

Intraspecific variation in the relationship between weather and masting behavior in valley oak, *Quercus lobata*

Walter D. Koenig, Johannes M.H. Knops, and William J. Carmen

Abstract: Masting behavior — variable and synchronized reproduction by a population of plants — has long been recognized as correlating with weather. How and why weather conditions influence seed production is, however, poorly understood. We investigated the relationships between acorn production and both local weather and long-term climate in 10 populations across the geographic range of the valley oak (*Quercus lobata* Née), a California endemic that matures acorns in a single season. Acorn production was larger following a cold spring in the prior year and dry conditions in the winter and spring immediately preceding acorn maturation; similar patterns were also found, with minor differences, at all 10 individual sites. The strength of the relationships varied geographically in the case of the correlation between winter rainfall and annual acorn production, which was stronger (more negative) at wetter sites. Thus, in contrast to a recent study in *Quercus petraea* (Matt.) Liebl., weather had generally similar effects on acorn production throughout the range of *Q. lobata*. Similar to *Q. petraea*, however, the strength of the relationship between site-level annual acorn production and one of the weather factors affecting acorn production (winter rainfall in the case of *Q. lobata*) varied geographically in ways that may be related to differences among sites in the degree of pollen limitation. Understanding the mechanisms by which weather affects seed production is challenging but critical if we are to understand how climate change will affect masting behavior in the future.

Key words: acorn production, masting, *Quercus lobata*, valley oak, variable reproduction.

Résumé : Il est depuis longtemps reconnu que la reproduction synchronisée et variable dans une population de plantes (« masting ») est corrélée avec les conditions météorologiques. Cependant, on comprend mal comment et pourquoi les conditions météorologiques influencent la production de semences. Nous avons étudié les relations entre la production de glands et les conditions météorologiques locales ainsi que le climat à long terme chez 10 populations dans l'aire de répartition du chêne lobé (*Quercus lobata* Née), un chêne endémique de la Californie dont les glands arrivent à maturité en une seule saison. La production de gland était plus abondante à la suite d'un printemps froid l'année précédente et des conditions sèches durant l'hiver et le printemps précédant immédiatement la maturation des glands. Des patrons similaires ont été observés, avec des différences mineures, dans l'ensemble des 10 stations individuelles. La force de la relation variait géographiquement dans le cas de la corrélation entre la chute de pluie hivernale et la production annuelle de glands; la corrélation était plus forte (plus négative) dans les stations plus humides. Par conséquent, contrairement à une étude récente qui portait sur *Quercus petraea* (Matt.) Liebl., les conditions météorologiques avaient généralement des effets similaires sur la production de glands partout dans l'aire de répartition de *Q. lobata*. Comme avec *Q. petraea* cependant, la force de la relation entre la production annuelle de glands à l'échelle de la station et un des facteurs météorologiques qui influencent la production de glands (chute de pluie hivernale dans le cas de *Q. lobata*) variait d'un endroit à l'autre. Cette variation pouvait être reliée à des différences entre les stations concernant la disponibilité du pollen. Il est difficile mais essentiel de comprendre les mécanismes par lesquels les conditions météorologiques influencent la production de semences si nous voulons comprendre de quelle façon le changement climatique affectera la reproduction synchronisée dans le futur. [Traduit par la Rédaction]

Mots-clés : production de glands, masting, *Quercus lobata*, vallée du chêne, reproduction variable.

Introduction

Variable, synchronized seed production, known as mast-fruiting or masting behavior, is commonly observed in many taxa of plants and is particularly widespread among temperate and boreal trees. The evolutionary drivers of masting behavior are generally thought to be one or more “economies of scale” (Kelly 1994); these include predator satiation (Janzen 1971), increased pollination efficiency (Kelly and Sork 2002), and enhanced efficiency of seed dispersal (Carmen 2004; Pesendorfer et al. 2016). More controversial are the proximate drivers of masting behavior (Crone and Rapp 2014; Pearse

et al. 2016; Bogdziewicz et al. 2020). Two factors are believed to be involved: one to drive the year-to-year variability in the resources that plants devote to reproduction, for which stored resources are generally thought to be critical (Isagi et al. 1997; Crone and Rapp 2014; Pearse et al. 2016; Bogdziewicz et al. 2018); and the second to synchronize reproduction among individuals, which can be expressed over distances of hundreds or even thousands of kilometres (Koenig and Knops 2013; Vacchiano et al. 2017).

The phenomenon most prominently implicated as being important to geographic synchrony in reproduction is pollen coupling,

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the potential advantage of investing heavily in seed production at the same time as other individuals in the population are investing in pollen, thereby reducing pollen limitation and enhancing pollination efficiency (Satake and Iwasa 2000, 2002a, 2002b). Pollen coupling is a density-dependent phenomenon that is thought to vary with the internal resource dynamics of plants and, thus, is not necessarily weather-dependent. As previously mentioned, pollen coupling is an economy of scale and a potential ultimate driver of masting (Satake and Iwasa 2000, 2002b; Crone et al. 2005; Pearse et al. 2016).

