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Environmental correlates of acorn production by four species of Minnesota oaks

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Abstract We measured acorn production by four species of oaks in central Minnesota over a 17-year period with the goal of understanding the proximate drivers of masting behavior. All four species exhibited significant annual variation and within-population synchrony of acorn production, although masting behavior was more pronounced in the two species that require 1 year to develop acorns ('1-year' species) than the two species that require 2 years ('2-year' species). There was also strong synchrony between species that require the same number of years to mature acorns, but not between species requiring different numbers of years. Acorn production by three of the four species correlated with spring or summer conditions, while no significant environmental correlate of acorn production was detected for the fourth species. Acorn production by none of the four species correlated significantly with variables calculated from the differences in weather conditions from 1 year to the next. These results, combined with prior studies of oaks, suggest that environmental conditions during key periods of acorn development frequently correlate with acorn production, as expected if such factors bear a direct mechanistic relationship to seed production. On the other hand, the environmental factors involve vary greatly both among species and even among populations of the same species, a result consistent with the hypothesis that environmental correlates are simply cues used by plants to synchronize reproductive investment. In

either case, our results do not support the recent proposition that variables based on differences in environmental conditions from 1 year to the next serve as a general cue for masting behavior.

Introduction

Masting or mast-fruiting—the annually variable production of seeds by a population of plants—is a widespread phenomenon particularly common in, but not limited to, temperate and boreal regions (Curran and Leighton 2000; Koenig and Knops 2000; Kelly and Sork 2002). Given that masting can be spatially synchronous over large geographic areas (Koenig and Knops 1998, 2013), it is unsurprising that the huge pulse of resources resulting from masting events can have significant ecological consequences within their respective communities (Ostfeld and Keesing 2000; Kelly et al. 2008). The proximate and ultimate factors driving masting thus have important implications for understanding the function of ecological communities.

In numerous masting systems it has been found that weather factors correlate with subsequent seed production (Sork et al. 1993; Koenig et al. 1996; Schauber et al. 2002). Only recently, however, has interest focused on the implications of such correlations in terms of the proximate factors driving this phenomenon (Pearse et al. 2013). Particularly important is the issue of whether environmental factors act merely as a cue—that is, a signal used by the plants to determine investment in flower or seed production

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that is arbitrary in that there is no direct link between the cue and the mechanism involved in the production of those structures—or whether the environmental factors that correlate with seed production do so because they have a direct physiological link to the mechanisms driving flower or seed production. If the former is true, then it is likely that climate change will have little or no effect on masting patterns (Kelly et al. 2013). In contrast, if there is a direct mechanism linking weather to seed production, then changes in climate will potentially influence variability, if not overall productivity, of seed production (Pearse et al. 2013).

We studied acorn production in four species of oaks in southeastern Minnesota, USA, from 1995 to 2011. Here we describe the masting patterns of these species, attempt to identify the environmental factors correlating with acorn production, and compare results with prior studies of oaks.

Our primary goals in these analyses are twofold. First, using the four species we studied in conjunction with studies of other oak species, we address the question of whether environmental factors act merely as cues or are instead related to some mechanism directly affecting acorn production. This latter hypothesis predicts that the environmental correlates of acorn production should in general be related to critical periods of flowering or acorn development and are likely to be similar among populations and species with comparable developmental patterns. In contrast, the cue hypothesis is consistent with the finding that environmental correlates of acorn production are highly variable and not necessarily related to any particular critical period of development.

Alternatively, a cue important to masting may extend generally across species, as recently suggested by Kelly et al. (2013). Our second goal is to examine the Kelly et al. (2013) hypothesis that differences in environmental factors from 1 year to the next (here called 'differential' or 'Δ' weather variables) serve as general proximate cues for masting by testing the relative efficacy of differential weather variables as predictors of masting in the four species of oaks studied.

