

Weather cues associated with masting behavior dampen the negative autocorrelation between past and current reproduction in oaks

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PREMISE OF THE STUDY: The influence of weather conditions on masting and the ecological advantages of this reproductive behavior have been the subject of much interest. Weather conditions act as cues influencing reproduction of individual plants, and similar responses expressed across many individuals lead to population-level synchrony in reproductive output. In turn, synchrony leads to benefits from economies of scale such as enhanced pollination success and seed predator satiation. However, there may also be individual-level benefits from reproductive responses to weather cues, which may explain the origin of masting in the absence of economies of scale. In a previous study, we found support for a mechanism whereby individual responses to weather cues attenuate the negative autocorrelation between past and current annual seed production—a pattern typically attributed to resource limitation and reproductive tradeoffs among years.

METHODS: Here we provide a follow-up and more robust evaluation of this hypothesis in 12 species of oaks (*Quercus* spp.), testing for a negative autocorrelation (tradeoff) between past and current reproduction and whether responses to weather cues associated with masting reduce the strength of this negative autocorrelation.

KEY RESULTS: Our results showed a strong negative autocorrelation for 11 of the species, and that species-specific reproductive responses to weather cues dampened this negative autocorrelation in 10 of them.

CONCLUSIONS: This dampening effect presumably reflects a reduction in resource limitation or increased resource use associated with weather conditions, and suggests that responses to weather cues conferring these advantages should be selected for based on individual benefits.

KEY WORDS acorn production; deciduous; evergreen; precipitation; *Quercus*; resource limitation; synchrony; temperature.

Mast seeding (or masting) is defined as the intermittent, synchronous production of large seed crops across many individuals within a plant population (Silvertown, 1980; Kelly, 1994). This phenomenon is present across a wide spectrum of plant taxonomic groups and terrestrial ecosystem types and has been a subject of much interest by ecologists (reviewed by Pearse et al., 2016). Still, the mechanisms that underlie masting events are not well understood and several nonmutually exclusive explanations have been put forward.

From an evolutionary perspective, the fitness advantages of masting are thought to originate from economies of scale associated with

population-level reproductive synchrony (Silvertown, 1980; Kelly, 1994). For example, there is evidence that synchronous flowering during masting events leads to increased pollination efficiency and greater reproductive success among flowering individuals (Kelly et al., 2001; Rapp et al., 2013; Moreira et al., 2014) (Fig. 1). Likewise, synchronous seed production may result in seed predator satiation and therefore increase the chance of seed escape during masting events (Linhart et al., 2014; Moreira et al., 2016; Greenberg and Zarnoch, 2018) (Fig. 1). The outcome of these dynamics for a given species may in turn be contingent on the seed predator functional