Pollen coupling is likely to be important in wind-pollinated, obligate outcrossing species such as many temperate and boreal trees, among which mast-fruiting is common and pollen can be limiting for a variety of reasons. This is particularly the case for “flowering masting” species in which the seed crop is primarily determined by flower production (Bogdziewicz et al. 2019a), but pollen limitation can also be important in “fruit-maturation species” in which seed production is largely determined by the variable ripening of a relatively constant flower crop (Pearse et al. 2016).

Alternatively, geographic synchrony may be driven by correlated environmental factors, known as Moran effects. The general idea is that weather, itself highly spatially correlated over large geographic distances (Koenig 2002), can affect the availability of pollen via density-independent processes known as “pollination Moran effects” (Pearse et al. 2016; Bogdziewicz et al. 2017a, 2017b).

Two nonexclusive hypotheses for how pollination Moran effects might be important are (i) phenological synchrony, the idea that how synchronously trees flower within a population determines pollen availability and thus acorn production (Koenig et al. 2015); and (ii) pollen washout, which proposes that weather conditions — particularly rain but potentially humidity and wind — affect pollen availability by washing pollen out of the air column (García-Mozo et al. 2007). Other “environmental veto” mechanisms can play important proximate roles in masting as well, both in the form of flower-killing freezes (Sharp and Chisman 1961) and by other forms of pollination Moran effects (Bogdziewicz et al. 2019b).

Thus, weather appears to play a key role in driving masting synchrony, but what weather variables are important and how variable they are among and within species need to be determined. Two recent studies are particularly relevant. The first compared 15 species of oaks (*Quercus* spp.) from North America and Spain, finding that differences in the relationship between weather and the acorn crop were phylogenetically conserved and statistically consistent within leaf habit, subcontinental region, and whether acorns matured in one or two years (Koenig et al. 2016). Thus, similar proximate mechanisms may be driving acorn production, at least within groups of species that are related phylogenetically, ecologically, or geographically. The second, by Bogdziewicz et al. (2019a), compared the weather factors correlating with reproduction across a series of French populations of European beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). These authors found that the same weather factors correlated consistently with successful reproduction in *F. sylvatica* across sites, but that correlations between local weather and acorn production were highly variable in *Q. petraea*. This difference was hypothesized to be because seed production in *F. sylvatica*, a flowering masting species, is potentially dependent more on resources driving flower abundance and less on local weather factors, while seed production in *Q. petraea*, a fruit-maturation species, is presumably highly sensitive to the exact timing of extreme weather conditions occurring during the flower-to-fruit transition, factors that potentially vary considerably among sites. Their analyses also revealed a significant climatic gradient, with the correlation between weather and seed crop size in *Q. petraea* being stronger at colder sites. They concluded that the relationship between weather and masting may be understandable and predicted, both across and within species.

Here we investigate the relationship between weather and reproduction in 10 populations across the geographic range of a single species endemic to California, valley oak (*Quercus lobata* Née). Prior work on this species has shown that there is both considerable variation in annual flower abundance (although not as great as annual variation in acorn production) and high flower abortion rates (Pearse et al. 2015). Thus, exhibiting characteristics of both a flowering masting and a fruit-maturation masting species, the predictions of Bogdziewicz et al. (2019a) as to whether there should be consistency across sites in the relationship between weather and acorn production based on this aspect of its ecology is ambiguous. *Quercus lobata* does, however, exhibit highly significant spatial synchrony of acorn production among populations (Koenig and Knops 2013), consistent with the hypothesis that similar, if not identical, weather factors are driving reproduction throughout its range.

Specifically, we address the following questions:

- (1) How similar are the masting metrics among different populations?
- (2) How concordant are the relationships between weather and acorn production?
- (3) Do differences among populations in the observed relationships between acorn production and weather exhibit interpretable geographic patterns and do they suggest functional differences in how weather affects seed production in different populations?

Methods

Study sites and species

We studied 10 populations of *Q. lobata* encompassing almost the entirety of its range (Table 1). Habitat at all sites was oak woodland and oak savanna, but environmental conditions ranged considerably, with the 30-year mean annual rainfall ranging from a near desert of 290 mm (Kaweah Oaks) to a temperate rain forest of 1328 mm (Tower House), and 30-year mean annual temperature ranging from 14.0 °C (Hopland) to 17.3 °C (Kaweah Oaks). Within these populations, we conducted visual acorn surveys each year through 2018 starting in 1980 (for Hastings Reservation), 1989 (for Jasper Ridge and Pozo), and 1994 (most of the remaining sites), estimating the acorn crop on a total of ~275 trees. (Numbers varied from year to year due to mortality and minor changes to the study; see Table 1 for details.)