Methods

Study site and species

The study was conducted at Cedar Creek Ecosystem Science Reserve in Bethel, MN, USA. We quantified acorn production each year between 1995 and 2011 for 212 marked trees of four species, including bur oak (*Quercus macrocarpa* Michx., $N = 90$), Northern pin oak (*Q. ellipsoidalis* E.J.Hill, $N = 90$; subsequently referred to as pin oak), white oak (*Q. alba* L., $N = 11$), and red oak (*Q.*

rubra L., $N = 21$). Trees that died during the study were not replaced; the number of trees remaining at the end of the study was: 82 (bur), 63 (pin), 11 (white), and 18 (red). Bur and white oaks are members of the white oak section of the genus (section Quercus) and mature acorns in a single season ('1-year' species), while pin and red oaks are members of the red oak section (section Lobatae) and require 2 years to mature acorns ('2-year' species). All are wind pollinated. *Quercus ellipsoidalis* and *Q. rubra* hybridize but are generally separated ecologically (Gailing et al. 2012). *Quercus macrocarpa* and *Q. alba* are distinct both morphologically and at the population genetics level (Craft and Ashley 2006), but are not always genetically distinct at the individual level (Craft and Ashley 2006) and are also known to hybridize (Biagi and Jensen 1995).

Trees of three of the four species (all except for *Q. alba*) were divided among six burn units differing in size from 2.4 to 30 ha and varying in the frequency of prescribed burning. Prescribed burns occurred in April or May after the snow melted but before trees leafed out; fire intensity varied depending on the weather and fuel load but was typically of low intensity (Reich et al. 2001; Cavender-Bares and Reich 2012). Fire frequency ranged from 0 to 12 fires during the 17-year study depending on the unit. Fires generally decreased acorn production the following autumn for both bur and pin oaks but were followed by larger crops the subsequent year in bur oaks (K. Funk et al., unpublished data). Thus, in order to avoid confounding effects, we eliminated trees growing within units burned either the previous spring (year 0) or the spring of the prior year (year -1). This issue primarily affected bur and pin oaks; no white oaks and only 3 of 21 (14 %) of red oaks were in burn units.

Data collection and analysis

Acorn production was quantified between late July and late August from 1995 to 2011 using visual surveys in which two observers scanned different parts of each tree canopy and counted as many acorns as they could in 15 s (Koenig et al. 1994a). Counts for the two observers were added (N30) and log-transformed ($\ln[N30 + 1] = LN30$) to reduce the correlation between the mean and the variance (Koenig et al. 1994b).

Summary statistics for the four species are described in Koenig et al. (2003) and included the population mean annual coefficient of variation (CV_p), the mean CV of individual trees ($\overline{CV_i}$), the mean pairwise correlation coefficient among trees ($\bar{r}_p$), the temporal lag-1 autocorrelation, and the partial (i.e., controlling for lag-1) temporal lag-2 autocorrelation. These latter two variables were calculated as the mean of all individuals in the survey ($\overline{ACF1_i}$

Table 1 Weather variables used in the analyses along with the relevant phenology of the two kinds of species studied

Season	Description	Variable name	Species	Phenology (1-year spp.)	Phenology (2-year spp.)
Spring, year −2	Mean maximum temperature in May 2 years earlier	MaxSprTemp2	Pin, red		Flower bud initiation
	Mean minimum temperature in May 2 years earlier	MinSprTemp2	Pin, red		
Summer, year −2	Mean maximum temperature, 1 May–31 July 2 years earlier	MaxSumTemp2	Pin, red		Flower bud initiation
	Rainfall 1 May–31 July 2 years earlier	SumRain2	Pin, red		
Spring, year −1	Mean maximum temperature in May 1 year earlier	MaxSprTemp1	All	Flower bud initiation	Anthesis and pollination
	Mean minimum temperature in May 1 year earlier	MinSprTemp1	All		
Summer, year −1	Mean maximum temperature, 1 May–31 July 1 year earlier	MaxSumTemp1	All	Flower bud initiation	
	Rainfall 1 May–31 July 1 year earlier	SumRain1	All		
Spring, year 0	Mean maximum temperature in May	MaxSprTemp	All	Anthesis, pollination, and fertilization	Ovule development and fertilization
	Mean minimum temperature in May	MinSprTemp	All		
Summer, year 0	Mean maximum temperature, 1 May–31 July	MaxSumTemp	All	Acorn maturation	Acorn maturation
	Rainfall, 1 May–31 July	SumRain	All		

Exact timing of flower bud initiation is unknown, but assumed to be either in the spring or summer of year −1 (1-year species) or of year −2 (2-year species)

and $\overline{PACF2_i}$) rather than at the population level, since they are potentially indicative of resource depletion at the individual tree level. Only trees that were alive for at least 6 years were included in the calculations involving individuals.