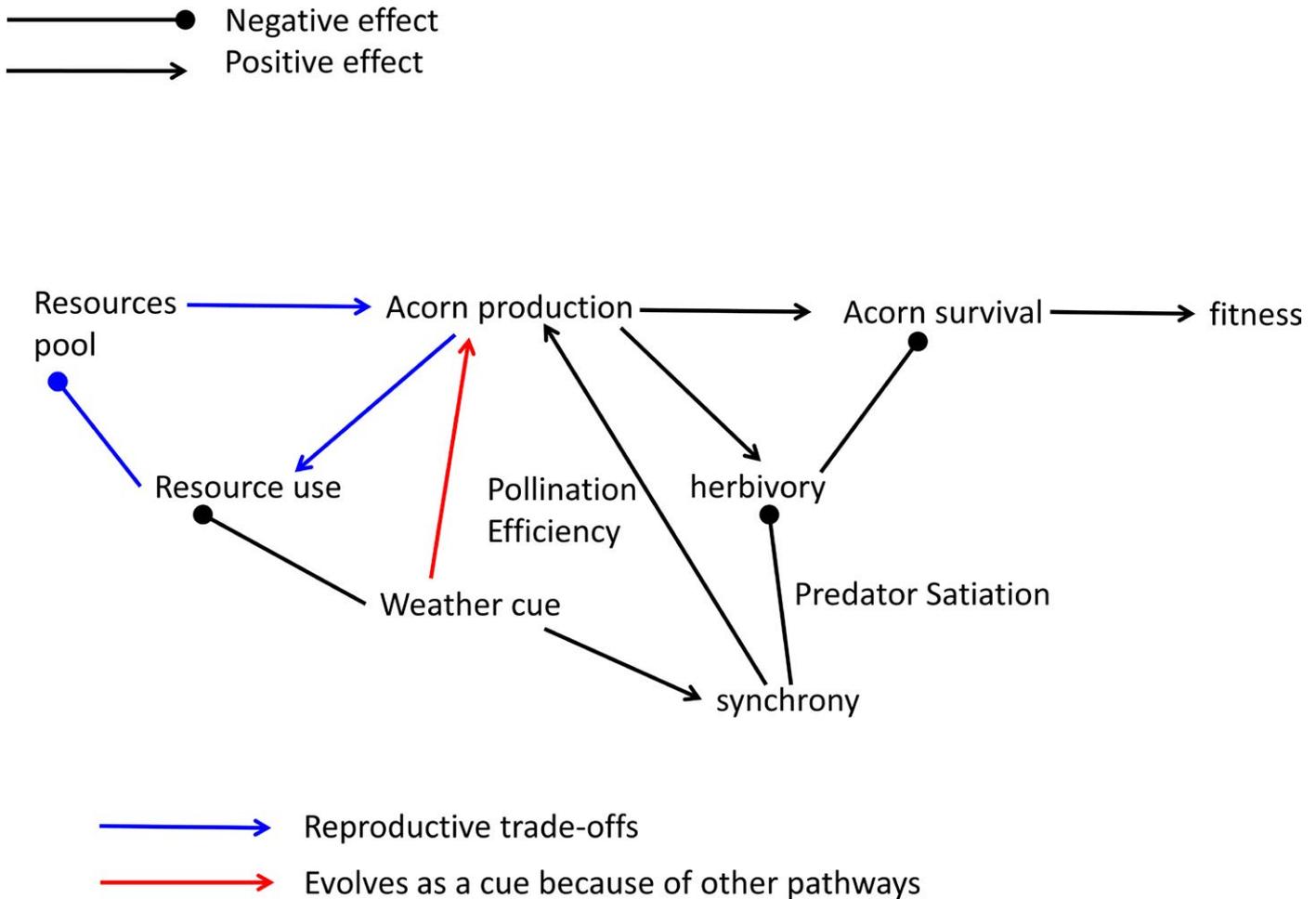


FIGURE 1. Conceptual diagram linking weather cues (e.g., temperature and precipitation), external (e.g., accumulation in the soil) and internal (e.g., acquisition, storage and allocation) plant resource dynamics, and economies of scale from population-level reproductive synchrony (pollination efficiency and predator satiation) to masting behavior via acorn production, acorn survival and plant fitness.

group or reproductive synchrony with other co-occurring species (Moreira et al., 2017). Together, these mechanisms represent fitness benefits to individuals stemming from population-level dynamics.

Another line of research has focused on the proximate drivers of masting by addressing how weather conditions trigger masting events (Mooney et al., 2011; Kelly et al., 2013; Roland et al., 2014; Vacchiano et al., 2017). Several authors have proposed that weather conditions act as arbitrary cues to which individuals respond simultaneously to initiate flowering, leading to synchrony in reproductive output (Kelly and Sork, 2002; Kelly et al., 2013; Roland et al., 2014) (Fig. 1). Under this scenario, the benefits from economies of scale represent a collateral outcome of groups of individuals responding synchronously to the same weather cues (Moreira et al., 2015; Pearse et al., 2016). Nevertheless, it is unclear how a reproductive response to weather conditions would evolve without it providing an individual-level benefit.

A number of studies have shown that weather conditions are strongly associated with interannual variability in resource availability in the soil (either carbohydrates or mineral nutrients), as well as in plant resource acquisition, allocation, storage, and depletion (e.g., Monks et al., 2016; Allen et al., 2017) (Fig. 1). Based on this, it is possible that individual-level responses to weather cues result

in direct benefits (in terms of resource availability and acquisition) to individuals that are independent of any economy of scale. For example, negative autocorrelations between past and present reproduction have been reported in many studies, and have frequently been taken as evidence for resource limitation (Smaill et al., 2011; Sala et al., 2012; Allen et al., 2017), thus preventing individuals from producing sequentially large crops. It has been proposed that plants respond to weather cues because it either increases resource gain or lowers the resource threshold for reproduction (i.e., Resource Budget Model; Isagi et al., 1997; Satake and Iwasa, 2000). Responses to the “right” weather cues could thus result in faster rebuild of energy and dampen the negative effects of last year’s reproduction. Accordingly, results from previous work of ours with ponderosa pine (*Pinus ponderosa*) suggest that individual-level responses to weather cues confer a direct advantage through attenuation of the negative autocorrelation between past and current annual seed production (Moreira et al., 2015). Results from other recent studies appear to support this mechanism. For example, Bogdziewicz et al. (2017) found that precipitation preceding acorn maturation was positively related to seed production in holm oak (*Quercus ilex*), mitigating apparent resource depletion following high crop production in the previous year (see also Fernández-Martínez et al., 2015).

These responses to weather cues would, over the long-term, result in higher lifetime seed production, and would be presumably selected to the extent that individual variation in such responses is underlain by genetic variation (Moreira et al., 2016). This pattern of responses to weather cues could be associated with the presence of “super-producers” within tree populations, i.e., individuals with high reproductive output that overcome strong resource limitation (Minor and Kobe, 2017). As such, this climate-driven process would represent an eco-evolutionary mechanism that potentially bridges weather cues, benefits to individuals, and group-level benefits occurring through economies of scale (Fig. 1).

A previous study of ours reported on the association between weather variables and masting behavior in 12 species of oaks (*Quercus* sp.) that encompass a broad range of attributes, including differences in leaf habit (deciduous or evergreen) and length of time needed for seed maturation (1 or 2 years) (Koenig et al., 2016). Here we use these oak species to test for the proposed individual-level benefits from responding to weather cues investigated previously for *P. ponderosa* (Moreira et al., 2015). Specifically, we tested for a negative autocorrelation between past and current reproduction in these species, and if responses to weather cues triggering masting dampened this negative autocorrelation, presumably through some mechanism associated with greater resource gain or reduced resource depletion (i.e., weaker resource limitation). Overall, this study provides an assessment of the relationship between weather cues and patterns of reproduction in long-lived oak species, and tests a potentially widespread mechanism associated with responses to weather cues that may help explain the origin and maintenance of masting.