Quercus lobata, a “white oak” in the section *Quercus* (Pearse and Hipp 2009), is wind-pollinated, an obligate outcrosser, matures acorns in a single season, and is winter deciduous. Its range encompasses foothill regions ringing the Central Valley of California at elevations up to ~1800 m (Griffin and Critchfield 1972) (Fig. 1). Within this range, stands tend to consist of relatively few large trees (White 1966; Bolsinger 1988). Hybridization with the closely related *Quercus douglasii* Hook. & Arn. occurs but is relatively uncommon (Craft et al. 2002; Abraham et al. 2011).

Acorn production was estimated each year using visual surveys in which two observers scanned different parts of the canopy of each tree and counted as many acorns as they could in 15 s (Koenig et al. 1994a, 1994b). The two 15 s counts were added together (N30) and natural log (ln) transformed (LN30) to reduce non-normality. Values within a site were then averaged (LN30) to estimate acorn production for each year and site.

Weather variables

We used records of monthly rainfall, mean maximum temperature, and mean minimum temperature matched geographically to each site from the PRISM climate database (Oregon State University, Corvallis, Oregon; <http://prism.oregonstate.edu>). Based on prior work investigating the relationship between weather and acorn production in *Q. lobata* (Koenig et al. 1996, 2016), we analyzed six weather variables. In seasonal order (where year x is the

Table 1. Sampling localities.

Site (abbreviation)	Latitude (N)	Longitude (W)	30-year mean annual rainfall (mm)	30-year mean annual temperature (°C)	No. of trees
Tower House Historic District (Tower House)	40°38'	122°34'	1328	14.0	17
Dye Creek Preserve (Dye Creek)	40°08'	122°00'	751	16.6	18
Sierra Foothills Research and Extension Center (Sierra Foothills)	39°15'	121°25'	884	16.1	9 ^a
Hopland Research and Extension Center (Hopland)	38°58'	123°07'	1210	14.5	10 ^b
Jasper Ridge Biological Station (Jasper Ridge)	37°24'	122°13'	601	15.3	39
Kaweah Oaks Preserve (Kaweah Oaks)	36°19'	119°10'	290	17.3	10 ^b
Hastings Natural History Reservation (Hastings)	36°12'	121°33'	675	14.2	86
Pozo	35°16'	120°16'	594	15.6	24
Liebre Mountain (Liebre Mtn.)	34°44'	118°41'	377	14.9	11
Sedgwick Reserve (Sedgwick)	34°43'	120°02'	638	16.6	12; 26 ^c

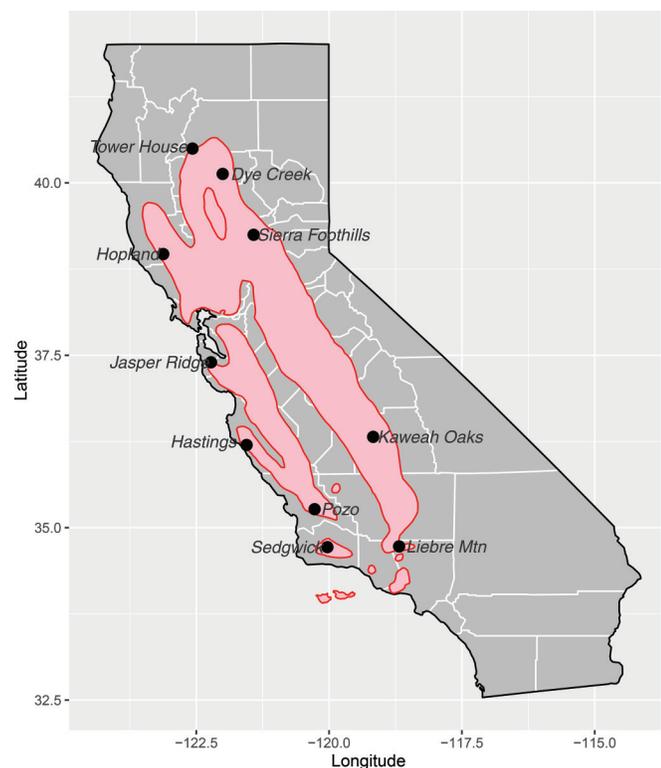
Note: Sites were sampled each year between 1994 and 2019, inclusive, except where noted.

^aAdded in 2001.

^bAdded in 1999.

^cTwelve trees surveyed in 1994–2007; 14 additional trees added in 2008.

Fig. 1. The geographic range of *Q. lobata* (outlined) and the sites used in this study. Base map from the R packages maps and ggplot2 (Hadley 2016). [Colour online.]



calendar year of the acorn crop being addressed), these were (i) mean spring temperature in the prior year (year $x - 1$), (ii) mean autumn temperature in the prior year, (iii) winter rainfall (starting in year $x - 1$ and extending into year x), (iv) mean spring temperature the current year (year x), (v) spring rainfall in the current year, and (vi) summer rainfall in the current year.