Values for $\bar{r}_p$ were tested statistically by bootstrapping the complete set of pairwise correlations 100 times, each time choosing a subset of values that included one random pairwise correlation from each tree. Significance was then estimated from the mean ± SD of the trials. Significance of $\overline{ACF1_i}$, and $\overline{PACF2_i}$ was estimated with binomial tests assuming the null expectation that half of the trees would exhibit positive and half negative values for these variables. Values were compared to the mean ± SE of 59 populations of a wide variety of taxa summarized by Koenig et al. (2003).

Weather variables generally paralleled those used by Sork et al. (1993) in their study of oaks in Missouri. Several modifications were made both to account for apparent differences in phenology and to reduce the number of variables so that analyses could be made using the actual variables rather than statistical composites (i.e., principle component loadings). Variables, chosen to represent the seasons potentially important to each species for the development of acorns in each of the species (Sork et al. 1993; Cecich 1997), included four during the year acorns were produced (year 0), four during the prior year (year −1),

Table 2 Weather variables used in the analyses combining data from successive years

Season	Description	Variable name	Species
Spring, year −1	MaxSprTemp1– MaxSprTemp2	ΔMaxSprTemp1	Pin, red
	MinSprTemp1– MinSprTemp2	ΔMinSprTemp1	Pin, red
Summer, year −1	MaxSumTemp1– MaxSumTemp2	ΔMaxSumTemp1	Pin, red
	SumRain1–SumRain2	ΔSumRain1	Pin, red
Spring, year 0	MaxSprTemp– MaxSprTemp1	ΔMaxSprTemp	All
	MinSprTemp– MinSprTemp1	ΔMinSprTemp	All
Summer, year 0	MaxSumTemp– MaxSumTemp1	ΔMaxSumTemp	All
	SumRain–SumRain1	ΔSumRain	All

and (for the 2-year species only) four from two years earlier (year −2) (Table 1).

Two sets of analyses were performed for each species, the first involving the eight (12 for the 2-year species) weather variables listed in Table 1 and the second involving differential (Δ) weather variables representing the difference between the same variable from 1 year to the

next. We included four Δ variables for all species consisting of the value in year -1 subtracted from the value in year 0, plus four additional Δ variables for the 2-year species consisting of the value in year -2 subtracted from the value in year -1 (Table 2). This second set of analyses was conducted in order to test the suggestion by Kelly et al. (2013) that such differential weather variables act as general cues for masting behavior.

In order to determine the environmental correlates of acorn production, we constructed sets of candidate approximating models (two sets for each species) consisting of the maximal (full) model with all weather variables, the null model including only the intercept, and a series of models that included each weather (or differential weather) variable individually. We then ranked the models within each set of analyses using the Akaike information criterion corrected for sample size (AIC_c) and summarized the model with the greatest support ($w = \text{Prob}\{H|\text{data}\}$) within each set using the 'AICctab' function in the R package 'bbmle' (Bolker 2012). Finally, we compared the models with the greatest support within each of the two sets of analyses for each species (the first involving the weather variables and the second involving the differential weather variables) and present the relative support for each based on model weights, again calculated using the 'AICctab' function.

All analyses were conducted in R 2.15.1 (R Development Core Team 2012).

Results

Synchrony was generally high not only between burn units for the same species but also between the pairs of species that require the same length of time to mature acorns (Table 3). In contrast, there was no significant correlation between bur and pin oaks within the same burn unit, nor between the 1-year and 2-year species in general (Table 3; Fig. 1). Summary statistics indicated several differences among the species related to the developmental period of acorns, with the 1-year species exhibiting considerably greater variability and synchrony than the 2-year species (Table 4). For the 1-year species, lag-1 temporal autocorrelations were significantly negative while the lag-2 temporal autocorrelations were not, whereas for the 2-year species lag-1 temporal autocorrelations were variable (one negative and one positive) while the lag-2 temporal autocorrelations were both significantly negative.

