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What drives masting? The phenological synchrony hypothesis

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Abstract. Annually variable and synchronous seed production, or masting behavior, is a widespread phenomenon with dramatic effects on wildlife populations and their associated communities. Proximally, masting is often correlated with environmental factors and most likely involves differential pollination success and resource allocation, but little is known about how these factors interact or how they influence seed production. We studied masting in the valley oak (*Quercus lobata* Née), a California endemic tree, and report evidence that phenological synchrony in flowering driven by microclimatic variability determines the size of the acorn crop through its effects on pollen availability and fertilization success. These findings integrate two of the major factors believed to influence seed production in wind-pollinated species—environmental conditions and pollen limitation—by means of a coherent mechanistic hypothesis for how highly variable and synchronized annual seed production is accomplished. We illustrate how, by means of a simulation based on the mechanism proposed here, climate change may influence masting patterns through its effects on environmental variability.

Key words: Hastings Natural History Reservation, coastal California, USA; mast fruiting; masting; phenological synchrony; phenology; pollen limitation; *Quercus lobata*; valley oak.

INTRODUCTION

Masting or mast fruiting consists of both highly variable seed production between years and synchrony in seed production within years among individuals within a population (Koenig and Knops 2000, Kelly and Sork 2002, Koenig et al. 2003). Within communities, masting can have dramatic effects. For example, work in eastern deciduous forests has demonstrated that the variable acorn crop initiates a “chain reaction” of responses that cascade through the ecosystem, affecting densities of deer, mice, ground-nesting birds, gypsy moths, and the tick vectors of Lyme disease (Elkinton et al. 1996, Ostfeld 1997, Jones et al. 1998, McShea 2000, Ostfeld and Keesing 2000). Equally dramatic effects of mast seeding on animal populations have been documented in European (Jedrzejewska and Jedrzejewska 1998, Satake et al. 2004), boreal (Koenig and Knops 2001), New Zealand (Kelly et al. 2008), and Malaysian dipterocarp forests (Curran et al. 1999, Curran and Leighton 2000).

Functionally, it is generally believed that masting serves to either reduce long-term seed predation by limiting predator populations (the “predator satiation” hypothesis; Janzen 1971), or to increase pollination efficiency through synchronized flowering effort (Moraireira et al. 2014), an effect most likely to be observed in wind-pollinated species that make up a high proportion

of masting taxa (Smith et al. 1990, Kelly et al. 2001). Proximally, masting frequently correlates with environmental cues such as temperature or rainfall potentially associated with resources that are in turn allocated so as to exaggerate variation in seed production among years (Kelly and Sork 2002, Kelly et al. 2013). Notably, however, little attention has been paid to the mechanisms driving this process (Pearse et al. 2014), despite considerable work investigating the factors promoting the evolution of wind pollination (Regal 1982, Whitehead 1983, Cully et al. 2002). In valley oaks (*Quercus lobata*) in central coastal California, USA, for example, there is a strong positive correlation between mean maximum April temperature and subsequent acorn production (Fig. 1). How and why do temperatures, specifically in April, correlate with subsequent acorn production?

Here we propose a novel hypothesis linking temperature and variable seed production in the valley oak. The hypothesis involves annual variability in microclimatic conditions driving differences in phenological patterns in the population. The hypothesis is a mechanistic one, and assumes pollen limitation, which, although rarely tested in wind-pollinated species (Koenig and Ashley 2003), has been demonstrated to have an important effect on seed production in valley oaks (Koenig et al. 2012; Pearse et al. 2015). The hypothesis also provides an alternative to the “weather as a cue” hypothesis proposed by Kelly et al. (2013) by proposing that the correlation between weather and seed production in this species is due to a direct, mechanistic

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relationship linking these two factors (Pearse et al. 2014). The hypothesis is specifically at the proximate level, and thus is complementary to functional explanations for masting such as predator satiation and pollination efficiency.