MATERIAL AND METHODS

Natural history

We compiled data on 12 species of oaks, including eight from California (*Quercus lobata*, *Q. douglasii*, *Q. engelmannii*, *Q. garryana*, *Q. chrysolepis*, *Q. agrifolia*, *Q. wislizeni* and *Q. kelloggii*), two from Minnesota (*Q. macrocarpa* and *Q. ellipsoidalis*), and two from Spain (*Q. suber* and *Q. canariensis*). Data for each species was obtained from a single population. Five of the California species (*Q. lobata*, *Q. douglasii*, *Q. chrysolepis*, *Q. agrifolia*, and *Q. kelloggii*) were from Hastings Reservation in central coastal California;

the other three California species (*Q. engelmannii*, *Q. garryana*, and *Q. wislizeni*) were from other sites around the state (Koenig et al., 2016). The Minnesota species were studied at Cedar Creek Ecosystem Science Reserve (Koenig and Knops, 2014), whereas the sampled populations of the species in Spain (*Q. suber* and *Q. canariensis*) were located at the Aljibe Mountains, in southern Spain (Pérez-Ramos et al., 2015; Moreira et al., 2017).

These oak species vary in their leaf habit (eight deciduous species and four evergreen species) and length of time needed for seed maturation (eight species that require one year to mature acorns and four species that require two years) (Table 1). For each species, we sampled individuals located at one site (i.e., population), where the number of individuals per site ranging from 12–86 (total $N = 457$) and the number of years of data for each population ranging from 10–35 (total of 279 population years) (Table 1).

Measurements of acorn production and tree growth

We collected acorn crop data for individual trees in two different ways. For the 10 North American species, we estimated annual acorn production by visual surveys of each tree involving two researchers counting as many acorns as possible in 15 s and combining their counts for an estimate of relative annual acorn production (Koenig et al., 1994). In addition, we also measured annual radial growth for the five species sampled at the Hastings Reservation starting in 1994 (Barringer et al., 2013).

For the two Spanish species, we estimated annual acorn production by randomly placing four circular traps (0.5 m diameter) under the crown of each selected tree, avoiding overlap with neighboring plant crowns (Pérez-Ramos et al., 2014, 2015). Each trap consisted of a plastic mesh attached around an iron ring, which was soldered to an iron rod 1.5 m in height to prevent acorn removal by rodents (the main post-dispersal predators at the study area; Pérez-Ramos et al., 2013). Each year, we collected trap contents at the end of the acorn-drop period (February–March), counted the number of acorns, and estimated acorn density (number of acorns per square meters).

Weather data

Weather data were obtained from nearby weather stations, or, in the case of the three species of California oaks studied at sites other than Hastings Reservation, from the PRISM data set (Oregon State

TABLE 1. Oak species used in the study. Listed are the acorn type (length of time needed for seed maturation, one or two years), the leaf habit (deciduous or evergreen), the number of trees and years measured, and the geographical coordinates (decimal degrees) from the single population measured of each oak species.

Species	Acorn type (in years)	Leaf type	N trees	N years	Latitude	Longitude
<i>Q. lobata</i>	1	Deciduous	86	35	36.3793	-121.5666
<i>Q. douglasii</i>	1	Deciduous	56	35	36.3793	-121.5666
<i>Q. engelmannii</i>	1	Deciduous	19	21	33.5230	-117.2757
<i>Q. garryana</i>	1	Deciduous	12	13	40.6701	-122.8696
<i>Q. macrocarpa</i>	1	Deciduous	58	17	45.4020	-93.1994
<i>Q. canariensis</i>	1	Deciduous	20	10	36.3483	-5.6039
<i>Q. suber</i>	1	Evergreen	30	10	36.3483	-5.6039
<i>Q. chrysolepis</i>	2	Evergreen	21	35	36.3793	-121.5666
<i>Q. agrifolia</i>	1	Evergreen	63	35	36.3793	-121.5666
<i>Q. wislizeni</i>	2	Evergreen	12	16	39.2381	-121.2858
<i>Q. kelloggii</i>	2	Deciduous	21	35	36.3793	-121.5666
<i>Q. ellipsoidalis</i>	2	Deciduous	59	17	45.4020	-93.1994

