- Le Quesne, C., Stahle, D.W., Cleaveland, M.K., Therrell, M.D., Aravena, J.C., Barichivich, J., 2006. Ancient *Austrocedrus* tree-ring chronologies used to reconstruct central Chile precipitation variability from A.D. 1200 to 2000. *J. Clim.* 19, 5731–5744. <https://doi.org/10.1175/JCLI3935.1>.
- Martín, D., Vázquez-Piqué, J., Carevic, F.S., Fernández, M., Alejano, R., 2015. Trade-off between stem growth and acorn production in holm oak. *Trees* 29, 825–834. <https://doi.org/10.1007/s00468-00015-01162-y>.
- Monselesse, G.P., Goldschmidt, E.E., 1982. Alternate bearing in fruit trees: horticultural control of alternation. *Hort. Rev.* 4, 128–173.
- Mund, M., Herbst, M., Knohl, A., Matthäus, B., Schumacher, J., Schall, P., Siebicke, L., Tamrakar, R., Ammer, C., 2020. It is not just a 'trade-off': indications for sink- and source- limitation to vegetative and regenerative growth in an old-growth beech forest. *New Phytol.* 226, 111–125. <https://doi.org/10.1111/nph.16408>.
- Nicklen, E.F., Roland, C.A., Csank, A.Z., Wilmsing, M., Ruess, R.W., Muldoon, L.A., 2019. Stand basal area and solar radiation amplify white spruce climate sensitivity in interior Alaska: evidence from carbon isotopes and tree rings. *Global Change Biol.* 25, 911–926. <https://doi.org/10.1111/gcb.14511>.
- Norton, D.A., Kelly, D., 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Funct. Ecol.* 2, 399–408.
- Ostfeld, R.S., Keesing, F., 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.* 15, 232–237. [https://doi.org/10.1016/S0169-5347\(00\)01862-0](https://doi.org/10.1016/S0169-5347(00)01862-0).
- Patterson, T.W., Knapp, P.A., 2016. Stand dynamics influence masting/radial growth relationships in *Pinus palustris* Mill. *Castanea* 81, 314–322. <https://doi.org/10.2179/16-085>.
- Pearse, I.S., Koenig, W.D., Kelly, D., 2016. Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytol.* 212, 546–562. <https://doi.org/10.1111/nph.14114>.
- Pearse, I.S., Koenig, W.D., Knops, J.M.H., 2014. Cues versus proximate drivers: testing the mechanism behind masting behavior. *Oikos* 123, 179–184. <https://doi.org/10.1111/j.1600-0706.2013.00608.x>.
- Pearse, I.S., LaMontagne, J.M., Koenig, W.D., 2017. Inter-annual variation in seed production has increased over time (1900–2014). *Proc. R. Soc. B* 284, 20171666. <https://doi.org/10.20171098/rspb.20172017.20171666>.
- Pesendorfer, M.B., Koenig, W.D., Pearse, I.S., Knops, J.M.H., Funk, K.A., 2016. Individual resource limitation combined with population-wide pollen availability drives masting in the valley oak (*Quercus lobata*). *J. Ecol.* 104, 637–645. <https://doi.org/10.1111/1365-2745.12554>.
- R Development Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN3-900051-07-0, URL <http://www.R-project.org>.
- Rodríguez-Ramírez, E.C., Terrazas, T., Luna-Vega, I., 2019. The influence of climate on the masting behavior of Mexican beech: growth rings and xylem anatomy. *Trees* 33, 23–35. <https://doi.org/10.1007/s00468-00018-01755-00463>.
- Sala, A., Hopping, K., McIntire, E.J.B., Delzon, S., Crone, E.E., 2012. Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytol.* 196, 189–199. <https://doi.org/10.1111/j.1469-8137.2012.04257.x>.
- Santos-del-Blanco, L., Climent, J., 2014. Costs of female reproduction in a conifer tree: a whole-tree level assessment. *J. Ecol.* 102, 1310–1317. <https://doi.org/10.1111/1365-2745.12283>.
- Speer, J.H., 2001. Oak mast history from dendrochronology: a new technique demonstrated in the southern Appalachian region. Ph.D. thesis. University of Tennessee, Knoxville, TN, USA 241 pp.
- Staudhammer, C.L., Wadt, L.H.O., Kainer, K.A., 2013. Tradeoffs in basal area growth and reproduction shift over the lifetime of a long-lived tropical species. *Oecologia* 173, 45–57. <https://doi.org/10.1007/s00442-00013-02603-00441>.
- Stearns, S.C., 1989. Trade-offs in life-history evolution. *Funct. Ecol.* 3, 259–268.
- Stearns, S.C., 1992. *The Evolution of Life Histories*. Oxford Univ. Press, Oxford, U.K.
- Strong, C., Zuckerman, B., Betancourt, J.L., Koenig, W.D., 2015. Climatic dipoles drive two principal modes of North American boreal bird irruption. *Proc. Nat. Acad. Sci. (USA)* 112, E2795–E2802. <https://doi.org/10.1073/pnas.1418414112>.
- Swetnam, T.W., Thompson, M.A., Sutherland, E.K., 1985. Using dendrochronology to measure radial growth of defoliated trees. In: *USDA Agricultural Handbook*. 639 USDA Forest Service, Washington, D.C.
- Szabó, P., 2012. Sources and methods to reconstruct past masting patterns in European oak species. *Arbor. J.* 34, 203–214. <https://doi.org/10.1080/03071375.03072012.03749117>.
- Woodward, A., Silsbee, D.G., Schreiner, E.G., Means, J.E., 1994. Influence of climate on radial growth and cone production in subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). *Can. J. For. Res.* 24, 1133–1143. <https://doi.org/10.1139/x1194-1150>.
- Zwolak, R., Bogdziewicz, M., Rychlik, L., 2016. Beech masting modified the response of rodents to forest management. *For. Ecol. Manage.* 359, 268–276. <https://doi.org/10.1016/j.foreco.2015.10.017>.
- Żywiec, M., Zielonka, T., 2013. Does a heavy fruit crop reduce the tree ring increment? Results from a 12-year study in a subalpine zone. *Trees* 27, 1365–1373. <https://doi.org/10.1007/s00468-00013-00884-y>.

