

Environmental drivers of mast-seeding in Mediterranean oak species: does leaf habit matter?

Ignacio M. Pérez-Ramos^{1*}, Carmen M. Padilla-Díaz¹, Walter D. Koenig² and Teodoro Marañón¹

¹Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), CSIC, P.O. Box 1052, Sevilla 41080, Spain; and

²Lab of Ornithology and Department of Neurobiology and Behavior Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

Summary

1. Understanding the proximate factors that govern the widespread mast-seeding process is a question of considerable interest that remains poorly understood. The identity and effect of these factors may vary among coexisting species that differ in leaf habit, potentially resulting in temporally asynchronous patterns of seed production.

2. In this study, we aim to identify the proximate causes of mast-seeding using two oak species with contrasting leaf habit that coexist in southern Spain, the deciduous *Quercus canariensis* and the evergreen *Q. suber*. Simultaneously, we review the literature on environmental drivers of mast-seeding in Mediterranean oaks, distinguishing between evergreen and deciduous species.

3. Our results indicate that Mediterranean oaks are primarily sensitive to weather, mast-seeding being strongly correlated with water availability and air temperature, mainly in the spring and summer.

4. The two study oak species were affected by weather in quite different ways, most likely because of different abiotic requirements as well as contrasting functional strategies of resource use and biomass allocation. Specifically, annual seed production in *Q. canariensis* was more severely limited by drought than in *Q. suber*, but responded positively to warmer spring temperatures.

5. *Q. canariensis* showed a large interannual variability, whereas *Q. suber* exhibited much more constant seed production. These two species also exhibited a very low level of synchrony in their temporal patterns of seed crop size, most likely due to phenological differences in the processes of flowering and seed maturation.

6. *Synthesis.* Our results indicate that weather plays a crucial role as a proximate driver of mast-seeding in Mediterranean oaks. We hypothesize that the current abundance of co-occurring species that differ in leaf habit could be altered under future climate change scenarios. The decline of seed production with drier conditions will be potentially greater in deciduous species, particularly those inhabiting wetter sites. Alternatively, the expected warmer temperatures could negatively affect evergreen species as a consequence of their more conservative strategy of biomass allocation. Our findings suggest that understanding how species with different functional or phenological attributes adjust their reproductive abilities to weather may enable us to infer the effects of ongoing environmental changes on population recruitment and dynamics.

Key-words: climate change, drought, functional strategies, phenology, plant–climate interactions, *Quercus canariensis*, *Quercus suber*, recruitment, synchrony, temperature

Introduction

Understanding how and why many perennial plant species exhibit large interannual variability in seed production, known

as mast-seeding (Silvertown 1980; Kelly 1994), is a question of considerable ecological and evolutionary interest (Kelly & Sork 2002). For wind-pollinated species such as oaks, it is generally assumed that the ultimate, evolutionary causes of mast-seeding are satiating seed predators and/or increasing pollination efficiency (Janzen 1971; Smith, Hamrick & Kramer

*Correspondence author. E-mail: imperez@imase.csic.es

1990; Kelly & Sullivan 1997). However, the proximate drivers of masting, that is the factors that promote the temporal synchronization among individuals in their reproduction patterns, are much more poorly understood (Kelly *et al.* 2013).

Three general sets of proximate factors of masting have been identified as being important in at least some ecosystems: (i) environmental factors, such as air temperature and rainfall, with direct ('weather as a proximate driver' hypothesis; Pearse, Koenig & Knops 2014) and/or indirect ('weather as a cue' hypothesis; Kelly *et al.* 2013) effects on annual seed crop; (ii) pollen availability and fertilization success (Koenig & Knops 2005; Koenig *et al.* 2012); and (iii) temporal patterns of resource allocation and physiological costs of reproduction (Isagi *et al.* 1997; Crone, Miller & Sala 2009; Sala *et al.* 2012). These are non-exclusive hypotheses, and most likely interact in some way. For example, environmental factors are likely to affect pollen availability by influencing the annual amount of resources available for reproduction and thus reproductive success the following year. In general, little is known about either the relative importance of these proximate factors or the details of how they interact in any particular system.

