

Individual resource limitation combined with population-wide pollen availability drives masting in the valley oak (*Quercus lobata*)

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Summary

1. Masting, the synchronized production of variable seed crops, is widespread among woody plants, but there is no consensus about the underlying proximate mechanisms. To understand this population-level behaviour, it is necessary to dissect the behaviour of individual trees as well as the interactions that synchronize them.

2. Here, we test a model of masting in which variability in seed set is driven by resource limitation within trees and synchrony is driven by pollen limitation due to phenological asynchrony in some years.

3. We used a 35-year seed set data set and a 12-year phenological data set to analyse seed production of 84 valley oaks (*Quercus lobata*) in central coastal California. Individual trees varied tremendously in their seed production patterns; trees with high levels of seed production were less variable over time, but showed stronger negative autocorrelation between years, suggesting that they are more resource-limited than unproductive trees. In years of more asynchronous flowering, *Q. lobata* produced fewer seeds, consistent with the importance of phenological synchrony.

4. We parametrized a model with these results to investigate how individual resource limitation and population-wide pollen limitation – a consequence of asynchronous flowering during cold spring temperatures – interact to shape annual variation in seed production. The model illustrates that this proximate abiotic driver can synchronize the behaviour of individuals, resulting in population-wide seed production patterns that closely resemble the field data.

5. *Synthesis.* Our findings support the hypothesis that an interaction between two proximate mechanisms, individual resource limitation and environmental variation affecting population-wide pollen availability, drives masting in this population of *Quercus lobata*. This combination of internal and external proximate drivers may underlie masting behaviour in many wind-pollinated plants.

Key-words: mast fruiting, masting, pollen limitation, *Quercus lobata*, reproductive ecology, resource limitation

Introduction

The intermittent, synchronous production of large seed crops, known as mast fruiting or masting behaviour, is common to many perennial plants, particularly in temperate regions (Silvertown 1980; Koenig & Knops 2000; Kelly & Sork 2002). The resulting seed crops have ecosystem-wide consequences as the resource pulses (or failures) reverberate through multiple trophic levels (Jones *et al.* 1998; Ostfeld & Keesing

2000). Masting is thought to have evolved under the selective pressures of one or more economies of scale which include increased pollination success, satiation of predators, or improved seed dispersal by mutualists (Kelly 1994; Kelly & Sork 2002; Vander Wall 2010; Archibald *et al.* 2012). Despite broad interest in this population-level phenomenon, however, there is still a lack of consensus as to its mechanistic underpinnings or its generality across taxa and geographic regions (Kelly *et al.* 2013; Crone & Rapp 2014; Pearse, Koenig & Knops 2014; Koenig *et al.* 2015).

Masting can be captured by a series of key descriptors (Table 1), including the variability of population-level and

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Table 1. Description and statistical definition of parameters used to describe seed production and masting behaviour

Parameter	Description	Statistic
N30	Annual acorn crop	30-s acorn count, combined from 15-s counts by two observers
RCS	Individual relative crop size	Percentage of maximum N30 value for whole data set achieved by individual in any given year
RCS _{pop}	Population-level relative crop size	Average RCS of all trees within a population of plants achieved within a given year
CV _p	Population-level variability of seed production	Coefficient of variation of average seed production of trees within a population over time
CV _i	Individual-level variability of seed production	Coefficient of variation of seed production in individual tree over time
ACF _i	Relationship between preceding acorn crop and current crop of individual tree	Temporal autocorrelation function of seed production, to preceding year
ACF _p	Population-wide relationship between preceding average acorn crop and current crop	Temporal autocorrelation function of population-average seed production, to preceding year
r _p	Synchrony in seed production among individuals	Mean cross-correlation of seed production among all individuals in study population

individual-level seed crop size (CV_p and \overline{CV}_i) over time, temporal autocorrelation to preceding years of reproduction at the individual and population levels (ACF_i and ACF_p) and the degree of synchrony (r_p) among individual plants in a population (Herrera *et al.* 1998; Koenig & Ashley 2003). Comparisons of these parameters and their interactions among plant populations and species have provided important insights into the role of individual- and population-level processes that regulate masting. Moderate levels of CV_p occur in populations with high \overline{CV}_i and low synchrony, or alternatively when individuals are highly synchronized but have low \overline{CV}_i ; high levels of CV_p are only achieved when \overline{CV}_i and synchrony are both high (Koenig & Ashley 2003). The extent of temporal autocorrelation of seed crops of populations (ACF_p and \overline{ACF}_i) is more negative when the variability in seed production is high (CV_p and \overline{CV}_i ; Koenig & Ashley 2003). Furthermore, in species that produce seeds in the same year as flowers are pollinated, ACF values for the prior year ($t-1$) becomes more negative with increasing seed production levels, both among populations (Liebhold *et al.* 2004) and individuals (Barringer, Koenig & Knops 2013). Identifying the drivers of masting within a given study system thus requires identifying mechanisms that determine the variability in seed production of individuals (CV_i) and its cyclical nature (ACF_i), as well as the mechanism that determines synchrony of plants within a population.