Mean spring temperature was included because April was previously identified as a critical month correlating with *Q. lobata* acorn production at Hastings Reservation (Koenig et al. 1996). To accommodate potential phenological differences among sites, however, we adjusted this variable as follows. For the analysis of all sites combined, we used mean temperature from 1 March – 31 May to encompass the potential range of this critical period throughout the state. At the individual-site level, we first calculated Pearson correlations (henceforth “ r values”) between the acorn crop and mean March, mean April, and mean May temper-

atures (both year x and year $x - 1$), and subsequently included only mean temperature for the month yielding the largest r values for that site (positive for year x ; negative for year $x - 1$). For simplicity, we refer to all of these variables as “mean spring temperature.”

Annual rainfall was divided seasonally into winter, spring, and summer to identify specific seasons in which water availability, or the lack thereof, might be important. As we mixed temperature and rainfall variables, it is important to recognize that these variables are inversely related in the Mediterranean climate of California, particularly in the spring: among the sites surveyed here, r values between mean spring temperature and spring rainfall averaged -0.63 (range -0.70 to -0.54). Thus, wetter sites are colder sites and vice versa.

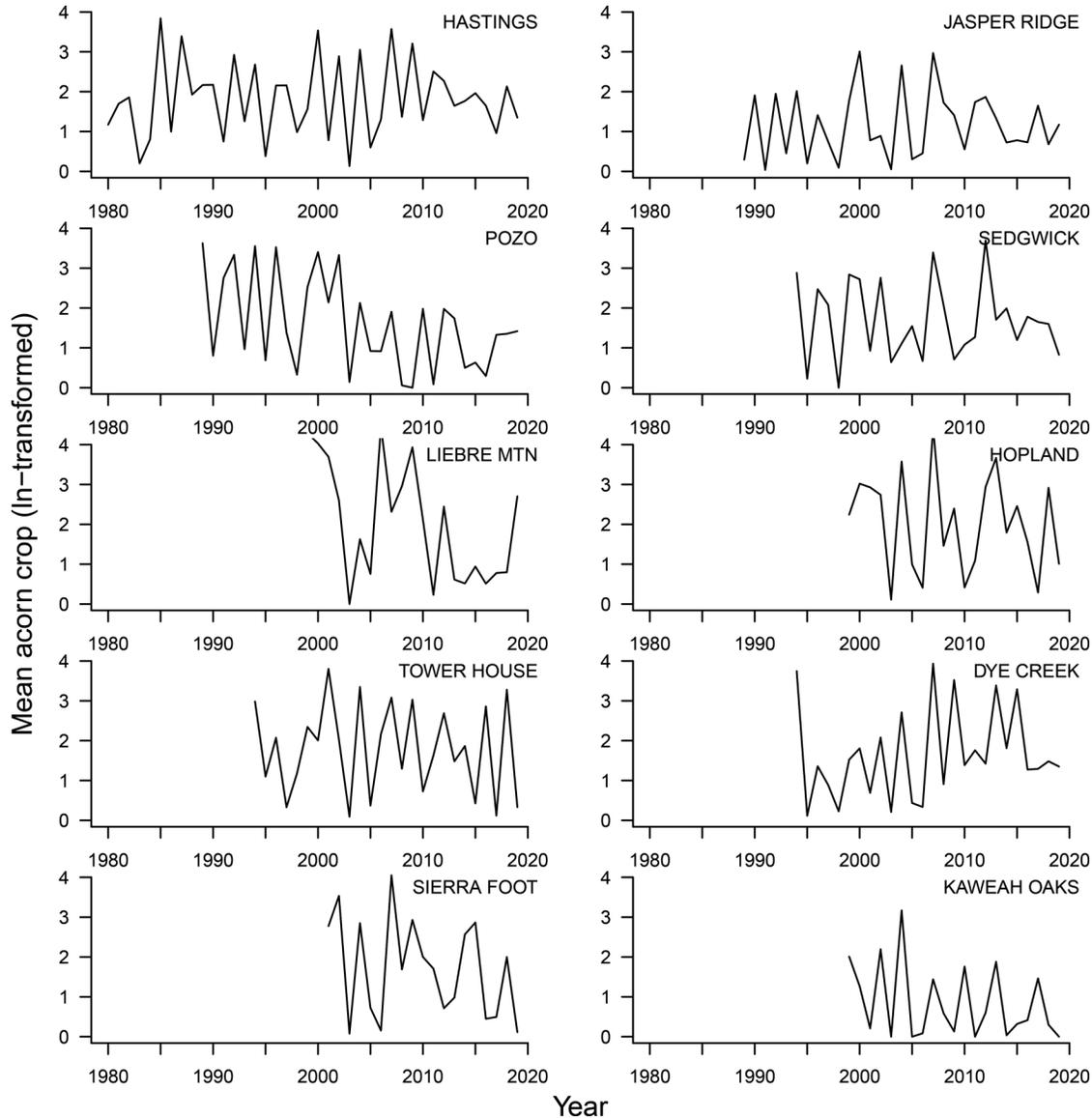
Weather variables encompassed the period from bud initiation to acorn maturity (Sork et al. 1993), with an emphasis on spring during flowering and fertilization — presumably the most vulnerable period for acorn production. For the acorn crop of year x , “autumn” was considered to be from 1 September (year $x - 1$) to 31 October (year $x - 1$); “winter” was from 1 November (year $x - 1$) to 29 February (year x); “spring” varied depending on the analysis as discussed above; and “summer” was from 1 June to 31 August (year x). We standardized all weather variables to mean = 0 and standard deviation = 1 prior to analysis, ensuring that their scales were comparable (Schielzeth 2010).