The valley oak is a deciduous, wind-pollinated, monoecious tree species endemic to California, widespread within the state (Griffin and Critchfield 1972), and of considerable conservation interest due to diminished recruitment (Tyler et al. 2006), the potentially adverse effects of climate change (Kueppers et al. 2005, Sork et al. 2010), and, in some sites, limited gene flow due to reduced pollen availability (Sork et al. 2002a). Selfing and hybridization with the closely related and often sympatric blue oak (*Q. douglasii*) are relatively rare (Craft et al. 2002, Sork et al. 2002b, Abraham et al. 2011). Meanwhile, annual variability in acorn production is high (mean annual coefficient of variation = 111.7%), is strongly correlated with mean maximum spring temperatures (Fig. 1; see Koenig et al. 1996), and is driven largely by annual differences in abortion rates among flowers caused by a combination of pollen limitation, resources, and other factors (Koenig et al. 2012; Pearse et al. 2015).

THE PHENOLOGICAL SYNCHRONY HYPOTHESIS

We propose four steps linking the strong, highly significant relationship between mean maximum spring temperature and the subsequent acorn crop (Fig. 2). First (step 1), we hypothesize that temperature during the spring correlates with the homogeneity of microclimatic conditions throughout the study area. Specifically, we propose that cold spring temperatures (which also tend to be wet, because there is a strong negative correlation between temperature and rainfall in this region) correlate with relatively heterogeneous microclimatic conditions throughout the study site, whereas warm, dry spring temperatures result in relatively homogeneous conditions. Second (step 2), we hypothesize that the differences in microclimatic heterogeneity proposed in step 1 drive differences in phenological variability, or synchrony, within the population. That is, during cold years when the heterogeneity in microclimate is great, variability in flowering is large and trees flower asynchronously, whereas in warm years the relatively homogeneous microclimate results in synchronous flowering and pollen production among trees in the population.

Third (step 3), we hypothesize that the differences in phenological synchrony proposed in step 2 drive differences in pollen availability. Specifically, synchronous flowering leads to relatively synchronous (and thus high) pollen availability because trees within the population tend to be flowering and producing pollen at the same time, whereas asynchronous flowering leads to relatively asynchronous and, thus, low pollen availability. Finally (step 4), we hypothesize that differences in pollen availability drive differences in

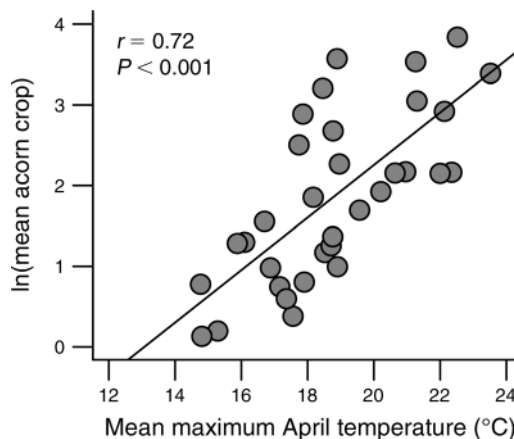


FIG. 1. Relationship between mean maximum April temperature and the mean (ln-transformed) acorn crop the following autumn for 84 valley oak (*Quercus lobata*) trees at Hastings Natural History Reservation in the Santa Lucia Mountains, central coastal California, USA. The observation period was $N = 33$ years (1980–2012). See *Materials and methods: Acorn production* for details on measuring crop size.

fertilization success, with low fertilization success and small acorn crops in cold years and high fertilization success and large acorn crops in warm years.

MATERIALS AND METHODS

Species and study site

We studied a population of 84 mature *Q. lobata* trees at Hastings Natural History Reservation, located in the Santa Lucia Mountains of central coastal California, between 1980 and 2012 (see Plate 1). *Q. lobata* is a winter-deciduous species in the white oak subgenus (*Quercus*) and matures acorns in a single season.