Environmental factors almost certainly play an important role in the masting process by influencing pollen or resource availability, with the impact expected to be stronger in resource-limited environments such as most Mediterranean ecosystems (Kelly & Sork 2002). The effects of environmental factors are complex, however, and are likely to vary not only among ecosystem types but also among species with contrasting leaf habit, flowering phenology or timing of seed maturation. For example, evergreen and deciduous species could respond to weather in different ways due to differences in resource use and biomass allocation (Mediavilla, Escudero & Helmeier 2001; Montserrat-Martí *et al.* 2009), which might interfere in their abilities to accumulate and mobilize resources for reproduction (Espelta *et al.* 2008). Alternatively, previous studies have shown that coexisting oak species differing in the time required for seed maturation exhibit strong asynchrony in their temporal patterns of seed production, presumably as a consequence of the interaction of weather with different phenological stages of reproduction (Koenig *et al.* 1994; Abrahamson & Layne 2003; Liebhold *et al.* 2004). Depending on such functional or phenological attributes and the link between weather and seed production, the impact of ongoing climate change on masting behaviour may be more or less important (Pérez-Ramos *et al.* 2010; Kelly *et al.* 2013; Pearse, Koenig & Knops 2014; Koenig *et al.* 2015). In a time of rapid global change, it is therefore timely to review the role of weather on this widespread phenomenon in order to gain a better understanding of the mechanisms underpinning mast-seeding in resource-limited ecosystems as well as of its vulnerability to future environmental scenarios.

In this study, we explore the spectrum of variation in mast-seeding in Mediterranean oaks (genus *Quercus*), and we aim to discern the proximate causes of this process by analysing

the role of weather at both the within- and between-species levels. *Quercus* species offer an ideal group for such analyses because this genus comprises some of the most dominant tree species in Mediterranean forests, exhibit large interannual variability in seed crop size and are frequently intermingled despite encompassing both deciduous and evergreen species. At the local scale, we present the results of a 10-year study on seed production in two Mediterranean oak species with different leaf habit (the deciduous *Quercus canariensis* Willd. and the evergreen *Q. suber* L.) that coexist in southern Spain. At the global scale, we review the literature on environmental drivers of mast-seeding in Mediterranean oak species with the principal aim of evaluating whether the identity and magnitude of these drivers differ between evergreen and deciduous species. Specifically, we address the following questions: (i) What are the strongest environmental drivers of mast-seeding in Mediterranean oak species? (ii) Is mast-seeding affected differently by weather in evergreen and deciduous species? (iii) How temporally concordant are co-occurring oak species with different leaf habits in their patterns of seed production? and (iv) What are the ecological implications of these findings for oak recruitment and forest dynamics under future climate change scenarios?

Materials and methods

STUDY AREA AND SPECIES

The study was conducted in the mixed-oak forests of Aljibe Mountains, near the Strait of Gibraltar, in southern Spain. Climate is subhumid Mediterranean type, with cool and wet winters alternating with warm and dry summers. Mean annual temperature ranges from 14.6 to 18.4 °C, with a mean maximum of 36 °C (in summer) and a mean minimum of 2 °C (in winter). Mean annual rainfall varies from 701 to 1331 mm (mean = 1056 mm for 15 weather stations over a 20 year period), with the heaviest rainfall occurring in winter (44.1%) and autumn (39%), followed by spring (15%) and summer (2.9%). Most of the forested area was protected in 1989 as Los Alcornocales Natural Park, covering about 1680 km².

Vegetation is dominated by evergreen cork oak (*Quercus suber*) forests, mixed with winter-deciduous oaks (*Quercus canariensis*), which are more abundant near streams (Urbietta, Zavala & Marañón 2008). *Q. canariensis* has marcescent leaves, a strategy that consists in retaining dead leaves in the crown during some months until the complete foliage abscission in late winter. Both *Q. suber* and *Q. canariensis* flower in spring (mainly in May). Acorn development occurs predominantly during summer (from June to September), and seedfall takes place in autumn (from October to February). Winter (from December to March) is potentially important for plant nutrient storage, particularly for the evergreen *Q. suber* that remains photosynthetically active during this season. These two species exhibit phenological differences in their endogenous dynamics of seed development at the study area, with *Q. suber* requiring a single year to mature acorns and *Q. canariensis* predominantly requiring two years (I. M. P.-R., personal observation). We did not detect the existence of biennial maturation in *Q. suber* in our study site, in contrast to reports in some particularly dry Mediterranean forests (Díaz-Fernández, Climent & Gil 2004; Pons & Pausas 2012).

SAMPLING DESIGN

In summer 2002, a total of 50 adult, healthy trees (20 individuals of *Q. canariensis* and 30 of *Q. suber*) were randomly selected and tagged within the study area. Selected trees had diameter at breast height (d.b.h.) ≥ 20 cm, and all had a dominant or co-dominant crown position in the forest canopy.