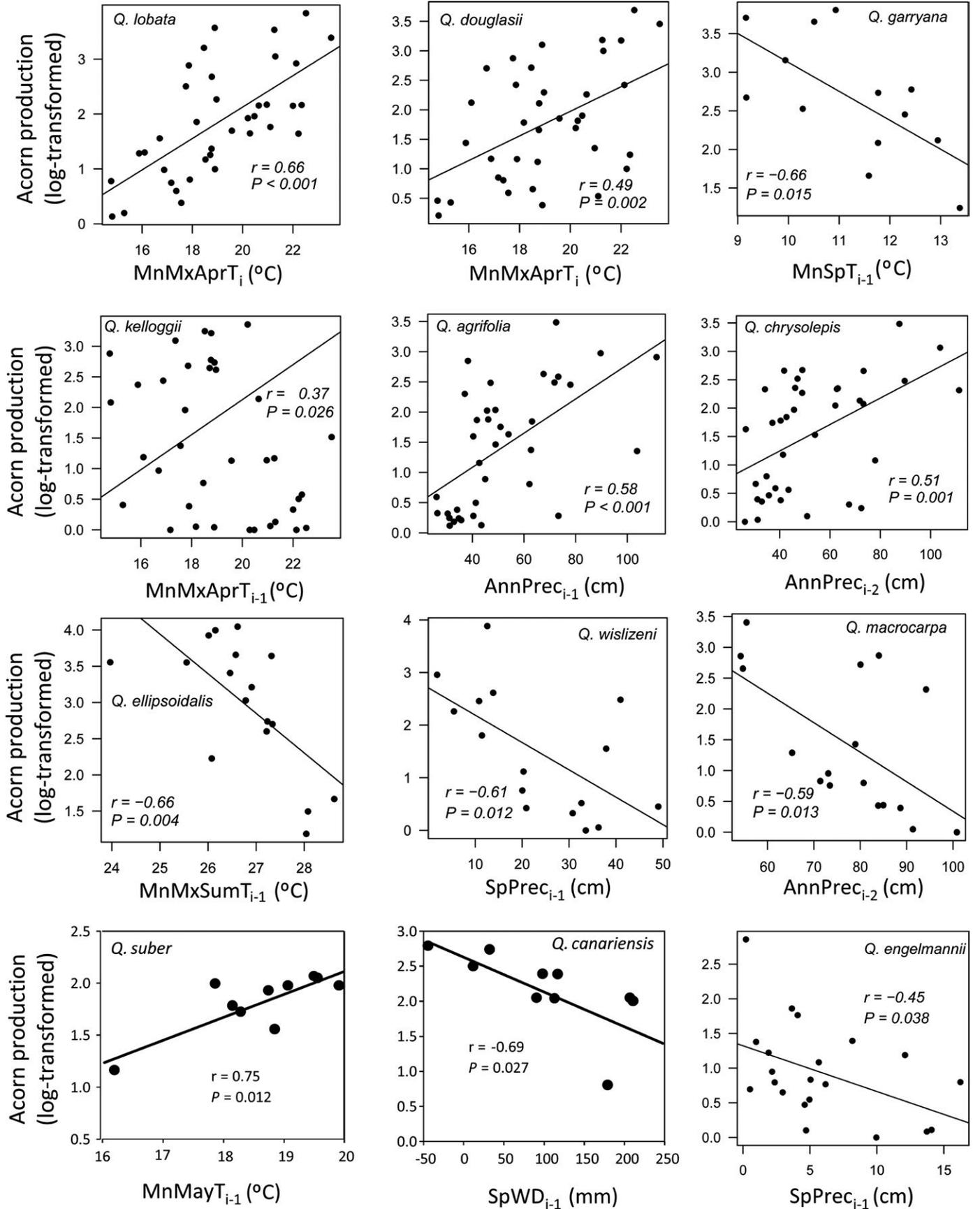


FIGURE 2. Relationships between acorn production at the population level and the weather variable that correlates with masting behavior with its abbreviation for 12 *Quercus* species. For details on statistical methods and criteria for selection of the weather cues see Pérez-Ramos et al. (2015) and Koenig et al. (2016). Points represent log-transformed mean values for each year ($N = 10\text{--}35$ years). Pearson r correlation coefficients and P -values are shown. The $MnMxAprT_i$ = unlagged mean maximum temperature in April, $MnSpT_{i-1}$ = one-year lagged mean spring temperature, $MnMxAprT_{i-1}$ = one-year lagged mean maximum temperature in April, $AnnPrec_{i-1}$ = one-year lagged annual precipitation, $AnnPrec_{i-2}$ = two-year lagged annual precipitation, $MnMxSumT_{i-1}$ = one-year lagged mean maximum temperature in summer, $SpPrec_{i-1}$ = one-year lagged spring precipitation, $MnMayT_{i-1}$ = one-year lagged mean temperature in May, $SpWD_{i-1}$ = one-year lagged spring water deficit, $SpPrec_{i-1}$ = one-year lagged spring precipitation.

University, Corvallis, Oregon, USA; <http://prism.oregonstate.edu>) (Koenig et al., 2016). For this study, we used weather variables previously identified as the best predictors of acorn production based on data collected at each local site for each species (Koenig et al., 2016). Acorn production was positively correlated with unlagged mean maximum temperature in April for *Q. lobata* and *Q. douglasii*, two-year lagged annual precipitation for *Q. chrysolepis*, one-year lagged mean maximum temperature in April for *Q. kelloggii*, one-year lagged annual precipitation for *Q. agrifolia*, and one-year lagged mean temperature in May for *Q. suber* (Fig. 2). Conversely, acorn production was negatively correlated with one-year lagged mean maximum temperature in summer for *Q. ellipsoidalis*, one-year lagged mean spring temperature for *Q. garryana*, one-year lagged spring precipitation for *Q. wislizeni*, two-year lagged annual precipitation for *Q. macrocarpa*, one-year lagged spring precipitation for *Q. englemanni*, one-year lagged spring water deficit (calculated as the difference between potential evapotranspiration and precipitation) for *Q. canariensis*, and one-year lagged spring precipitation for *Q. engelmannii* (Fig. 2). “Spring season” was defined as the period between spring equinox and summer solstice.

Weather effects on the negative autocorrelation between past and current reproduction

We evaluated the linkage between weather variables and total acorn production by testing whether the above species-specific weather cues influenced the negative autocorrelation between past and current reproduction (sensu Moreira et al., 2015). To the extent that this negative autocorrelation reflects the influence of resource limitation on reproduction where there is a trade-off between past and current reproduction (Isagi et al., 1997; Pesendorfer et al., 2016), an influence of weather on the strength of this autocorrelation suggests that weather alters the dynamics of resource availability and use. Individual-level analyses indicated that the magnitude of this negative autocorrelation (measured as the slope of current acorn output regressed onto past acorn output) is negatively associated with average acorn production (overall mean across the entire multiyear sampling period) for several of the oak species under study (Appendix S1). This means that trees with high reproductive output exhibit a stronger negative temporal autocorrelation than individuals with low output, which is suggestive of greater resource limitation in productive trees (Isagi et al., 1997; Pesendorfer et al., 2016). Accordingly, if weather cues dampen such autocorrelation, this would potentially reflect reduced resource limitation and thus a fitness advantage for the tree.