The variability and synchrony of seed production in some masting populations is thought to emerge from a mechanistic interaction between internal resource dynamics of individual plants and variable pollination success within populations (Isagi *et al.* 1997; Satake & Iwasa 2000, 2002; Crone & Rapp 2014), both of which have received independent empirical support (Sork, Bramble & Sexton 1993; Koenig *et al.* 2012; Pearse, Koenig & Knops 2014; Pearse *et al.* 2015). Seed production is energetically expensive, and the production of large crops appears to deplete a tree's resource storage (Crone, Miller & Sala 2009; Crone & Rapp 2014). Such resource depletion, in turn, is reflected in negative temporal autocorrelation in seed crop sizes, a pattern that is found for many masting species (Koenig & Knops 2000; Koenig & Ashley 2003; Liebhold *et al.* 2004). Resource limitation alone may thus explain the variability of seed production and its cyclical nature, both on the level of individuals and populations, but is insufficient to synchronize seed production across individuals or populations (Crone & Rapp 2014).

In addition to resource constraints, pollen availability has been shown to limit seed production in many plants, particularly those that are insect-pollinated, but also wind-pollinated species such as oaks (Koenig & Ashley 2003; Knight *et al.* 2005). Even in years when plants have abundant resources, abiotic conditions that prevent effective pollen transfer can hinder the production of large seed crops (Crone, Miller & Sala 2009). Flowering phenology data and pollen addition experiments in wind-pollinated oaks have recently demonstrated that pollen can be limiting in some years and suggest that pollen limitation provides the underlying mechanism for the relationship between spring temperatures and subsequent acorn crop size for valley oaks (*Quercus lobata*) in California (Koenig *et al.* 1996; Koenig *et al.* 2012; Pearse *et al.* 2015). In years of high spring temperatures, the microhabitat variability of temperature is significantly lower, resulting in more synchronous flowering of individual trees in a population, which in turn appears to reduce pollen limitation (Pearse, Koenig & Knops 2014; Koenig *et al.* 2015). Thus, this hypothesis proposes that phenological synchrony of trees may drive the synchrony of annual seed production among individuals in the population.

To investigate the proximate drivers of annual variation in seed production of individuals, we introduce a novel standardized metric of relative seed production in individuals, relative crop size (RCS). RCS scales the seed production of an individual tree in any given year to the maximum seed crop it produced during the study period (in our case, a 35-year period) and thus represents the percentage of a tree's potential crop size produced in any 1 year. Because there is broad variation in the maximum seed crops of individual tree, likely due to factors that may not be associated with masting such as age, size and access to limiting resources (Barringer, Koenig & Knops 2013), comparing RCS between years and individuals provides a relatively simple means to investigate temporally variable limitation of seed production.

Our goals here are threefold. First, we use RCS to investigate the interrelationships of the five masting descriptors

(CV_p , \overline{CV}_i , r_p , $ACF1_p$ and \overline{ACF}_i) in a 35-year data set on *Q. lobata*. Secondly, we test the phenological synchrony hypothesis using 12 years of flowering phenology to explore the role of individuals in shaping population-level effects of pollen limitation (Koenig *et al.* 2015). Thirdly, we use a set of simulation models to determine the relative contribution of resource limitation and pollen limitation to the variability and synchrony of population-level seed crop sizes observed in *Q. lobata* at Hastings Reservation.

Our models are based on that of Isagi *et al.* (1997). Resource limitation in our model is assumed to be access to water (Knops, Koenig & Carmen 2007; Barringer, Koenig & Knops 2013). To test whether pollen availability affects acorn production, we included spring temperature, the key determinant of pollen limitation in *Q. lobata* (Koenig *et al.* 2015). If resources and pollen are both limiting acorn production, we predicted that the combined model will recreate the actual pattern of seed production whereas the model of resource limitation alone would not.

Materials and methods

STUDY SYSTEM AND SITE

We studied seed production of 84 *Q. lobata* trees located on the Hastings Natural History Reservation, 40 km inland from the Pacific coast in central coastal California. The region has a Mediterranean climate with hot, dry summers, cool, wet winters, and highly variable annual rainfall (range over last 70 years: 153–1131 mm). The elevation of the *Q. lobata* trees at the study site ranges from 460 to 950 m *a.s.l.*, and they co-occur with *Q. douglasii* and *Q. agrifolia* throughout the reserve, as well as *Q. chrysolepis* and *Q. kelloggii* at higher elevations.