Statistical analyses

Analyses were conducted in R 3.5.3 (R Core Team 2019). Acorn production patterns were compared by standard masting metrics, including the mean acorn crop, annual variability measured as the coefficient of variation (CV) at both the population (CV_p) and mean individual (CV_i) levels, the mean pairwise correlation between acorn production of individuals in the population (mean r_p), and the temporal autocorrelation of acorn production lagged 1 year (lag-1 autocorrelation) (Herrera 1998; Koenig et al. 2003). We also calculated an additional more recently suggested metric, the “consecutive disparity index” (D) (Fernández-Martínez et al. 2018), for a total of six. D is a measure of temporal variability that resolves some of the problems of the CV, particularly its dependence on the mean (McArdle et al. 1990; Lepš 1993). In addition, D takes into account the order of values in the time series. Bias due to differing sample sizes was assessed by correlating the masting metrics with the number of trees and number of years of data at each of the sites.

We calculated correlations between population mean annual acorn production and each of the weather variables following the protocol recommended by Royama (1992; eq. 3.41) for the analysis of a density-independent perturbation (weather) on a stationary time series (acorn production). This procedure, which involves calculating the correlation between the second-order differences in acorn production and the weather variable being tested, has

Fig. 2. Annual mean acorn production (ln-transformed) at the sites.



been shown to be more effective at detecting the population-wide influence of a perturbation such as weather than alternative coefficients and, importantly, takes into account the autoregressive effects of temporal autocorrelation in acorn production. For further details, see Koenig et al. (2016).

To determine what weather variables were important to acorn production overall, we performed a linear mixed-effects model using the lmer procedure in the lme4 package (Bates et al. 2015). All six weather variables were included as fixed factors, while site was included as a random factor. Variance inflation factors (VIF) for the fixed factors were calculated using the usdm package (Naimi et al. 2014).

Next, we performed analyses on each of the 10 populations individually. To avoid collinearity, we calculated Pearson correlations between the six weather variables and mean annual acorn production at each of the sites. We assessed the concordance of the strength of the correlations of the six weather variables at the 10 sites using Kendall's coefficient of concordance. We did this both on the raw r values and on their absolute values. The former tested for agreement among the sites of the strength of the weather variables on acorn production taking the direction (pos-

itive or negative) into account, while the latter tested for agreement among the 10 sites of the effect strength of the weather variables irrespective of the direction of their effect.

Finally, we tested for geographic patterns in the strength of the relationship between mean annual acorn production and the six weather variables. This was done by calculating Pearson correlations between each of the six r values (one for each weather variable vs. mean annual acorn production) and the 30-year mean climate variables from the PRISM database. Climate variables included 30-year mean annual temperature (calculated from September of year $x - 1$ to August of year x), mean spring temperature, and mean annual, winter, and spring rainfall values, where spring was defined as 1 March – 31 May and winter was defined as 1 November (year $x - 1$) – 29 February (year x).

Statistical significance was set at $p < 0.05$.

Results

Population metrics

All populations exhibited typical masting behavior (Fig. 2). Population metrics varied considerably, however, across the 10 popu-

Table 2. Masting metrics for the sites and Pearson correlation coefficients (p value) between the metrics and sample sizes at each site.

Site	Mean acorn crop (ln-transformed)	Population CV (CV _p , %)	Mean individual CV (CV _i , %)	Consecutive disparity index (D)	Lag-1 auto-correlation	Mean synchrony (mean r_p)
Tower House	1.79	63.1	99.1	0.688	-0.50	0.53
Dye Creek	1.65	69.0	103.8	0.565	-0.32	0.62
Sierra Foothills	1.72	72.7	92.8	0.607	-0.20	0.41
Hopland	2.02	61.3	83.7	0.606	-0.28	0.62
Jasper Ridge	1.17	71.9	143.3	0.538	-0.32	0.41
Kaweah Oaks	0.85	109.3	196.5	0.666	-0.42	0.24
Hastings	1.83	53.1	104.4	0.520	-0.52	0.43
Pozo	1.60	73.6	101.1	0.585	-0.11	0.65
Liebre Mtn.	2.01	73.0	85.3	0.485	0.35	0.18
Sedgwick	1.69	57.5	93.4	0.495	-0.32	0.17
No. of individuals	-0.148 (0.68)	-0.021 (0.95)	-0.634 (0.049)	0.512 (0.13)	0.530 (0.12)	0.464 (0.18)
No. of years	-0.218 (0.55)	-0.443 (0.20)	0.625 (0.053)	-0.545 (0.10)	-0.564 (0.09)	-0.520 (0.12)