First, we evaluated the relationship between past and current reproduction by running separate linear mixed models for each species where current acorn production was predicted by acorn production during the previous year. A negative correlation between reproductive investment in consecutive years is expected (Isagi et al., 1997; Koenig et al., 2015; Pesendorfer et al., 2016),

especially in masting species where high investment of annual resources in a given year is predicted to result in subsequently smaller investment in reproduction the next year (Sala et al., 2012). For species that require two years for seed maturation (Table 1), we ran models that included acorn production during the previous year and two years before current acorn production as predictors of current acorn production (Appendix S2). However, because results from these models remained qualitatively unchanged for a subset of these species (i.e., same sign and thus interpretation for cue by predictor interaction; Appendix S3) relative to those from models using only reproduction the prior year (Table 2), we present results only for the simpler models including reproduction in the previous year as a predictor. We also note that a negative autocorrelation between past and current reproduction may also be determined by processes such as resource storage or tradeoffs between growth and reproduction (Monks and Kelly, 2006; Barringer et al., 2013). Accordingly, for the five species for which radial growth was available, we tested whether growth altered the autocorrelation between past and current reproduction. We did so by running models where current acorn production was predicted by acorn production in the previous year, and annual radial growth in the current year. If a significant effect of acorn production in the previous year on current acorn production turned nonsignificant after including growth in the models, this suggested that the negative autocorrelation in reproduction was set in motion by resources that were diverted from growth to reproduction (i.e., a growth-reproduction trade-off; Pearse et al., 2016), rather than by dynamics exclusively associated with reproductive allocation (e.g., reproductive trade-offs).

Second, we tested whether the strength of the negative autocorrelation between past and current acorn output was mediated by weather variables. We restricted these analyses to the 11 oak species that exhibited a significant negative autocorrelation between past and current reproduction (see *Results* section). For each of these species, we ran a model where current acorn production was predicted by acorn production during the previous year, the weather cue associated with masting for the species, and their interaction. We standardized both predictor variables (mean = 0, SD = 1) to allow meaningful comparison of the magnitude of the parameter estimates. The interaction term in each of these models tested whether the relationship between past and current reproduction was contingent on the weather cue associated with masting behavior; that is, if the weather cue influenced the magnitude of the negative autocorrelation. A positive value for the interaction parameter indicated that as values for the weather cue increase, the relationship between past and current acorn production becomes less negative (i.e., there is a weaker negative autocorrelation between past and current reproduction), or alternatively, that as the effect of the weather cue decreases, the negative autocorrelation becomes more negative (i.e., stronger) (Fig. 3A). Contrarily, a negative value for the interaction parameter indicated that as values for the weather cue decrease, the relationship between past and current acorn production becomes

TABLE 2. (A) Linear mixed model testing for a relationship between current acorn production (N_i) and acorn production during the previous year (N_{i-1}) for 12 *Quercus* sp. (B) Linear mixed model testing for the effects of acorn production during the previous year, weather cue associated with masting behavior, and their interaction for 12 *Quercus* sp. Statistical analyses of both models were performed at the individual tree level using a mixed model with tree as a random factor. To approach normality of residuals in our models, acorn production was log-transformed. The slope estimator (β) with the standard error (inside brackets), t -values with the degrees of freedom (inside brackets), and P -values are shown. Significant predictors ($P < 0.05$) are in bold. Abbreviations of the weather cues associated with masting behavior are shown in Fig. 2. We standardized the acorn production during the previous year (N_{i-1}) and the weather cue associated with masting (mean = 0, SD = 1) to allow meaningful comparison of the magnitude of the parameter estimates.