DATA

Acorn production

Starting in 1980, annual acorn production of 84 individual trees was quantified in early to mid-September using the visual survey method (Koenig *et al.* 1994b): two observers using binoculars counted as many acorns as they could in 15 sec, and their counts were added together to constitute N30, the annual acorn crop estimate for a tree. To calculate relative crop size (RCS) for each year, we divided N30 by the tree's maximum N30 value over the 35-year study period (1980–2014) and multiplied by 100. In contrast to other indices, RCS therefore represents the percentage of a tree's potential acorn crop produced in a specific year. To quantify the population-wide acorn crop and its variability, we calculated the mean RCS across all individuals for each year and determined the coefficient of variation of mean RCS values (CV_p) over the study period.

Phenology

From 2003 to 2014, we determined the flowering phenology of each tree by conducting weekly surveys beginning with the budburst of the first trees in the population in mid-February or early March. Using binoculars, we scored each tree based on budburst, percentage of crown leafed out, catkin stage and catkin abundance. Here, we use

the first calendar week of pollen dehiscence as the flowering date and the absolute difference of each tree from the mean flowering date of the population as the measure of flowering synchrony.

Masting metrics

To characterize masting behaviour, we calculated the mean RCS, the coefficient of variation (CV), and the lag-1 (ACF1) and lag-2 (ACF2) temporal autocorrelation of RCS for each individual and for population means (Table 1). In addition, we estimated the synchrony of population-wide acorn production by calculating the mean pairwise cross-correlation of RCS values over all trees (Bjørnstad, Ims & Lambin 1999).

Statistical analysis

All analyses were conducted in R (R Development Core Team 2015). We used Pearson correlations to determine the relationships between tree and population parameters. To isolate the effect of flowering phenology on acorn production, we constructed linear mixed models with RCS as the dependent variable, absolute relative flowering date as a fixed effect, and year as a random effect. To account for repeated sampling of the same individuals, the models also included tree ID as a random effect. We used Wald type II tests (library *car*, Fox & Weisberg 2010) to calculate χ^2 and *P*-values associate with fixed effects. Cross-correlations were calculated using the *mSynch* function in the *ncf* package, version 1.1-5 (Bjørnstad 2013) and linear mixed models were constructed in *lme4*, version 1.1-7 (Bates *et al.* 2014).

SIMULATION MODELS

Resource limitation as driver of variation

Following Isagi *et al.* (1997), our model assumed that each tree obtains a fixed amount of surplus energy (P_s) from photosynthesizing, and when the stored energy surpasses a threshold (L_t), the surplus (C_f) is invested in flowers. The pollinated flowers then bear fruit (C_a), whose production cost (R_c) is proportional to the amount of flowers, so that $L_t - C_a = L_t - R_c C_f$. After resources are depleted by flowering and fruiting, the tree accumulates P_s energy annually until it surpasses the threshold again.

By running the model across a range of parameter values, Isagi *et al.* (1997) concluded that the relative cost of fruit production (R_c) played the most important role in shaping the temporal patterns of fruit production in individual trees, because when $R_c \geq 1$, masting patterns appeared, and with increasing cost, the interval among mast years increased and more variable seed production patterns appeared. They also noted that lag-1 autocorrelation values became less negative as R_c increased. When replicating the model, we found first that ACF1_i values were strongly negatively correlated with mean RCS values of trees ($r = -0.99$; Fig. S1) in patterns that closely resembled the Hastings data (Fig. 1d), and second, that mean RCS values declined in a log–log manner as R_c values increased ($r = -0.91$; Fig. S2).

To parameterize the population-wide resource limitation model, we took advantage of the observed log–log relationship between R_c and RCS to estimate R_c values corresponding to the mean RCS values of the 84 individual *Q. lobata* trees in our data. This allowed us to model the temporal sequence of acorn production under the assumption that resource limitation alone drives variation in seed production. We simulated the seed production over the 76 years for which we