lations (Table 2). For example, mean annual productivity ranged from 0.85 to 2.02 (2.4-fold on a ln scale), mean individual CV (CV_i) ranged from 83.7% to 196.5% (2.4-fold), and mean pairwise synchrony (mean r_p) ranged from 0.17 to 0.65 (3.8-fold). Less variable was the consecutive disparity index (D ; range 0.485–0.688, 1.4-fold). Lag-1 autocorrelations were all negative, with the exception of the Liebre Mountain site.

Correlations between the masting metrics and sample sizes, although statistically significant in only one case, were sufficiently strong ($r < -0.5$ or $r > 0.5$) as to be important factors driving many of these differences (Table 2). In particular, CV_i increased as fewer trees and more years were sampled, while the opposite was true for D , lag-1 autocorrelations, and mean pairwise synchrony (significant for the number of years).

Weather variables

Including data from all sites, acorn production was larger following a cold spring in the prior year and a dry winter and spring in the current year (Table 3). With site included as a random factor, nearly half the variance in annual acorn production was explained by the weather variables (conditional $R^2 = 0.48$). VIFs ranged from 1.2 to 3.3, indicating moderate correlations among the fixed factors in the model (Hair et al. 1995).

Correlations between the weather variables and annual acorn production for each of the sites individually are summarized in Table 4. As in the mixed model including all data, acorn production was greater following cold spring in the prior year (all populations, five significant), followed by dry conditions during the winter (nine populations, four significant) and spring (all populations, six significant). In parallel with the negative relationships between acorn production and spring rainfall, all populations (four significant) exhibited a positive correlation between acorn production and mean spring temperature. None of the correlations with summer rainfall was statistically significant, although all were negative, and the correlations between mean autumn temperature and acorn production were variable and were significant at one site.

Overall, concordance among the sites as to the strength and direction of the r values of the weather variables was highly significant (Kendall $W = 0.67$, $\chi^2 = 33.7$, $df = 5$, $p < 0.001$); concordance remained significant using absolute r values (Kendall $W = 0.26$, $\chi^2 = 12.9$, $df = 5$, $p = 0.02$). Thus, in general, the weather factors important to acorn crop size in the mixed model were similarly important at each of the individual sites.

Correlations between the strength of the relationship of acorn production with the six annual weather variables at each of the sites vs. the 30-year mean climatic variables were all nonsignificant (Supplementary Table S1¹), with the exceptions of those be-

Table 3. General linear mixed model of mean annual acorn production (ln-transformed) for *Q. lobata* at the 10 sites on six weather factors; “site” was included as a random factor.

Fixed factors	Model estimate	Standard error	p value
Mean spring temperature year $x - 1$	-0.596	-0.093	<0.001
Mean autumn temperature	0.004	0.086	0.96
Winter rainfall	-0.276	0.093	0.003
Mean spring temperature	0.147	0.120	0.22
Spring rainfall	-0.409	0.090	<0.001
Summer rainfall	-0.061	0.069	0.38

Note: Marginal $R^2 = 0.29$; conditional $R^2 = 0.48$. Statistically significant factors are in boldface type.

tween winter rainfall and the 30-year mean annual, winter, and spring rainfall values (Fig. 3). Thus, winter rainfall had a stronger (more negative) effect on acorn production at wetter sites.

Discussion

Variability and geographic patterns of masting metrics

Masting metrics were generally consistent with what Kelly (1994) referred to as “normal” masting behavior, with high annual variability and strong within-site synchrony (Koenig and Knops 2000). Masting metrics, however, differed considerably among the 10 populations, varying over twofold in productivity (measured on a ln scale) and nearly fourfold in mean pairwise synchrony. Neither the overall mean acorn crop nor the population CV was strongly influenced by sample sizes, but many of the other metrics were significantly affected by the number of individuals sampled or the number of years included, or both. Thus, a critical comparison of intraspecific differences in masting metrics should equalize both factors as much as possible.

Relationships between weather and acorn production

Overall, acorn production was greatest following a cold spring in the prior year and a dry winter and spring immediately preceding maturation. With few differences, similar conditions correlated with the acorn crops at each of the individual sites, a conclusion confirmed by analyses indicating that the rank order of the strength of the effects of the weather variables on the acorn crop at the 10 sites was statistically significant.