	A. $N_i = N_{i-1}$			B. $N_i = N_{i-1} + \text{weather cue} + N_{i-1} \times \text{weather cue}$		
	β (s.e.)	t -value (df)	P	β (s.e.)	t -value (df)	P
<i>Quercus lobata</i>						
N_{i-1}	-0.243 (0.017)	-13.96 (1, 2989)	<0.001	-0.247 (0.028)	-8.94 (1,2987)	<0.001
MnMxAprT _i	-	-	-	0.605 (0.023)	25.72 (1,2987)	<0.001
$N_{i-1} \times \text{MnMxAprT}_i$	-	-	-	0.079 (0.024)	3.37 (1,2987)	<0.001
<i>Quercus douglasii</i>						
N_{i-1}	-0.167 (0.015)	-15.94 (1, 1943)	<0.001	-0.232 (0.034)	-6.77 (1,1941)	<0.001
MnMxAprT _i	-	-	-	0.441 (0.028)	15.50 (1,1941)	<0.001
$N_{i-1} \times \text{MnMxAprT}_i$	-	-	-	0.142 (0.029)	4.92 (1,1941)	<0.001
<i>Quercus engelmannii</i>						
N_{i-1}	-0.123 (0.036)	-3.41 (1, 721)	<0.001	-0.151 (0.051)	-2.96 (1,719)	0.003
SpPrec _{i-1}	-	-	-	-0.159 (0.045)	-3.54 (1,719)	<0.001
$N_{i-1} \times \text{SpPrec}_{i-1}$	-	-	-	-0.146 (0.046)	-3.17 (1,719)	0.002
<i>Quercus garryana</i>						
N_{i-1}	-0.216 (0.082)	-2.62 (1, 128)	0.010	-0.249 (0.120)	-2.07 (1,126)	0.040
MnSpT _{i-1}	-	-	-	-0.436 (0.091)	-4.78 (1,126)	<0.001
$N_{i-1} \times \text{MnSpT}_{i-1}$	-	-	-	-0.289 (0.090)	-3.19 (1,126)	0.002
<i>Quercus macrocarpa</i>						
N_{i-1}	-0.220 (0.040)	-5.54 (1, 548)	<0.001	-0.261 (0.278)	-0.94 (1,546)	0.367
AnnPrec _{i-2}	-	-	-	-0.491 (0.312)	-1.34 (1,546)	0.204
$N_{i-1} \times \text{AnnPrec}_{i-2}$	-	-	-	0.432 (0.372)	1.16 (1,546)	0.268
<i>Quercus canariensis</i>						
N_{i-1}	-0.178 (0.049)	-3.61 (1, 121)	<0.001	-0.087 (0.046)	-1.90 (1,119)	0.060
SpWD _{i-1}	-	-	-	-0.297 (0.042)	-7.06 (1,119)	<0.001
$N_{i-1} \times \text{SpWD}_{i-1}$	-	-	-	-0.142 (0.067)	-2.13 (1,119)	0.035
<i>Quercus suber</i>						
N_{i-1}	-0.188 (0.067)	-2.78 (1, 179)	0.006	-0.081 (0.059)	-1.37 (1,177)	0.172
MnMayT _{i-1}	-	-	-	0.173 (0.049)	3.54 (1,177)	<0.001
$N_{i-1} \times \text{MnMayT}_{i-1}$	-	-	-	0.204 (0.051)	4.02 (1,177)	<0.001
<i>Quercus chrysolepis</i>						
N_{i-1}	-0.237 (0.035)	-6.81 (1, 727)	<0.001	-0.356 (0.054)	-6.59 (1,725)	<0.001
AnnPrec _{i-2}	-	-	-	0.444 (0.049)	9.08 (1,725)	<0.001
$N_{i-1} \times \text{AnnPrec}_{i-2}$	-	-	-	0.113 (0.049)	2.31 (1,725)	0.021
<i>Quercus agrifolia</i>						
N_{i-1}	-0.084 (0.021)	-3.99 (1, 2171)	<0.001	-0.160 (0.031)	-5.22 (1,2169)	<0.001
AnnPrec _{i-1}	-	-	-	0.563 (0.028)	20.14 (1,2169)	<0.001
$N_{i-1} \times \text{AnnPrec}_{i-1}$	-	-	-	0.089 (0.032)	2.82 (1,2169)	0.005
<i>Quercus wislizeni</i>						
N_{i-1}	-0.115 (0.037)	-3.10 (1, 626)	0.002	-0.431 (0.066)	-6.51 (1,624)	<0.001
SpPrec _{i-1}	-	-	-	-0.393 (0.058)	-6.77 (1,624)	<0.001
$N_{i-1} \times \text{SpPrec}_{i-1}$	-	-	-	-0.230 (0.060)	-3.83 (1,624)	<0.001
<i>Quercus kelloggii</i>						
N_{i-1}	0.100 (0.039)	2.57 (1, 604)	0.010	-	-	-
MnMxAprT _{i-1}	-	-	-	-	-	-
$N_{i-1} \times \text{MnMxAprT}_{i-1}$	-	-	-	-	-	-
<i>Quercus ellipsoidalis</i>						
N_{i-1}	-0.220 (0.040)	-5.54 (1, 548)	<0.001	0.006 (0.055)	-4.69 (1,517)	<0.001
MnMxSumT _{i-1}	-	-	-	-0.560 (0.050)	-11.26 (1,517)	<0.001
$N_{i-1} \times \text{MnMxSumT}_{i-1}$	-	-	-	-0.250 (0.053)	-4.73 (1,517)	<0.001

less negative (i.e., there is a weaker negative autocorrelation between past and current reproduction), or alternatively, that as the effect of the weather cue increases, the negative autocorrelation becomes stronger (Fig. 3B). If the direction of the relationship between acorn output and the cue (i.e., positive or negative slope, Fig. 2) coincides

with the direction of the pattern described by the interaction (positive or negative), this would indicate that the weather cue dampens the negative autocorrelation.

The above models were conducted at the individual level, because this is the level at which resource limitation on acorn production

occurs (Pearse et al., 2014; Moreira et al., 2015). For species requiring two years for seed maturation that exhibited a significant effect of reproduction two years before on current reproduction (Appendix S2), we also ran models that included reproduction two years before current reproduction and its interaction with the weather cue as predictors (Appendix S3). Because the interpretation of the results in these cases did not change relative to findings from models using only reproduction the prior year and its interaction with the weather cue, we again present results for the simpler models including only reproduction one year previously.

Past and current acorn production were log-transformed to achieve normality of residuals in all the models. In addition, we used “tree ID” as a random factor in all models to account for repeated measures on each individual (Pearse et al., 2014; Moreira et al., 2015). Analyses were performed in R 3.2.0 (R Core Team, 2014).

RESULTS

There was a significant negative autocorrelation between past and current acorn production for 11 of the 12 oak species (Table 2A), the only exception being *Q. kelloggii*. For these 11 species, we then proceeded to test the influence of weather cues on the negative autocorrelation. For the five species with radial growth measurements, the negative autocorrelation remained significant after including growth in the model suggesting that the observed negative autocorrelations were not associated with trade-offs between growth and reproduction in these species (Appendix S4).

Results from the models—including weather cues—indicated a significant interaction between acorn production in the previous year and the weather cue for 10 species (Table 2b), i.e., the negative autocorrelation was contingent on the weather cue. The parameter value for the interaction was positive for *Q. lobata*, *Q. douglasii*, *Q. suber*, *Q. agrifolia* and *Q. chrysolepis* (Table 2B), indicating that as values of the weather cue increased, the relationship between past and current acorn production became less negative (i.e., weaker negative autocorrelation) (Fig. 3A). For each of these species, the weather cue was positively related to acorn output (Fig. 2), which is in accordance with positive parameters for the interaction and indicates that higher values of the weather cue decreased the strength of the negative autocorrelation (Fig. 3A).