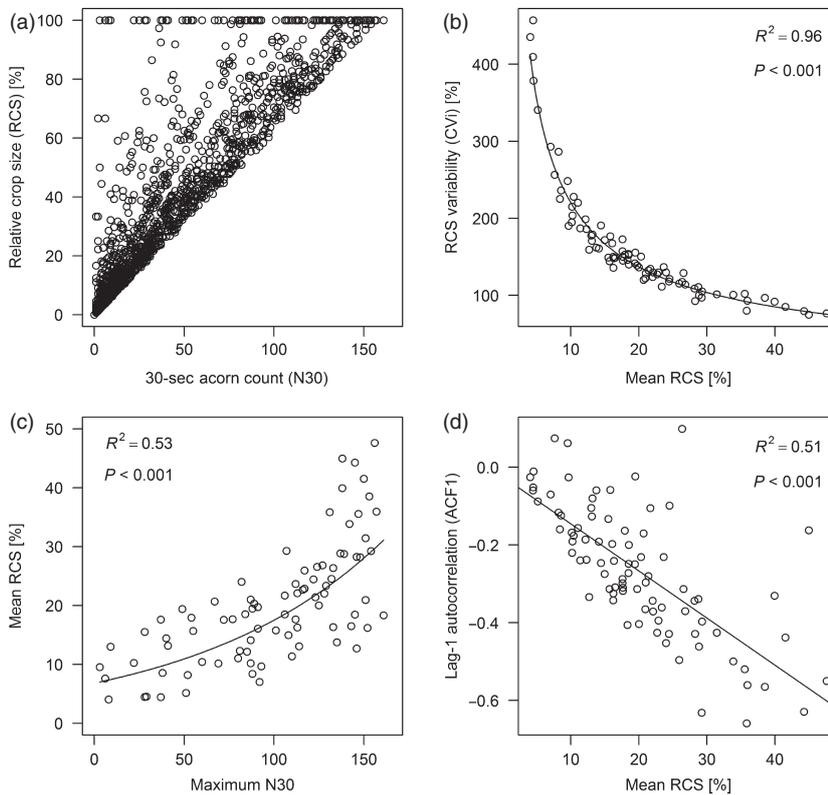


Fig. 1. Relationships among seed production and masting parameters for *Q. lobata* trees at Hastings Natural History Reservation. (a) For trees with low maximum acorn production, small acorn counts (N30) can represent high relative crop size (RCS; data for 84 trees over 35 years). Because all trees have years with complete crop failures (N30 = 0), RCS values cannot fall below the diagonal plain; (b) trees with high mean RCS produce less variable seed crops (log–log fitted curve, $n = 84$ trees); (c) trees with large maximum acorn counts consistently produce higher relative crop sizes (fit: $\log(\text{mean RCS}) \sim \text{max}(N30)$; $n = 84$ trees); (d) trees with large mean relative crop size show stronger negative lag-1 autocorrelation ($ACF1_i$; linear fit; $n = 84$ trees).

have temperature data at Hastings Natural History Reservation (see below). However, we only used the final 35 years for comparisons, which is the period for which we also had data on *Q. lobata* seed production. All trees started with the same initial settings ($P_{s,i} = 3$, $P_s = 6$, $L_t = 6$, $Cf_i(0) = 2.5$), and for each tree we calculated RCS ($C_{a,i}/C_{a,max}$) for every year and mean RCS, $CV(RCS)$ and $ACF1_i$ for the final 35 years. Similarly, we calculated all five masting metrics (CV_p , \overline{CV}_i , \bar{r}_p , $ACF1_p$ and \overline{ACF}_i) for the simulated population over the 35-year period (Table 2).

Pollen limitation as a driver of variation and synchrony

To investigate the effect of pollen limitation on the variation of seed production in individual trees, we combined the resource limitation

model with a modified version of the model derived in Koenig *et al.* (2015) linking annual population-wide acorn crop size to the mean maximum daily temperature of April (\bar{T}_{max}) by simulating the key mechanism that affect flowering synchrony. The first step links \bar{T}_{max} to the variability of microclimate (CV_{temp}) among trees, the second step links CV_{temp} to the variability in flowering initiation dates (CV_{flow}), and the third step links CV_{flow} the acorn crop. To simulate the same mechanism on the level of individual trees in the absence of flowering phenology data available for the entire time period, we scaled each tree's annual acorn crop calculated by the resource limitation model to \bar{T}_{max} by multiplying $C_a \times (100 - 10 \times (\max(\bar{T}_{max}) - \Delta\bar{T}_{max}))/100$ (R code of simulation model provided in supplementary materials). This allowed us to model the effect of resource and pollen limitation over the 76-year period for which temperature

Table 2. Masting parameters for real and simulated populations of 84 *Q. lobata* trees: (A) population level and (B) individual level*

Masting metric	Data	Short model		Long model		
		Resources only	Resources & pollen	Resources only	Resources & pollen	
(A) Population level						
Mean acorn crop	(\overline{RCS}_p)	20.0	17.7	18.9	17.4 ± 0.1	14.0 ± 0.3
Variability	(CV_p)	91.5	20.1	72.9	18.2 ± 2.7	79.3 ± 14.3
Autocorrelation	$(ACF1_p)$	-0.53	-0.28	-0.41	-0.43 ± 0.1	-0.43 ± 0.10
Synchrony	(r_p)	0.56	0.26	0.48	0.00 ± 0.00	0.29 ± 0.10
(B) Individual level						
Mean acorn crop	(\overline{RCS})	19.9	17.8	18.2	17.4 ± 0.1	14.4 ± 0.4
Variability	(CV_i)	163.7	193.3	150.3	198.5 ± 3.0	155.8 ± 11.0
Autocorrelation	$(ACF1_i)$	-0.31	-0.33	-0.36	-0.33 ± 0.01	-0.34 ± 0.05

Acorn crop size, variability and lag-1 autocorrelation for population means, as well as the means calculated across all individuals for the same time span. Synchrony was calculated as mean pairwise cross-correlation for all trees. *Short Model*: measures for last 35 years of 76-year simulations; *Long Model*: measures for 965 35-year intervals from 1000-year simulation.