Two factors in particular stand out, both related to spring conditions. First, the strong, positive effect of warm, dry springs in year x is consistent with the hypothesis that such conditions facilitate successful pollination and fertilization (Koenig et al. 2015; Pearse et al. 2015). Alternatively, one can consider the negative effects of a cold, wet spring in year x as a “veto” limiting pollina-

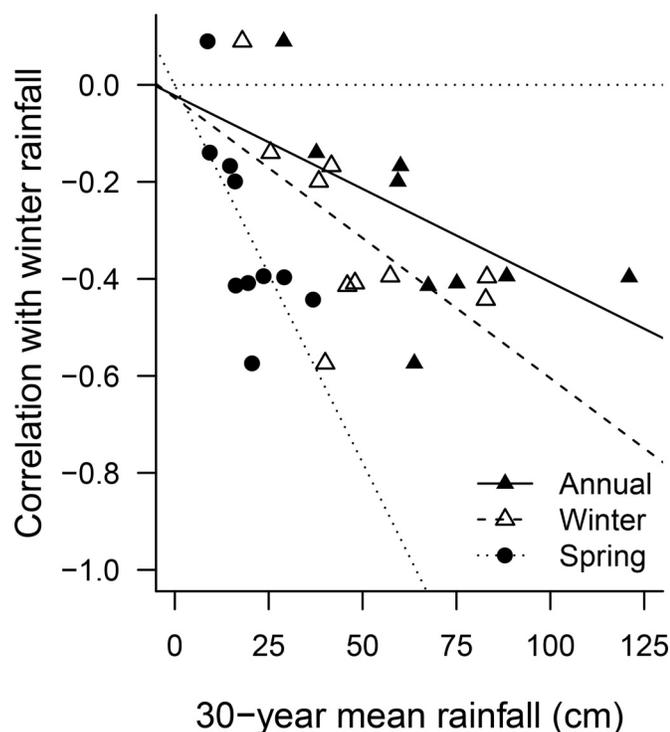
¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2020-0098>.

Table 4. Pearson correlations between mean annual acorn production (ln-transformed) and the six weather variables at each of 10 sites.

Season	Variable	Tower House	Dye Creek	Sierra Foothills	Hopland	Jasper Ridge	Kaweah Oaks	Hastings	Pozo	Liebre Mtn.	Sedgwick
Spring (year $x - 1$)	Mean temperature	-0.464*	-0.299	-0.277	-0.366	-0.528**	-0.550**	-0.355*	-0.423*	-0.370	-0.220
Autumn	Mean temperature	0.147	0.438*	0.037	0.406	0.032	0.347	0.230	-0.128	-0.362	0.037
Winter	Rainfall	-0.443*	-0.409*	-0.395	-0.396	-0.167	0.090	-0.414**	-0.199	-0.140	-0.574**
Spring	Mean temperature	0.268	0.595**	0.413	0.537*	0.402*	0.239	0.581***	0.223	0.272	0.314
Spring	Rainfall	-0.268	-0.633***	-0.594**	-0.700***	-0.491**	-0.505*	-0.496**	-0.074	-0.095	-0.373
Summer	Rainfall	-0.230	-0.123	-0.312	-0.135	-0.114	-0.130	-0.145	-0.260	-0.006	-0.323

Note: Significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Statistically significant values are in boldface type.

Fig. 3. Scattergrams of 30-year mean annual, winter, and spring rainfall on the x axis vs. the Pearson correlation coefficients (r values) between winter rainfall and mean acorn production on the y axis. All three $p < 0.05$.



tion and subsequent investment in reproduction (Pearse et al. 2016; Bogdziewicz et al. 2019b); either way, this result is indicative of a strong pollination Moran effect. Second, the opposite (negative) effect of spring temperature in the prior year is consistent with a strong negative autocorrelation between acorn crops in the prior year and the current year (Pearse et al. 2014) — that is, a warm, dry spring in year $x - 1$ fosters a large crop in year $x - 1$, which subsequently depresses crop size in year x . Thus, these results support the view that spring weather conditions, in both the current year and prior year, are proximate drivers that have direct, mechanistic relationships to acorn crop size in this species (Pearse et al. 2014, 2015).

The strength of the correlations between weather and the acorn crop across the 10 sites generally did not correlate significantly with long-term climatic variables, with the exception of winter rainfall, which was stronger (more negative) at wetter sites.

Mechanisms relating weather to seed production

What do these results reveal about the mechanism by which spring conditions affect pollination and subsequent acorn production? The phenological synchrony hypothesis proposes that differences in microclimate correlated with spring temperatures drive differences in flowering synchrony and thus pollen limita-

tion (Koenig et al. 2015). The positive effect of mean spring temperature (mean $r = 0.38$, range 0.223–0.595), significant at four of the sites, is consistent with this hypothesis. Supporting the alternative pollen washout hypothesis, however, is the negative effect of spring rainfall (mean $r = -0.42$, range -0.700 to -0.074), significant at five of the sites.