In contrast, the parameter value for the interaction was negative for *Q. engelmannii*, *Q. garryana*, *Q. canariensis*, *Q. ellipsoidalis*, and *Q. wislizeni* (Table 2B), indicating that as values of the weather cue decreased, the relationship between past and current acorn production became less negative (i.e., weaker negative autocorrelation) (Fig. 3B). For each of these species, the weather cue was negatively related to reproductive output (Fig. 2), which is in accordance with

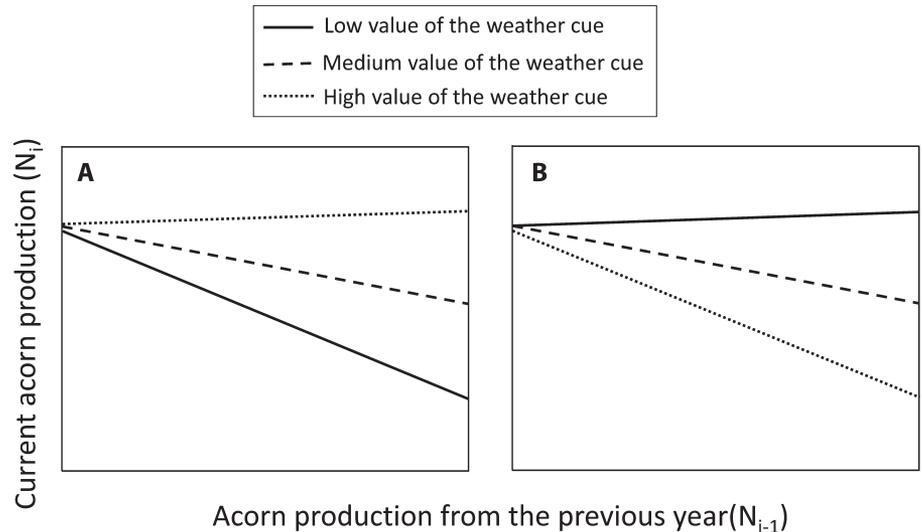


FIGURE 3. Predictions of current acorn production (N_i) based on acorn production from the previous year (N_{i-1}) at high, medium and low values of the weather cues associated with masting behavior. (A) Panel showing a case where we found a positive relationship between acorn production and the weather cue (*Q. lobata*, *Q. douglasii*, *Q. suber*, *Q. chrysolepis*, and *Q. agrifolia*; Fig. 2) and a positive value for the parameter of the interaction between acorn production during the previous year and the weather cue (Table 2). This would indicate that as values for the weather cue increase, the relationship between past and current acorn production becomes less negative (i.e., there is a weaker negative autocorrelation between past and current reproduction), or alternatively, that as the effect of the weather cue decreases, the negative autocorrelation becomes more negative (i.e., stronger). (B) Panel showing a case where we found a negative relationship between acorn production and the weather cue (*Q. engelmannii*, *Q. garryana*, *Q. canariensis*, *Q. ellipsoidalis* and *Q. wislizeni*; Fig. 2) and a negative value for the parameter of the interaction between acorn production during the previous year and the weather cue (Table 2). This would indicate that as values for the weather cue decrease, the relationship between past and current acorn production becomes less negative (i.e., there is a weaker negative autocorrelation between past and current reproduction), or alternatively, that as the effect of the weather cue increases, the negative autocorrelation becomes more negative (i.e., stronger). Figure modified from Moreira et al. (2015).

a negative parameter for the interaction and suggests that lower values of the weather cue in such species dampen the negative autocorrelation (Fig. 3B).

Finally, we did not find a significant interaction between acorn production in the previous year and the weather cue for *Q. macrocarpa* (Table 2B).

DISCUSSION

We found a strong negative autocorrelation between past and current reproduction for 11 of the 12 oak species, which agrees with reports for other long-lived masting tree species such as pines (*Pinus*) and oaks (*Quercus*) (Sork et al., 1993; Crone et al., 2009; Moreira et al., 2015). The prevailing interpretation for this result has been that the production of a large acorn crop depletes stored resources and that these take more than a year to replenish, resulting in allocation constraints or tradeoffs across years (Crone et al., 2009; Sala et al., 2012; Han et al., 2014). The degree to which plants invest resources in reproduction during masting events has been modeled as the “depletion coefficient” (Kelly, 1994) or “cost of flowering” (Isagi et al., 1997). If the depletion coefficient is high, reserves are exhausted and plants are not able to reproduce again for some time

or reproduce less subsequently (Kelly, 1994). It is important to note that the negative autocorrelation between past and current reproduction might depend on the extent to which resources are diverted from growth to reproduction. Allocation to growth (vs. reproduction) may result in an apparent tradeoff between past and current reproduction that is caused by allocation constraints between vegetative growth and reproduction (Pearse et al., 2016). However, for five of the studied species, the effect of past reproduction remained significant after including radial growth in the models, suggesting that the negative autocorrelation between past and current reproduction was not influenced by growth-reproduction tradeoffs.

In accordance with previous findings for other tree species (e.g., Chen et al., 2018), we also found that oak masting behavior is triggered by species-specific weather variables. We observed that reproductive output by each of these species was associated with a variety of different weather cues, presumably reflecting interspecific variation in the relationships between weather conditions and masting behavior. This suggests differences in the specific traits and processes underlying reproductive responses to weather in oaks depending on the weather conditions to which each species has adapted. Having said this, we also found differences in weather cues associated with masting for sympatric species with similar life histories growing under similar climates. This suggests that there is not necessarily a strict link between functional strategies or traits and weather cues associated with reproduction. It therefore appears that rather than a single type of weather cue-reproduction association under specific climatic types, there may be a suite of different associations representing alternative ecological mechanisms among sympatric species.