*Mean \pm standard deviation.

data was available. To compare the performance of the two simulation models to the *Q. lobata* population at Hastings, we calculated RCS values and other masting metrics for the final 35-year period and used Pearson correlations to compare population-level RCS values.

In order to quantify concordance between the simulation models and the field data, we used expanded simulation models ('long models') to estimate variability in the 35-year masting simulations. First, we ran the two simulation models (resource limited only vs. resource and pollen limited) of the seed production of the 84 trees over a 1000-year time period, starting with the same values as the 76-year models ('short models'). To simulate realistic levels of pollen limitation, we randomly drew 1000 mean maximum April temperature values (\bar{T}_{\max}) from the 76 years of Hastings weather data with replacement after excluding outliers beyond the 95% CI of the mean. Using a sliding 35-year sliding window, we then calculated masting metrics for 965 iterations of simulated seed production and report their mean and standard deviation. For each iteration, we also calculated correlation coefficients (Pearson's r) between the simulated population-wide RCS and the Hastings *Q. lobata* data. Because the random drawing of temperature data for the extended simulation effectively permuted the pollen limitation aspect of the model, we were able to compare the correlation coefficients of the short models (parameterized with the actual temperature data) and the field data to the distribution of the correlation coefficients from the long model (Fig. S6). To test whether the short model coefficients were significantly non-random, we calculated the 97.5% quantile of the distribution of long model correlation coefficients, assuming a two-tailed $\alpha = 0.05$.

Results

VARIATION AMONG INDIVIDUAL TREES

Individual trees varied considerably in the extent and temporal variability of acorn production. The mean (\pm SD) maximum N30 value over 35 years was 99.2 ± 42.9 . Relative crop size (RCS) correlated strongly with N30 values ($r = 0.94$), and revealed that, for some trees, even low N30 values can constitute a large proportion of their maximum acorn crop (Fig. 1a).

Over the full 35-year period, mean RCS for individuals ranged from 4.1% to 47.6%, with a mean (\pm SD) of

$19.9\% \pm 9.9\%$. CV_i of acorn production ranged from 74.9% to 457.0% (mean \pm SD = $163.7\% \pm 76.4\%$), and $\ln(CV_i + 1)$ declined with $\ln(\overline{RCS})$ of individual trees (Fig. 1B; $F_{1,83} = 1,934$; $P < 0.001$). Trees with large maximum N30 values had higher average RCS, and the relationship was best described by a regression of $\ln(\overline{RCS} + 1)$ on maximum N30 values (Fig. 1c; $F_{1,83} = 95.2$; $P < 0.001$).

Productive trees with high mean RCS values exhibited a stronger negative autocorrelation with acorn production the previous year ($ACF1_i$) but not the year before that ($ACF2_i$) (Fig. 1d; $ACF1_i$: $F_{1,83} = 91.5$, $P < 0.001$, $ACF2_i$: $F_{1,83} = 0.7$, $P = 0.39$). To confirm that this was not a mathematical consequence of higher average RCS values, we shuffled the order of RCS values for each tree 100 times, calculated the $ACF1_i$ value and averaged it across all repetitions. The simulated data showed no correlation between \overline{RCS} values and average $ACF1_i$ values of randomized counts (Fig. S3; $F_{1,83} = 0.8$; $P = 0.36$), indicating that the specific temporal sequence of RCS resulted in the significant correlation with $ACF1_i$.

Similarly, we detected a significant positive relationship between individual variability in seed production (CV_i) and lag-1 autocorrelation ($ACF1_i$: $r = 0.64$; $F_{1,83} = 60.3$; $P < 0.001$). Trees with less overall variation in seed production were more negatively autocorrelated in their seed production in relation to the previous year, but not the year before that ($ACF2_i$: $F_{1,83} = 1.7$; $P = 0.19$).

POPULATION-LEVEL METRICS OF MASTING

Over the full 35-year period, the population-wide RCS ranged from 0.3% to 72.5% with a mean (\pm SD) of $20.0\% \pm 18.3\%$ (Fig. 2a; Table 2A). The population-level variability of acorn crops was higher and negative autocorrelation stronger than the average across individual trees (Table 2A). Mean pairwise synchrony in the 12-year data set was $\bar{r}_p = 0.49$ (range: 0.41–0.55); using the full 35-year data set (range: 0.49–0.62).