Results of the analyses investigating environmental relationships indicated that acorn production in bur oak was greater following cooler summers (Table 5). Acorn production in pin oak was greater following wet summers 2 years earlier, while that of red oak was greater following

Table 3 Pairwise synchrony among burn units and between taxa depending on the time required to mature acorns

Comparison	Taxa compared	Mean ± SE r value	N pairs	P value
Across burn units	Bur vs. bur	0.79 ± 0.08	15	<0.001
Across burn units	Pin vs. pin	0.65 ± 0.15	15	<0.001
Within burn units	Bur vs. pin	−0.09 ± 0.25	6	ns
Species	Bur vs. white; pin vs. red	0.45 ± 0.08	2	–
Species	1-year vs. 2-year species	−0.18 ± 0.18	4	ns

Bur oak and white oaks are '1-year' species; pin oak and red oak are '2-year' species
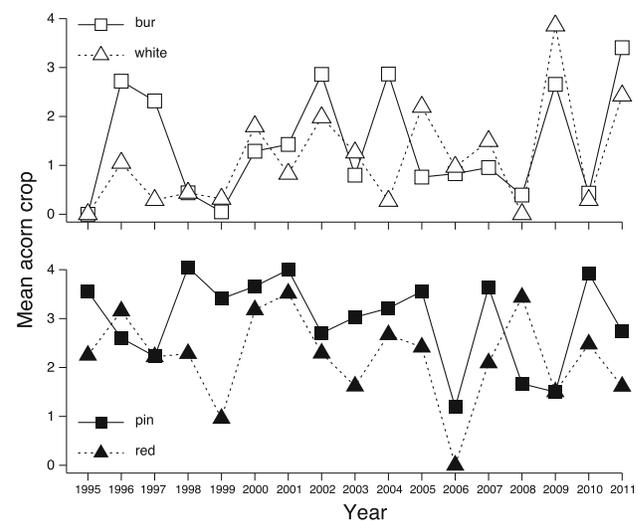

Fig. 1 Annual pattern of acorn production by four species of oaks at Cedar Creek Ecosystem Science Reserve, Minnesota, 1995–2011

warm springs 2 years earlier. The null model had the most support in the analysis of white oak acorn production. In the analyses involving the Δ weather variables the difference in mean maximum summer temperature had the most support in both of the 1-year species (although in the case of white oak, the ΔAIC_c value for the model was equivalent to that of the null model) while the null model gained the most support in both of the 2-year species.

In three of the species, models including the differential weather variables failed to outperform the null model. The exception was bur oak, in which support for the model including mean maximum summer temperature (the unmodified weather variable with the greatest support) received over five times the support of the model including the differential in mean maximum summer temperature from year 0 to year -1.

Table 4 Summary statistics for the four species of oaks studied along with mean values of 59 populations of various taxa (data ln-transformed) analyzed by Koenig et al. (2003)

	Bur oak (1-year)	White oak (1-year)	Pin oak (2-year)	Red oak (2-year)	Mean $\pm$ SE of 59 populations
CV_p	79.4	91.5	30.1	40.8	68.8 ± 5.3
$\overline{CV_i}$	118.0	137.8	50.0	70.2	105.0 ± 6.6
$\bar{r}_p$	0.48***	0.60***	0.34***	0.39***	0.54 ± 0.02
$\overline{ACF1_i}$	−0.13***	−0.30*	−0.07	−0.06	-0.22 ± 0.03
$\overline{PACF2_i}$	−0.07**	0.17*	−0.16***	−0.32***	-0.28 ± 0.03