Hastings is ~40 km inland and ranges in elevation from 460 to 950 m. The region has a mediterranean climate of dry summers and wet winters; annual rainfall ranges from 153 to 1131 mm (over 73 years, from 1940 to 2012, inclusive), with a mean (\pm SD) of 526 ± 192 mm. Oak (genus *Quercus*) is the dominant genus throughout the study site. Five species are common, including *Q. lobata*, *Q. douglasii*, and *Q. agrifolia* at lower elevations, joined by *Q. chrysolepis* and *Q. kelloggii* at higher elevations.

Data

Overall environmental conditions were measured by a weather station located at Hastings Reservation headquarters. Three sets of data were gathered on each tree, from which we calculated variability in microclimate and phenology.

Microclimate.—Small automated temperature recorders (iButtons; Maxim Integrated Products, Sunnyvale, California, USA) were located on the north side of each tree ~1.5 m above ground, thus providing a measure of microclimate that was consistent across trees. iButtons were programmed to record temperatures at 4-h

intervals starting at 04:00 hours each day; thus, six recordings were made daily at 04:00, 08:00, 12:00, 16:00, 20:00, and 24:00 hours. For the analyses performed here, we calculated the mean of the daily maximum temperatures for each tree for each year between 1 March and 30 April, encompassing the period when budburst takes place in this population (Koenig et al. 2012). iButtons were first deployed in 2004 and were available for all trees by 2009 (minimally for 59 of the trees in 2005 and 2006).

Phenology.—Each spring from 2003 to 2012, starting on or before 1 March, we surveyed trees weekly for budburst and flowering activity. Each tree was examined with binoculars and scored based on budburst, catkin stage, and catkin number. For the analyses performed here, budburst was used as a proxy for flowering and pollen production, which follow budburst by an average of 12.3 days (Koenig et al. 2012). Budburst was used as the measure of phenology because it was relatively easy to quantify objectively and was thus likely to entail the least error. Analyses conducted here involve the Julian date in each year when a tree was determined to have undergone budburst, defined as the first date on which at least 5% of the tree had leafed out and was green.

Acorn production.—Acorn production was determined in early- to mid-September starting in 1980 by means of visual surveys in which two observers counted as many acorns as they could on each tree in a 15-s period, a technique that has been found to provide a good index of acorn availability under most conditions (Koenig et al. 1994a). Counts of acorns were added together (variable “N30”) and ln-transformed ($\ln(N30 + 1) = LN30$) in order to reduce the correlation between the mean and the variance.

Estimating variability.—For each year, we calculated variability among trees (estimated by the coefficient of variation; $CV = \text{standard deviation} \times 100/\text{mean}$) for two sets of variables: (1) the mean maximum daily temperature in microclimate during the spring budburst and flowering period (1 March–30 April, $N = 9$ years), and (2) mean budburst date ($N = 10$ years). CVs were used as the standard measure of relative variability used in studies of masting (Koenig et al. 2003). However, in order to avoid the statistical problems of using a ratio variable when correlated against the original scaling variable (Lewontin 1966, Atchley et al. 1976), we also report results using the standard deviation of the ln-transformed values of relative microclimatic variability vs. mean maximum spring temperature in the analysis where this is an issue.

Relationships were determined by Pearson correlations. All analyses were conducted in R2.15.1 (R Development Core Team 2012).

Simulation of acorn production

In order to estimate how climate change might be expected to influence masting behavior of *Q. lobata*, given the mechanism linking weather and masting

proposed here, we conducted simulations estimating variability in acorn production for each of seven mean maximum spring (1 March–30 April) temperatures (16–23°C; observed mean \pm SD for the years 1980–2012 = $17.9^\circ \pm 2.0^\circ\text{C}$; range between 1939 and 2012 was 13.6–22.3°C). For each set of trials, we started with the mean (ln-transformed) acorn crop chosen randomly from the observed distribution (mean \pm SD) of 1.87 ± 1.05 . We then simulated 33 years of acorn production (matching the length of the observed data) using the following iterative procedure:

- 1) We randomly chose a value for the mean maximum spring temperature from a distribution centered on the mean for the run (16° to 23°C) and a SD equal to the observed value of 2.0°C. Then, based on the relationships in the actual data, we:
- 2) calculated the CV in spring microclimate using the mean maximum spring temperature chosen in step 1;
- 3) calculated the CV in flowering phenology (phenological synchrony) using the CV in microclimate determined in step 2; and
- 4) determined the size of the current year’s acorn crop using the CV in flowering phenology determined from step 3 along with the prior year’s acorn crop.