Trees produced larger acorn crops when they flowered in synchrony with the population. In the 12-year phenology data set, RCS values declined with absolute relative flowering date

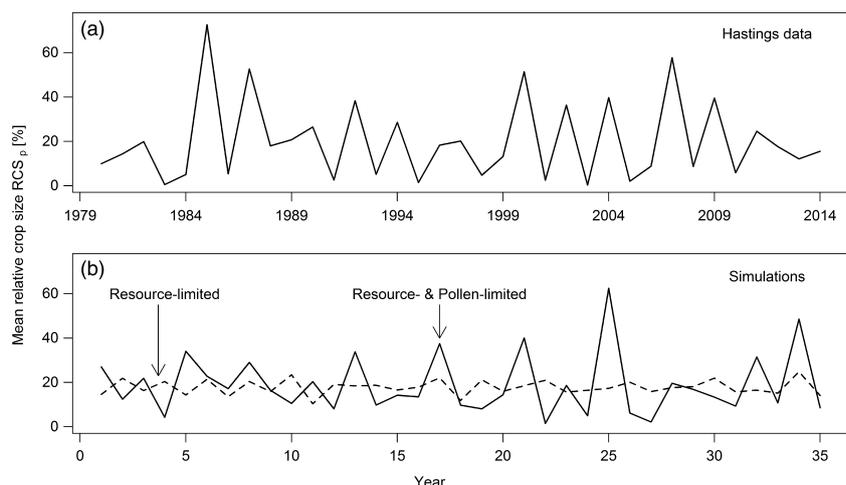


Fig. 2. Population-wide seed production (RCS_p) over 35 years for (a) Hastings population of *Q. lobata* and (b) simulated populations of resource-limited (dashed line) and resource- and pollen-limited (solid line) trees. Simulations were run over 76 years; last 35 years are shown for comparison. ($n = 84$ trees).

when controlling for year (Fig. 3; LMM; $\chi^2 = 12.7$, $df = 1$, $P < 0.001$).

SIMULATION MODELS

The simulated population limited by pollen and resources exhibited masting metrics that closely resembled those of the Hastings *Q. lobata* trees, while the simulated population that was only resource limited failed to do so (Figs 2 and S4). Over the 35-year period, the RCS values of the combined model correlated significantly with the data ($r = 0.43$, $P = 0.009$), while values simulated in the resource limitation model did not ($r = 0.1$, $P = 0.6$). CV_p , \overline{CV}_i and r_p were all more accurately replicated in the model of the pollen limited population, which also behaved in a similar manner as the Hastings population (Table 2).

The long models that simulated the tree population's behaviour over a period of 1000 years confirmed the findings from the shorter 76-year model (Fig. S5), with the exceptions that mean RCS values and synchrony were lower (Table 2). Population-level and individual-level variability (CV_p and \overline{CV}_i) estimates as well as the lag-1 autocorrelation ($ACF1_i$ and $ACF1_p$) of the combined (resource- and pollen-limited) short model and the data both were within a standard deviation of the combined long model means, while the data estimates were all more than five standard deviations from the estimates of the resource-only model. Synchrony was lower in the long models than in the short models (Table 2). In addition, we found that the correlation coefficients between the Hastings *Q. lobata* data and the simulated RCS_{pop} values in the short model were significantly higher than expected, as illustrated by the model that contained the permuted spring temperature values (Fig. S6).

Discussion

To identify the proximate mechanisms underlying population-wide seed production patterns in masting species, it is necessary to dissect the behaviour of individual plants as well as the interactions that synchronize their behaviour (Herrera *et al.* 1998; Koenig & Ashley 2003; Crone & Rapp 2014).

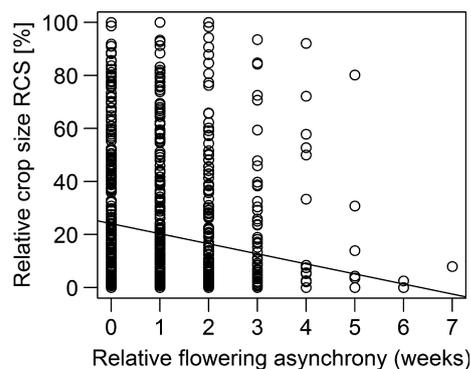


Fig. 3. Relative crop sizes (RCS) decline significantly with relative flowering asynchrony (LMM with random effect year; $\chi^2 = 12.7$, $df = 1$, $P < 0.001$). Data for 84 trees over 12-year time span.

Here, we investigated the drivers of masting behaviour in a population of *Q. lobata* using data from 84 individual trees over a 35-year period. By combining the effects of resource limitation in individual trees and population-wide pollen limitation in a simulation model, we found that pollen limitation can synchronize individual trees in this population that are resource limited, ultimately leading to realistic population-wide masting patterns.