CV, coefficient of variation (%); $\bar{r}_p$, mean pairwise correlation coefficient; $\overline{ACF1_i}$, mean lag-1 autocorrelation; $\overline{PACF2_i}$, mean partial lag-2 autocorrelation. Subscript "p" refers to the population mean; subscript "i" refers to individual trees. Statistical tests (see text) were made for $\bar{r}_p$, $\overline{ACF1_i}$, and $\overline{PACF2_i}$

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 5 Results of linear models comparing the best-supported models using individual weather variables (model 1) vs. the differential variables combining data from successive years (model 2)

Species	Model	Variables in model	P value	ΔAIC_c	df	Model weight
Bur	1	MaxSumTemp (−)	0.016	0.0	3	0.84
	2	ΔMaxSumTemp (−)	0.079	3.2	3	0.16
White	1	(null model)	–	0.0	2	0.50
	2	ΔMaxSumTemp (−)	0.110	0.0	3	0.50
Pin	1	SumRain2 (+)	0.043	0.0	3	0.71
	2	(null model)	–	1.8	2	0.29
Red	1	MaxSprTemp2 (+)	0.029	0.0	3	0.79
	2	(null model)	–	2.6	2	0.21

Model 1 used variables in Table 2; model 2 used those in Table 3. The models were then chosen as described in the text; the two best models in each category were then compared using AIC$_c$ values. The sign in parentheses indicates whether the variable correlated positively (+) or negatively (−) with acorn production

Discussion

Acorn production was relatively synchronous both within species (across burn units within the study site) and among species requiring the same length of time to mature acorns, but not between species requiring different numbers of years to mature acorns (Table 3). Similar results have been reported in previous studies of oaks (Sork et al. 1993; Koenig et al. 1994b).

Summary statistics for the four species indicated several substantive differences related to the length of time species require to mature acorns (Table 4). In general, the 1-year species were relatively more variable from year to year, both at the population (CV_p) and individual ($\overline{CV_i}$) levels than the 2-year species, both of which exhibited considerably less variability than the mean of 59 populations (both oak and non-oak taxa) summarized by Koenig et al. (2003). Individuals of all four species produced acorns synchronously, but the 1-year species were more synchronized (mean $\bar{r}_p = 0.54$, exactly equal to the mean of 59 species analyzed by Koenig et al. 2003) than the 2-year species (mean $\bar{r}_p = 0.37$). The mean individual lag-1

temporal autocorrelations ($\overline{ACF1_i}$) were all negative, significantly so for the 1-year species, while the lag-2 temporal autocorrelations ($\overline{PACF2_i}$) were significantly negative for both 2-year species.

These patterns most likely reflect some combination of interspecific differences in (1) the developmental pattern of acorns, (2) cues used to initiate the processes involved in flower or acorn production, and (3) the different effects of those cues on the mechanisms of acorn production. Differences in the temporal autocorrelations are plausibly related to the impact of resource depletion on subsequent floral initiation and acorn development, a process that takes place over a period of approximately 1.4 years (spring of year −1 to autumn of year 0) in the 1-year species and 2.4 years (spring of year −2 to autumn of year 0) in the 2-year species. Such resource depletion has been inferred from negative temporal autocorrelations in acorn production found in prior studies of oaks (Sork et al. 1993; Koenig et al. 1994b; Barringer et al. 2012) and has considerable theoretical (Isagi et al. 1997; Satake and Iwasa 2000) as well as some experimental (Crone et al. 2009; Crone 2013) support. It has not, however, been supported by recent

Table 6 Environmental factors correlating with acorn production in various tree oak species