Although not included elsewhere in the model, the prior year’s acorn crop was included in step 4 because previous analyses have shown that acorn production in several species of oaks is negatively autocorrelated with a 1-yr time lag (Koenig et al. 1994b), a relationship implying that acorn production requires a significant investment in resources requiring more than a year to recover (Sork et al. 1993). In the case of *Q. lobata*, both the acorn crop in year $x - 1$ and mean maximum April temperature in year x are significantly related to the size of the acorn crop in year x (linear regression of the mean acorn crop [ln-transformed] on spring temperature and the prior year’s acorn crop using data from 1980 to 2012 [$N = 33$ years]; for April temperature, $P < 0.001$; for prior year’s acorn crop, $P = 0.02$).

In order to standardize productivity across trials, acorn crop size was adjusted to the same mean productivity (mean ln-transformed acorn crop = 2.0) at the completion of each trial. In order to obtain estimates of variability of acorn production, we conducted 100 complete sets of trials, in which each trial consisted of a set of 33 years for each integer value of mean maximum spring temperature from 16° to 23°C. For each of the trials, we calculated the coefficient of variation (CV) of acorn production, and then, using all 100 trials at each temperature value, we calculated the mean \pm SE of the CVs to yield an index of masting. The simulation, written in R, is provided in the Supplement.

Given the potential for future climate change to increase climate variability (Meehl and Tebaldi 2004, Schär et al. 2004), additional runs were conducted, varying the standard deviation of the mean maximum