INDIVIDUAL VARIATION IN SEED PRODUCTION

To describe annual seed production of individual trees, we calculated a new metric, relative crop size (RCS), by scaling annual acorn counts (N30) to each tree's maximum acorn count in our 35-year data set. This focused our analyses on the mechanistic underpinnings of interannual variation in seed set rather than factors that determine variation in seed production of trees within a year (such as water potential; Barringer, Koenig & Knops 2013). The absolute number of seeds produced is important when considering predation- and dispersal-related fitness benefits and costs (Kelly & Sork 2002; Vander Wall 2010), but RCS values provide a standardized metric that sheds light on the temporal patterns of internal resource dynamics of individual trees. For example, if two trees have the same N30 value in a given year, one may only have reached half of its potential acorn crop ($RCS = 50$), while the second tree produced its maximum acorn crop ($RCS = 100$; Fig. 1A). When comparing reproduction and its synchrony among a population of trees that vary tremendously in size, access to water or light, and competition with other species, RCS thus provides a tool to determine the proportional impact of temporally limiting factors.

We found that trees that produced large acorn crops (large maximum N30) did so on a consistently high level (high \overline{RCS}) with less variability (CV_i low) than trees that only produced few acorns throughout the study period. Most importantly, we found that these prolific trees also exhibited the strongest negative autocorrelations with the RCS of the previous year ($ACF1_i$), supporting a role for resource limitation in shaping temporal patterns of seed production in individual trees (Sork, Bramble & Sexton 1993; Koenig *et al.* 1994a; Crone & Rapp 2014).

POLLEN LIMITATION SYNCHRONIZES SEED PRODUCTION AMONG INDIVIDUALS

Recent work suggests that, in addition to resource limitation, annual variation in pollen limitation affects population-wide seed crop size in oaks (Pearse *et al.* 2015), which may also explain the strong relationship between spring temperature and seed production in this species (Koenig *et al.* 1996; Pearse, Koenig & Knops 2014). We found additional support for this phenological synchrony hypothesis by analysing data on the trees' flowering phenology and synchrony over a 12-year period. In addition to the established relationship between population-wide flowering synchrony and RCS, our results showed that more asynchronous trees also produced

lower RCS than synchronously flowering trees (Fig. 3). This finding further supports a central role of pollen limitation in shaping the seed production patterns of individuals in this population (Koenig *et al.* 2015; Pearse *et al.* 2015).

To investigate how resource limitation of individual trees may interact with population-wide pollen limitation to determine seed production patterns, we parameterized the model of Isagi *et al.* (1997) with data derived from the *Q. lobata* Hastings population. We first modelled a population of individual trees that are resource limited in a way that reflects the ACF1_i of the 84 trees in our study, but without pollen limitation. While the simulated trees showed realistic $\overline{\text{RCS}}$ and $\overline{\text{CV}}_i$ values, population-level metrics, such as RCS variability ($\text{CV}_p = 20.1$) and synchrony ($\bar{r}_p = 0.26$), were much lower than the field data (Fig. 2B; Table 2). Thus, as expected, resource limitation alone was enough to drive individual variability but not population-wide synchrony (Isagi *et al.* 1997; Satake & Iwasa 2002; Crone & Rapp 2014).

Including the abiotic variable that correlates most strongly with pollen limitation in *Q. lobata* (mean maximum April temperature; Koenig *et al.* 2015) dramatically improved the simulation model. Mean individual and population-level variability of RCS in the simulated population were only slightly lower than in the field data ($\overline{\text{CV}}_i = 150.3$; $\text{CV}_p = 72.9$ compared to $\overline{\text{CV}}_i = 163.7$; $\text{CV}_p = 91.5$), and the level of synchrony was twice as high compared to the resource model and similar to the field data ($\bar{r}_p = 0.47$ compared to $\bar{r}_p = 0.56$). The simulated population behaved in a way that resembled the field data, although it does not fully reproduce it (Fig. 2, Table 2).

These simulation models do not test hypotheses about the proximate mechanisms underlying masting in oaks, but serve to illustrate that the interaction of individual-level, cyclical behaviour, combined with a synchronizing mechanism that affects the whole population such as the variation of abiotic conditions, can reproduce population-level behaviour that closely resembles the masting dynamics of a population. It is important to note that the synchronizing mechanism in our model (spring temperature) is not autocorrelated ($\text{ACF1} = 0.04$ over the study period) and thus, by itself, cannot drive cyclical behaviour observed in the seed production of the population. Similarly, the model confirms that resource limitation alone does not recreate real-world behaviour of the plants. Rather, a combination of internal resource limitation and environmental constraints on flowering or seed production, which are common in plants, can drive mast-seeding behaviour comparable to that observed in natural populations (Rees, Kelly & Bjørnstad 2002; Crone & Rapp 2014). What sets our model apart from previous work, however, is that the mechanism that connects the variation in the abiotic parameter to the reproductive success is well understood. Spring temperatures drive the variation among the microhabitats of individual trees, which in turn affects flowering synchrony that determines the population-wide degree of pollen limitation (Koenig *et al.* 2012; Koenig *et al.* 2015; Pearse *et al.* 2015).