Species	Locality	Variables related positively to the acorn crop	References
1-year species			
White oak	Pennsylvania	Warm spring	Sharp and Sprague 1967
White oak	Missouri	Warm, wet summer Warm, dry spring	Sork et al. 1993
White oak	Missouri	Cool, humid springs	Cecich and Sullivan 1999
White oak	Minnesota	(None detected)	This study
Bur oak	Minnesota	Cool summer	This study
Valley oak (*Q. lobata*)	California	Warm spring	Koenig et al. 1996
Blue oak (*Q. douglasii*)	California	Warm spring	Koenig et al. 1996
Coast live oak (*Q. agrifolia*)	California	Rainfall (year −1)	Koenig et al. 1996
Holm oak (*Q. ilex*)	Spain	Wet summer; heavy spring rains	Pérez-Ramos et al. 2010
Holm oak	Spain	Wet spring; cold winter before flowering	García-Mozo et al. 2007
Holm oak	Spain	Annual and seasonal rainfall; mid-summer water potential	Alejano et al. 2008
Holm oak	Spain	Summer water availability	Espelta et al. 2008
Cork oak (*Q. suber*)	Spain	Lack of spring frost	García-Mozo et al. 2001
Cork oak (annual acorns only)	Spain	Warm spring; shorter summer	Pons and Pausas 2012
Downy oak (*Q. humilis*)	Spain	Summer water availability	Espelta et al. 2008
Kashiwa oak (*Q. dentata*)	Japan	Warm spring; warm winter	Masaka and Sato 2002
Mizu-nara (*Q. crispula*)	Japan	(None detected)	Maeto and Ozaki 2003

Table 6 continued

Species	Locality	Variables related positively to the acorn crop	References
2-year species			
Red oak	Missouri	Wet summer; warm spring	Sork et al. 1993
Red oak	Minnesota	Warm spring (year −2)	This study
Pin oak	Minnesota	Wet summer (year −2)	This study
Black oak (*Q. velutina*)	Missouri	Wet summer; warm spring	Sork et al. 1993
Canyon live oak (*Q. chrysolepis*)	California	Rainfall (year −1); rainfall (year −2)	Koenig et al. 1996
California black oak (*Q. kelloggii*)	California	Warm dry spring (year −1)	Garrison et al. 2008
Japanese evergreen oak (*Q. acuta*)	Japan	(None detected)	Hirayama et al. 2012
Japanese willowleaf oak (*Q. salicina*)	Japan	(None detected)	Hirayama et al. 2012
Tsukubane-gashi (*Q. sessilifolia*)	Japan	(None detected)	Hirayama et al. 2012

'1-year' species mature acorns the same year flowers are produced; '2-year' species mature acorns the year after flowers are produced. "None detected" indicates that none of the environmental variables tested correlated significantly with acorn production

studies of carbon use in masting trees (Hoch et al. 2013; Ichie et al. 2013), possibly because of complications related to their modular structure and the importance of other key nutrients such as nitrogen or phosphorus (Miyazaki 2013). Clearly more work on the role of stored resources and resource depletion in masting species is needed.

The work presented here is one of a relatively large number of studies conducted on oaks in the genus *Quercus* investigating the relationship between weather and productivity. We summarized such studies in order to look for patterns that might illuminate the role that environmental factors play in driving acorn production. Although probably not comprehensive, our search revealed 15 studies encompassing 26 populations of 18 different species across three continents (Table 6).

The most striking conclusion emerging from this compilation is the diversity of environmental factors correlating with acorn production. Nonetheless, a few generalizations are possible. In particular, conditions during the spring

immediately prior to acorn maturation are important for a high proportion species, primarily those that mature acorns in a single year [10 of 17 (59 %) studies], although spring conditions were also significant for four of the nine (44 %) 2-year species, in one case lagged 1 year and in one case lagged 2 years. In the majority of these cases acorn production correlated positively with warm springs [11 of 14 (79 %)], but in the remaining three studies acorn production correlated with wetter or cooler springs instead. Summer was also an important period, correlating significantly with acorn production in nine of the studies (35 % of 26), most frequently following wet conditions [6 of 9 (67 %) studies]. No significant weather correlate of acorn production was detected in five of the studies (19 % of 26).

These results suggest that environmental factors potentially correlate with, and thus presumably influence, nearly any or all stages of acorn production, from the period of flower bud initiation (red oak in this study) to the period of acorn maturation (the nine studies for which summer conditions immediately prior to when acorns mature was important). Most frequently for the 1-year species, conditions during the spring of year 0 when anthesis, pollination, and fertilization are taking place were important, but this was not the case for the 2-year species, which were highly variable. Such variability was expressed in the four species studied here, for which the most important weather variables included maximum summer temperature in year 0 (bur oak), maximum spring temperature in year −2 (red oak), and summer rainfall in year −2 (pin oak), while none of the weather variables explained a significant amount of the variation in white oak acorn production.