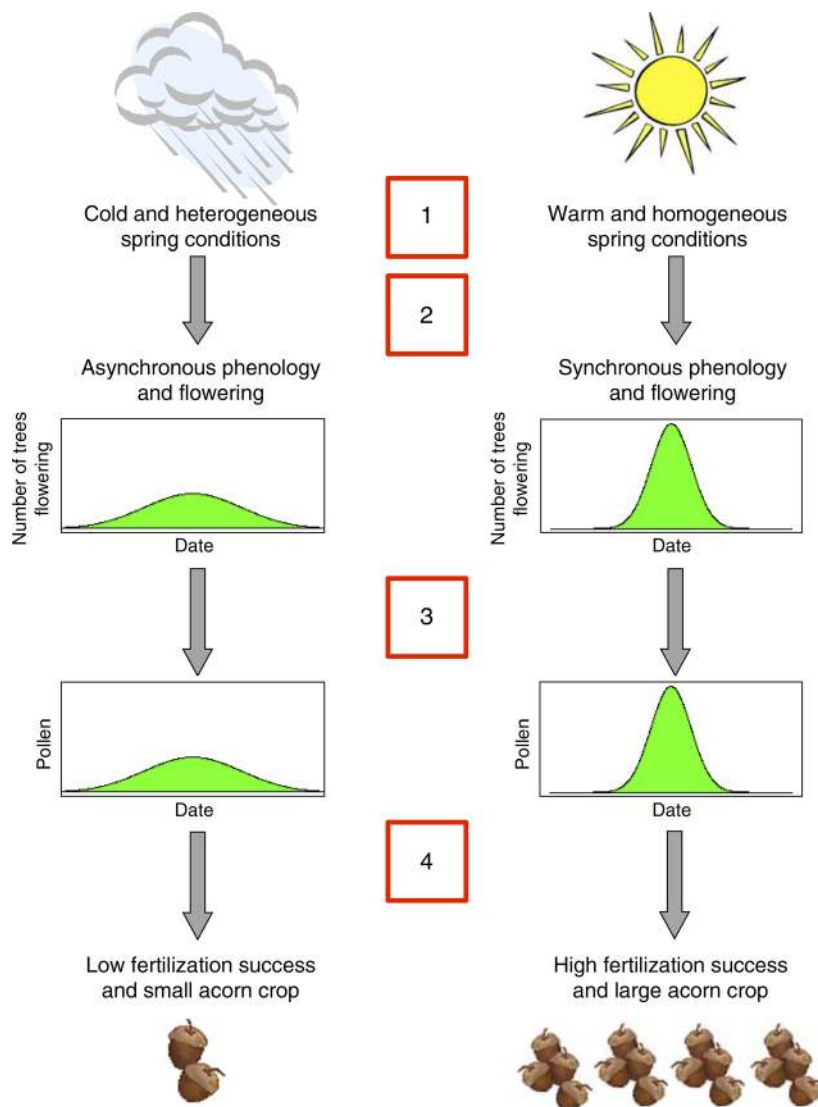


FIG. 2. Proposed relationships linking spring weather conditions to acorn production in *Quercus lobata*. Cold, wet springs (left side) correlate with spatially heterogeneous microclimatic conditions, asynchronous budburst and flowering, protracted and thus generally low pollen availability, poor fertilization success, and ultimately a small acorn crop. Warm, dry springs (right side) correlate with spatially homogeneous microclimatic conditions, synchronous budburst and flowering, and thus high pollen availability, good fertilization success, and ultimately a large acorn crop.

early spring temperature. These changes did not alter the conclusions and are not discussed further.

RESULTS

Mean temperature vs. microclimate homogeneity (step 1)

The correlation between the mean maximum temperature from 1 March to 30 April (as measured by the on-site weather station) and homogeneity of microclimate during the same time period (as estimated by the CV of mean maximum temperatures measured at each tree by the automated temperature recorders) was significantly negative ($r = -0.78$, $N = 9$ years, $P = 0.012$; Fig. 3a). Results were similar using the standard deviation of the ln-transformed mean maximum temperature rather than

the CV of the untransformed data ($r = -0.81$, $N = 9$ years, $P = 0.009$). Thus cold, wet weather in spring during the flowering period was associated with more variable and heterogeneous microclimatic conditions across the study site during the spring flowering period.

Microclimatic homogeneity vs. phenological synchrony (step 2)

Phenology of individual trees was correlated with microclimatic conditions, with trees in warmer microsites undergoing budburst and flowering earlier than trees in colder microsites (Fig. 4). Thus, step 2 in the hypothesis is that cold, heterogeneous spring conditions result in asynchronous budburst in the population,