The mechanisms by which weather influences masting are not well understood. Over shorter time scales, it has been proposed that weather conditions act as proximate arbitrary cues that stimulate the onset of reproduction and reproductive synchrony, and that the advantage of individual plants responding similarly (in amount and timing) to such cues originates from economies of scale associated with reproductive synchrony (Kelly et al., 2013) (Fig. 1). These reproductive benefits from synchrony are suggestive of natural selection favoring responses to a common weather cue, but it is difficult to explain an evolutionary basis for climate-seeding relationships without the presence of individual-level benefits from responses to these same cues (Pearse et al., 2014; Moreira et al., 2015). In this sense, numerous studies have demonstrated that masting behavior relies on a combination of weather cues and external (e.g., accumulation in the soil) and internal (e.g., acquisition, storage and allocation) plant resource dynamics (reviewed by Allen et al., 2017) (Fig. 1). Based on this view, climate-driven processes should provide direct individual benefits (in terms of availability and acquisition of resources critical to reproduction) that are independent of any economy of scale (Moreira et al., 2015) (Fig. 1). Here we found that the individual-level responses to weather cues confer a direct advantage through the attenuation of the negative autocorrelation between past and current reproduction for 10 out of the 12 studied oak species. For five of these 10 species (Fig. 2), patterns were consistent with our work on *P. ponderosa* (Moreira et al., 2015), as well as with studies on beech (*Nothofagus solandri* var. *cliffortioides*) (Smaill et al., 2011) and holm oak (*Q. ilex*) (Bogdziewicz et al., 2017), showing that cooler or wetter conditions positively correlate with reproductive output. These patterns have been attributed, at least partly, to a reduction in resource limitation presumably through more efficient nitrogen acquisition and use (Smaill et al., 2011; Schaeffer et al., 2013; Bogdziewicz

et al., 2017). However, for the other five species, masting events were associated with high temperature or low precipitation during the spring (Fig. 2). It is perhaps not surprising that some of these species respond positively to high temperatures, considering that some habitats are not strongly limited by water availability and warm temperatures can induce flowering (e.g., Bogdziewicz et al., 2017). However, patterns observed for two species for which reproductive output was negatively associated with precipitation (Fig. 2) are more puzzling, because increasing aridity is expected to heighten resource limitation (Pérez-Ramos et al., 2010). In interpreting these results, it is important to keep in mind that weather cues associated with masting can be linked to resource availability in unexpected ways. For example, studies have found that the change in temperature between two previous consecutive years correlates strongly with current reproductive output, suggesting that trees integrate information on weather cues across multiple seasons (rather than temperature or precipitation during a single season) when allocating to current reproduction (Kelly et al., 2013). Nonetheless, previous analyses of our oak populations demonstrated that a model testing for averaging effects did not provide a better fit in predicting acorn production than a model that included the climatic cue alone (Koenig and Knops, 2014; Pérez-Ramos et al., 2015). This suggests that averaging effects are not the sole mechanism behind temporal patterns in reproductive output in these species.

It is also possible that plant responses to weather cues are related to other mechanisms not strictly linked to resource limitation but are fundamental to masting, such as flower induction and pollination success. These mechanisms may respond to different weather conditions relative to those associated with resource use and availability. For example, Koenig et al. (2015) found that warm spring conditions increased male and female flowering synchrony in valley oak (*Q. lobata*), which in turn resulted in greater pollination success and acorn production during the subsequent autumn. In contrast, García-Mozo et al. (2007) found that high precipitation during flowering events interfered with pollen dispersal and limited the pollination success of holm oaks (*Q. ilex*).

Our results call for further studies involving long-term measurements of resource use and reproduction. In performing such endeavors, a desirable feature is to sample multiple populations per species to assess whether associations between reproductive patterns, plant traits, and related weather cues remain consistent across sites. An examination of plant functional traits associated with nutrient acquisition and use is recommended (Abe et al., 2016), and this could be achieved by comparing closely related species with contrasting growth strategies, longevities, and nutrient economies. These comparisons would yield insight into how differences in life-history strategies determine the occurrence and magnitude of resource limitation and its relationship with weather cues. Other candidate mechanisms besides resource limitation, including abiotic control on pollen dispersal and germination or on seed maturation, should also be investigated because they determine individual-level fitness benefits associated with reproductive responses to weather cues.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

APPENDIX S1. Correlation at the individual tree level between the slope estimator of current reproduction regressed onto past reproduction (lag 1) and total acorn production (log-transformed data) for 12 *Quercus* species.

APPENDIX S2. Linear mixed model testing for the effects of acorn production during the previous year (N_{i-1}) and two years before current reproduction (N_{i-2}) on current acorn production (N_i) in three *Quercus* species requiring two years for seed maturation.

APPENDIX S3. Linear mixed model testing for the effects of acorn production during the previous year (N_{i-1}), acorn production two years before current reproduction (N_{i-2}), the weather variable acting as the masting cue, and their two-way interactions for two *Quercus* species requiring two years for seed maturation (and for which a significant effect of reproduction two years before on current reproduction was observed).

APPENDIX S4. Linear mixed model testing for the effects of acorn production during the previous year (N_{i-1}), two years before current reproduction (N_{i-2}) (in the case of species requiring two years for seed maturation) and current annual radial growth (D_i) on current acorn production (N_i) in five *Quercus* species.

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