The strong inverse relationship between spring temperature and rainfall in this region makes it difficult to distinguish these hypotheses, which are only likely to be testable by experimental studies (Bogdziewicz et al. 2020). It is, however, possible that both proximate mechanisms are important; for example, phenological synchrony may be important under most circumstances but may be overshadowed by pollen washout when heavy rains take place during the spring.

The biological significance of the negative effect of winter rainfall on acorn production is less clear. To some extent, it may be a consequence of wet winters correlating with wet springs: correlations between winter rainfall and spring rainfall across the 10 sites were all positive, averaging 0.23 (range 0.001–0.494). Thus, the significance of winter rainfall may be primarily as a proxy for the negative effects of generally wet years.

We also found a significant correlation between acorn production and mean autumn temperature at one site (Dye Creek). It is possible that the generally positive effect of temperature during this season (r values were positive at eight sites) is related to warm temperatures facilitating flower bud initiation in this 1-year species (Sork et al. 1993).

Conclusion and comparison with Bogdziewicz et al. (2019a)

Considerable progress in understanding the proximate mechanisms driving seed production in masting species has been made in recent years (Crone and Rapp 2014; Pearse et al. 2016; Bogdziewicz et al. 2020). Nonetheless, much remains to be learned about how and why masting species respond to weather. Here we investigated how the masting behavior of different populations of *Q. lobata* located throughout its geographic range respond to local weather and long-term climate.

Despite the variability in masting behavior among sites, all sites generally exhibited similar relationships with weather: acorn production was best following dry winters and warm, dry springs in the current year and cold (and thus wet) springs in the previous year. These results are consistent with the high degree of spatial synchrony exhibited across sites in this species (Koenig and Knops 2013; Koenig et al. 2017).

The concordance between weather and the acorn crop among sites differed from *Q. petraea*, where the relationship between crop size and the critical weather factor — spring temperature — was highly variable among sites (Bogdziewicz et al. 2019a). These authors hypothesized that this was the result of the flower-to-fruit transition in this fruit-maturation species being sensitive to the precise timing of extreme weather events that varied considerably among sites, thus being strong at sites where key events happened to be within the spring time period analyzed and weak or absent where they were not. Results for *Q. lobata* more closely matched those reported for *Fagus sylvatica*, a flowering masting

species in which the same weather factor (summer temperature of the prior year) correlated with seed production across its range in France.

Both *Q. lobata* and *Q. petraea* are in the *Quercus* section of oaks (Hipp et al. 2020). Thus, intraspecific variation in the relationships between weather and seed production does not coincide with the phylogenetic relationships among these three species (the two oaks and the beech). The distinction between being a flowering masting or fruit-maturation masting species also provides little guidance; *Q. lobata* has characteristics of both, but the consistency in the correlations between weather and acorn production across populations more closely matches the flowering masting *Fagus sylvatica*.

More data are clearly needed to understand intraspecific variation in the relationship between weather cues and seed production in different populations of masting species. Similar to the variety of factors affecting this relationship interspecifically (Koenig et al. 2016), intraspecific differences are likely to be influenced by several variables. Whether a species is a flowering masting or a fruit-maturation masting species may be one such factor but will be of little help when masting is partly both, as for *Q. lobata* and probably many other species (Pearse et al. 2015; Bogdziewicz et al. 2019a).

Beyond the similarities in the relationships between weather and acorn production among sites, we found significant correlations between the strength of one of the weather factors affecting annual acorn production — winter rainfall — and long-term climatic conditions: the (negative) effect of winter rainfall was greater at generally wetter sites (Fig. 3). To some extent, this parallels the finding in *Q. petraea* that the strength of the correlation between spring temperature and acorn production was stronger (more positive) at colder sites (Bogdziewicz et al. 2019a).

Bogdziewicz et al. (2019a) proposed that this pattern was the result of two steps. First, following the logic of the phenological synchrony hypothesis (Koenig et al. 2015), warmer sites should exhibit greater average flowering synchrony and thus weaker pollen limitation. Second, greater average flowering synchrony could potentially weaken the correlation between spring temperature and the acorn crop, at least if annual variability were smaller as well, in which case, the error to signal ratio would be greater at warmer sites.

Applying similar logic to *Q. lobata*, the correlation between winter rainfall and the acorn crop should, as found here, be weaker (less negative) at drier sites, assuming that drier sites are subject to weaker pollen limitation. Whether this assumption is met remains to be tested.

There is still much to be learned about how weather and climate affect seed production in masting species. Particularly challenging will be conducting experimental analyses that go beyond the correlative results of this and most other studies to test the mechanisms by which weather and other environmental conditions affect pollination, fertilization, and ultimately seed production (Bogdziewicz et al. 2020). An understanding of these mechanisms is critical, however, especially for the understanding of how masting behavior may be affected by climate change (McKone et al. 1998; Kelly et al. 2013; Koenig et al. 2015; Pesendorfer et al. 2020).

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