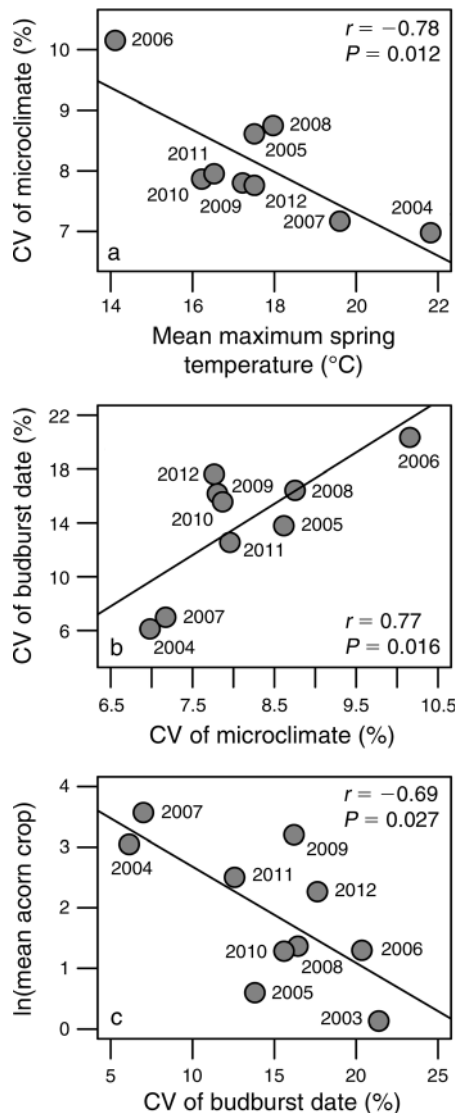


FIG. 3. Relationships between mean maximum spring temperature, variability of microclimate, variability of phenology, and the acorn crop, with correlation coefficients (r values) and P values. (a) The correlation between mean maximum temperatures during the spring flowering period (1 March–30 April) and the coefficient of variation (CV) in mean maximum microclimatic temperatures during the same period at individual *Q. lobata* trees; $N = 9$ years (2004–2012). (b) The relationship between the CV in mean maximum microclimatic temperatures during the spring flowering period at individual *Q. lobata* trees and the CV in budburst date of the same 84 trees; $N = 9$ years, 2004–2012. (c) The correlation between the CV in budburst date among the 84 individual *Q. lobata* trees and the mean acorn crop produced by the same trees the following autumn as measured by visual surveys (the ln-transformed number of acorns counted in 30 s); $N = 10$ years, 2003–2012.

whereas warm, homogeneous spring conditions result in relatively synchronized population phenology. The correlation between the CV of mean maximum temperature during the spring flowering period measured at the 84 individual trees and the CV of budburst date for the

nine years for which we have temperature data was highly significantly positive ($r = 0.77$, $P = 0.016$; Fig. 3b), as predicted.

Phenological synchrony vs. fertilization success (step 3)

Step 3 postulates a positive relationship between phenological synchrony and pollen limitation. Although no direct data on pollen availability or fertilization success are currently available, studies of *Q. ilex* and *Q. pubescens* in Spain found positive correlations between the proportion of trees with catkins and the amount of pollen in the atmosphere (Fernández-Martínez et al. 2012), and prior work has found that *Q. lobata* trees in our population that leaf out and flower in the middle of the season when more trees are in bloom produce more acorns than trees that flower early or late in the season (Koenig et al. 2012). Pollen supplementation in our population also increased acorn set in one of two years, providing experimental support for pollen limitation (Pearse et al. 2015). These results support the assumption that more pollen is available, and thus fertilization success is likely to be greater, when more trees are flowering, as occurs when budburst is more synchronized within the population. With the data currently available, however, we cannot exclude alternative hypotheses for factors that might drive a relationship between phenology variability and the success of female flowers, such as weather conditions affecting flower abortion independent of pollen availability.

Phenological synchrony vs. the acorn crop (step 4)

Finally, step 4 predicts that low pollen availability due to asynchronous flowering results in low fertilization success and a small acorn crop, whereas high pollen availability due to synchronized flowering results in high fertilization success and a large acorn

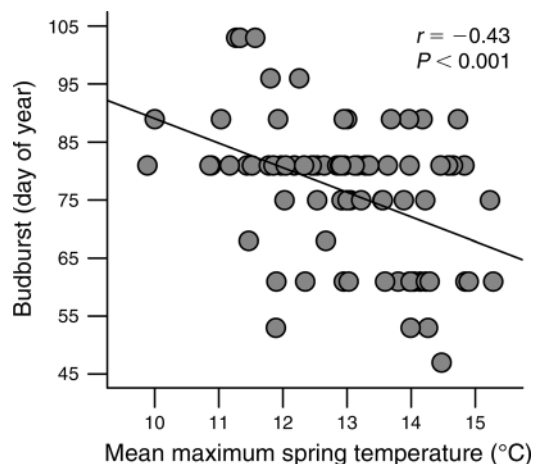


FIG. 4. Correlation between mean maximum early spring temperature at individual trees (1 January–28 February) and budburst of *Q. lobata* in 2010 ($N = 83$ trees).

crop. Prior studies have demonstrated a significant relationship between flower survivorship and the subsequent acorn crop both in valley oak (Pearse et al. 2015) and in other oak species (Sork et al. 1993, Pérez-Ramos et al. 2010), suggesting that the size of the acorn crop is at least partly determined by fertilization success of flowers. Thus, the key relationship predicted by this step is between phenological synchrony and the size of the subsequent acorn crop. With 10 years of data, this correlation is significantly negative ($r = -0.69$, $P = 0.027$; Fig. 3c), thus confirming that more asynchronous budburst correlates with smaller acorn crops, as well as completing the steps linking mean maximum spring temperatures to subsequent masting behavior.