This diversity of environmental correlates even extends to studies of the same species. We failed to find any significant correlate of acorn production in the white oaks we studied, whereas Cecich and Sullivan (1999) found that acorn production by white oaks in Missouri was enhanced by cool, humid springs, opposite the findings of Sharp and Sprague (1967) in Pennsylvania and Sork et al. (1993), also in Missouri, who found white oak acorn production to be greater following warm, dry springs. Warm spring conditions correlated with larger red oak acorn crops in both our study and that of Sork et al. (1993) in Missouri, but the timing (lag) differed, being unlagged in the Missouri study and in year −2 here. Thus, although there are some similarities in the ecological conditions influencing acorn production across the range of these species, there remain major unexplained differences that at the very least argue against a single, unified environmental driver of acorn production within species, much less across the genus *Quercus* or its subgenera.

Other differences in the environmental factors found to correlate with seed production in different species are apparently geographical. For example, conditions during the summer immediately preceding acorn maturation were important in a high proportion of studies conducted on populations in Spain [5 of 7 (71 %) studies; Koenig et al. 2013] and Missouri [3 of 4 (75 %) studies] but not in California (0 of 5 studies). Clearly more work focusing on the environmental factors correlating with acorn production are desirable, particularly in areas such as Japan, where environmental correlates of acorn production have been reported for only one of five species for which we found published analyses.

Results are thus inconclusive as to whether the environmental correlates of acorn production in oaks are simply cues or whether they are directly related to some mechanism driving acorn production. Supporting this latter hypothesis, acorn production by a high proportion of species [21 of 26 (81 %) summarized in Table 6] were found to correlate with some environmental factor during a potentially critical period of either flower production or acorn maturation. Supporting the cue hypothesis is the striking diversity of the environmental factors identified in the various studies, suggesting either that seed production by virtually every population of oaks is driven by a different set of environmental factors or that those factors are arbitrary and unrelated to the physiological drivers of acorn production, which are presumably similar at least among species whose acorns share the same developmental timing.

The resolution of this important issue will depend on more detailed studies of the proximate drivers of masting behavior, which potentially involves not only a complex combination of environmental factors affecting the phenological events leading up to the seed crop—flower bud initiation, flowering, pollen production, pollination, fertilization, and acorn maturation—but also resource storage (Isagi et al. 1997; Miyazaki 2013) and pollen production by conspecifics (pollen coupling; Satake and Iwasa 2000; Crone 2013). Thus far a specific mechanism relating environmental factors to seed production has only rarely been proposed (García-Mozo et al. 2007; W.D. Koenig et al., unpublished data).

Recently Kelly et al. (2013) suggested not only that that the environmental correlates of masting are arbitrary cues used by the trees to synchronize reproductive investment, but that temperature differentials between years is the principal cue used by masting species to time investment in reproduction. We tested this differential-cue hypothesis using a series of variables encompassing the difference in spring and summer conditions both between year 0 and year −1 (for all species) and between year −1 and year −2 (the 2-year species only). In only one of the four species did models including the differential weather variables receive greater support than the null model, and in the fourth species, a model including the (unmodified) weather

variable received considerably greater support than the model with the differential weather variable. Thus, results from none of the four species supported this hypothesis. Kelly et al. (2013) found that the climate sensitivity of the species they considered was positively related to seedfall variability (CV_i), and thus the failure of the differential-cue hypothesis is perhaps not surprising, at least for the pin and red oaks, which exhibited relatively low variability in seed production (Table 4). This was not the case for bur and white oaks, however.

We conclude that the differential-temperature hypothesis of Kelly et al. (2013) is not applicable to any of the four species of *Quercus* studied here. Careful examination of other taxa are clearly needed in order to determine the extent to which the differential weather model applies to species other than those examined by Kelly et al. (2013). More work is also needed investigating the role that environmental factors play in driving patterns of seed production in masting species, which remains an important unresolved issue.

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