MECHANISTIC AND CUE-BASED MODELS UNDER CLIMATE CHANGE

Our results and simulation models provide support for a mechanistic link between environmental conditions and seed production in a masting tree. In contrast to the recent suggestion that seed production in masting species is based on ΔT , the cue of differences in spring temperatures between the two preceding years (Kelly *et al.* 2013), the combination of pollen and resource limitation provides a mechanism that does not require individual plants to store information about past events (Pearse, Koenig & Knops 2014). The annual variation in environmental heterogeneity and its effect on phenological synchrony may be important in a number of species in which conditions during flowering and seed development correlate with subsequent seed production (Koenig *et al.* 2015). In addition to temperature, other abiotic drivers of individual plant behaviour, such as precipitation or water stress, may synchronize the seed production of resource-limited individuals of a population. As the understanding of proximate drivers of masting is increasing, we predict that a variety of combinations of mechanistic individual- and population-level drivers will be identified in study systems of masting.

The mechanistic hypothesis supported here and the cue-based model proposed by Kelly *et al.* (2013) make very different predictions about the potential effect of global change on masting behaviour. In masting based on differential cue variables such as ΔT , changes in mean temperature are predicted to have no effect on the intensity of masting, assuming that the variation around the mean remains comparable to the present (Kelly *et al.* 2013). If phenological synchrony drives population-wide synchrony and masting, however, an increase in mean temperature could reduce the microhabitat variability among sites, weaken the degree of pollen limitation and thus lower the intensity of masting (Koenig *et al.* 2015). In terms of our simulation models, the population-level variation in seed production would deviate from the combined model towards the resource limitation model (Fig. 2b).

Conclusion

A number of questions remain. What is the generality of the combination of resource limitation and environmental constraints across plant taxa? Crone & Rapp (2014) point out that, to date, both aspects have only been addressed in few masting systems. They also highlight the fact that there are a number of resources that could limit seed production between years. In *Q. lobata* (as well as *Q. douglasii* and *Q. agrifolia*), trees that are less water-limited, as measured by xylem water potential, have higher overall acorn productivity, and productive trees also display a stronger degree of negative autocorrelation (ACF1_i ; Barringer, Koenig & Knops 2013). In the Spanish *Q. ilex*, acorn production of individual trees was also correlated with hydraulic conductivity (Carevic *et al.* 2014), and is generally linked to water availability (Pérez-Ramos *et al.* 2010). At Hastings, soil nitrogen likely affects the photosynthetic capacity of individuals, as evidenced by a positive

relationship with summer nutrient levels in leaves (Knops & Koenig 1997).

Several recent studies also found that the carbohydrates used to produce mast seed crops are photosynthesized in the year of the crop, rather than previously stored (Hoch *et al.* 2013; Ichie *et al.* 2013). Trees with better access to water and nitrogen may therefore generally be able to photosynthesize more efficiently, allowing them to quickly accumulate resources, and in turn produce larger acorn crops. However, the internal resource dynamics that prevent trees with high mean RCS from producing large acorn crops every year, as evidenced by their strong degree of negative autocorrelation, are unclear.

In conclusion, we found evidence for resource limitation in individual trees, and for pollen limitation across the *Q. lobata* population in central coastal California. While the interaction of these two proximate mechanisms has previously been reported for experimental plant populations (Crone, Miller & Sala 2009) and for flowering in a natural population of snow tussocks (Rees, Kelly & Bjørnstad 2002), this study provides evidence for a direct, mechanistic link between variation in abiotic parameters, individual resource limitation and seed production in a natural population of masting trees.

Acknowledgements

We thank Dave Kelly and an anonymous referee for their comments. We also thank the Hastings Natural History Reserve director Vince Voegeli for continued support and Brian Barringer for collecting phenology data. This research was funded by NSF grant DEB-1256394 to WDK.

Data accessibility

Data deposited in Dryad repository: <http://datadryad.org/resource/10.5061/dryad.b58j2> (Pesendorfer *et al.* 2016).

R scripts: uploaded in online supporting information (Appendix S2).

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Received 20 October 2015; accepted 28 January 2016
 Handling Editor: Kenneth Whitney

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplemental figures S1–S5.

Appendix S2. R code for simulation models of masting in *Quercus lobata*

Figure S1. The relationship between mean crop size and autocorrelation to the acorn crop of the previous year in Isagi *et al.* (1997).

Figure S2. The relationship between mean RSC and the cost of flowering (R_c) in the model of Isagi *et al.* (1997).

Figure S3. Autocorrelation values depend on specific sequence of seed production values over time.

Figure S4. Proportional distribution of RCS_{pop} for Hastings data and 35-year simulations.

Figure S5. Proportional distribution of RCS_{pop} values over 1,000-year simulations.

Figure S6. Distribution of correlation coefficients between RCS_{pop} values of combined long model and Hastings *Q. lobata* data.