Simulation of the potential effects of climate change

The potential effects of climate change were estimated by simulations in which variability in the acorn crop over 33-yr periods was determined based on the observed relationships between mean maximum spring temperature, microclimatic variability, phenological synchrony, prior investment, and the size of the acorn crop. Results with varying mean spring temperatures from 2°C colder to 5°C warmer than the observed value clearly illustrate how annual variability in acorn production (masting behavior) is predicted to decrease as spring temperatures increase, independent of any change in overall mean productivity (Fig. 5).

DISCUSSION

These results provide support for a novel mechanistic hypothesis for how masting is accomplished within a population of forest trees. The hypothesis is explicitly proximate, and thus is compatible with predator satiation, pollination efficiency, and other functional (ultimate-level) hypotheses (Kelly 1994, Kelly and Sork 2002).

Several aspects of the hypothesis are of interest. First, it integrates environmental conditions and pollen limitation, the two major factors generally thought to influence seed production in wind-pollinated species (Kelly and Sork 2002). Second is the manner in which the hypothesis incorporates annual differences in microclimatic heterogeneity. Although microclimate is known to vary widely, depending on a variety of physiographic factors (Vanwalleghem and Meentemeyer 2009), and is recognized as having an important influence on species distributions (Suggitt et al. 2011), it is only recently that it has become feasible to quantify microclimatic variability, and this is one of the first times that interannual differences in microclimatic variability have been quantified or used in an ecological context. We predict that microclimatic variability will be found to play a far more important ecological role as its measurement becomes more widespread.

Third, our hypothesis postulates that acorn production is affected not by the onset or mean date of any

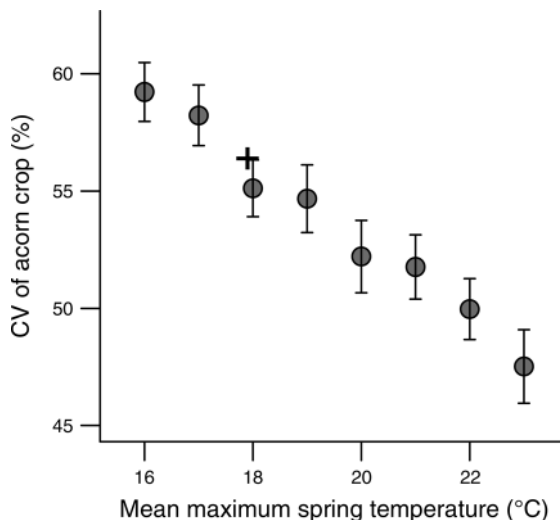


FIG. 5. The predicted masting pattern (mean \pm 2 SE of the CV of the mean annual acorn crop) of *Q. lobata* as a function of mean maximum spring temperatures as determined by computer simulations (100 runs of 33 years for each value of mean maximum spring temperature). Results are based on the observed relationships between spring temperatures, microclimatic heterogeneity, phenological synchrony, and acorn production. The overall mean acorn crop was constrained to a constant value across each set of runs. The observed value in the population is plotted as a “+.”

particular phenological event, but rather by the variability in the phenological response of the population, which we refer to as phenological synchrony. Although reproductive synchrony has long been known to be evolutionarily significant in a variety of contexts (Ims 1990) and there has been considerable study of the importance of the fitness consequences of phenological differences within populations (Schemske 1977, English-Loeb and Karban 1992, Koenig et al. 2012), the potential ecological consequences of phenological synchrony within plant populations have rarely been investigated (Augsburger 1981).

Fourth, the phenological synchrony hypothesis predicts that changes in mean temperature due to future climate change, by their effect on microclimatic variability, will alter patterns of phenological synchrony and variability in annual seed production by the population. Specifically, increased temperatures during the spring flowering period can be expected to result in a decrease in the intensity of masting. This contrasts with the temperature-differential cue hypothesis for masting recently proposed by Kelly et al. (2013), which postulates that the difference in mean temperature between years drives masting behavior, and thus that long-term changes in mean temperature are unlikely to affect variability of seed production. Although a plausible alternative to the phenological synchrony hypothesis, no mechanism by which temperature differences between years might be detectable by plants or by which plants would be able to respond with an



PLATE 1. Valley oak savanna at Hastings Reservation in Monterey County, California, USA, in the spring. Photo by W. D. Koenig.

appropriately sized acorn crop is currently known (Pearse et al. 2014).

No significant temporal changes in mean maximum spring temperatures have been observed at our study site since records were first kept in the late 1930s (correlation between mean maximum temperature 1 March–30 April and year for 1939–2012, $r = -0.01$, $P = 0.90$) or over the 33-yr period from 1980–2012 for which we have acorn production data ($r = -0.10$, $P = 0.57$). The potential effects of future climate change can be estimated, however, by means of computer simulations. Results demonstrate how the mechanism proposed here results in variability in annual acorn production (masting) decreasing as mean maximum temperatures increase, independent of their effects on overall productivity. Whether long-distance gene flow, as characterizes many wind-pollinated tree populations, might mitigate these effects (Kremer et al. 2012) remains to be seen, particularly given the variability in pollen flow observed in different populations of *Q. lobata* (Sork et al. 2002a, Abraham et al. 2011) and the potential for climate change to drive regional extinctions of this species (Kueppers et al. 2005, Sork et al. 2010).

Whether a similar mechanism integrating environmental conditions during flowering and subsequent seed production might be important in other masting systems remains to be determined. Studies in Spain attempting to relate pollen availability to acorn production in *Q. ilex* have yielded variable results (García-Mozo et al. 2007, Fernández-Martínez et al. 2012), in part due to the difficulties of measuring pollen availability; no study to

date has quantified pollen actually available to individual trees. It is, however, probable that factors beyond those considered here will be involved in the mechanisms driving masting behavior in other systems. In some cases these effects may be through their influence on phenology and pollen availability in ways parallel to those proposed here; for example, rainfall might affect phenological synchrony, and thus annual differences in pollen variability, in some systems rather than temperature. In other cases, however, completely different factors are likely to be involved. For example, water stress during the summer affecting seed maturation rather than factors related to pollen availability in the spring appears to be particularly important in several Spanish oak species (Espelta et al. 2008, Pérez-Ramos et al. 2010, Koenig et al. 2013), and it is likely that resource depletion in mast years often will affect seed production in ways that might either be in addition to or confound the effects of pollen availability (Satake and Iwasa 2000, 2002, Crone et al. 2009, Ichie and Nakagawa 2013, Miyazaki 2013). In the population of valley oaks studied here, experimental work has shown that the majority of female flowers are aborted even in the presence of excess pollen, consistent with resource depletion playing a role beyond that of pollen limitation (Pearse et al. 2015). Resource depletion is particularly likely to be important in alternate-bearing systems (Crawley and Long 1995, Crone 2013) and, more generally, systems in which there is temporal autocorrelation of seed crop size.

Although it is unlikely to be important in all systems, we predict that a mechanism based on phenological

synchrony driven by environmental heterogeneity may be important in determining variable seed production in many species in which conditions during the flowering period correlate with subsequent seed production, as is frequently the case (Koenig and Knops 2014). To the extent that phenological synchrony is involved in determining variable seed production, climate change is likely to have significant effects on patterns of seed production in other masting systems. Whether or not such changes alter overall productivity, they are likely to affect both the magnitude and frequency of resource pulses generated by masting events and thus have important ecosystem consequences.

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