To estimate annual seed production, four traps (0.50 m diameter) were placed under the crown of each of the 50 selected trees so as to avoid overlap with neighbouring plant crowns. 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 avoid post-dispersal acorn removal by rodents and beetles (the main acorn consumers at the study area; Pérez-Ramos *et al.* 2013a). The selected trees were located within fenced areas to avoid interference by large herbivores. Trap contents were collected annually over 10 consecutive years starting with the acorn crop of autumn 2002 through that of 2011. To characterize seedfall dynamics of the two oak species, censuses were carried out monthly over the seed-drop period (October–March) during the first three years. For the seven remaining years, trap contents were collected annually at the end of the seed-drop period in March. Acorns contained within each trap were counted and classified as aborted (incompletely or maldeveloped seeds with length < 13 mm or diameter < 7 mm) or mature acorns (attaining complete seed size).

WEATHER VARIABLES

Climate data were obtained from two meteorological stations located at the study area, one in the north part of the Park (Jimena de la Frontera; 5°27'20"W 36°26'00"N) and the other in the south (Pantano de Almodóvar; 5°38'59"W 36°09'11"N). Meteorological stations recorded air temperature (maximum and minimum), rainfall and wind velocity. Mean daily temperature was calculated as the average of maximum and minimum values. Data for missing days (typically < 8 days per month) were estimated from nearby meteorological stations (correlation coefficients ranged from 0.70 to 0.85).

Weather variables were chosen based on results from previous studies reporting their relationship to acorn production in Mediterranean oak species (see references in Appendix S2). For the mean temperature, we calculated annual and seasonal averaged values (spring: from 22 March to 21 June; summer: from 22 June to 22 September; autumn: from 23 September to 21 December; and winter: from 22 December to 21 March). In addition, we considered the minimum temperature in spring and the maximum in summer due to their potential influence on the processes of flowering and fruit ripening, respectively. For rainfall, we used the accumulated annual values as well as for spring and autumn due to their potential mechanical effects on pollination and premature seed abscission, respectively. Wind velocity was not included in our final analyses because none of the published studies in the Mediterranean that we compiled for the meta-analysis found a significant influence of this weather variable on the process of mast-seeding (Appendix S2).

As a proxy of water limitation, we computed two additional variables for the two principal time periods (spring and summer) where water is most likely to be limiting seed production: water deficit ($WD = PET - PCP$, where PCP is precipitation and PET is potential evapotranspiration, with higher WD values indicating drier conditions; adapted from Espelta *et al.* 2008) and a drought index ($DI = T - 0.33 PCP$, where T and PCP are the averaged daily values of temperature and precipitation for the time period considered; Sork, Bramble & Sexton 1993). All these derived variables were also calculated for May, corresponding to the time period where flowering and

pollination commonly occurs in the two focal species. Finally, we also calculated the difference between the values of the current and the previous year (hereafter Δ_{factor}) for all the above-described variables of temperature, rainfall and water limitation, according to the recent suggestion by Kelly *et al.* (2013) that such differential variables are widespread cues for masting behaviour.

DATA ANALYSES

Environmental drivers of mast-seeding at the local scale: Q. canariensis and Q. suber in southern Spain

Interannual variability in seed production was examined for the two focal oak species using the population-level coefficient of variation (CV_p), calculated as the ratio of the standard deviation to the annual mean value for all sampled trees (30 individuals of *Q. suber* and 20 of *Q. canariensis*). To identify the weather factors potentially driving interannual variability in seed production, we fitted linear and non-linear models with maximum likelihood techniques separately for each of the two species. We calculated seed production as the average number of initial (i.e. aborted + mature seeds) and final (mature) acorns produced per square metre of each crown's tree. These two variables and the percentage of abortions (%) were used as dependent variables, whereas the above-described weather factors were included as predictors. We also considered the same weather factors for the previous year due to the potential existence of acorns maturing in two years in *Q. canariensis*. We tested three alternative functional forms (linear, exponential and Michaelis-Menten) covering a wide range of possible forms (see equations in Appendix S1).

We first tested models for each weather factor and functional form independently, and the best of the three models was compared to the null model that assumed no effect of any factor. We then fitted bivariate and trivariate models using those weather factors that had an effect on seed production when evaluated singly. We compared alternative models in which the second factor was included either additively or multiplicatively. However, models including more than one weather factor are not reported due to their lower empirical support compared with univariate models. Models were parameterized with maximum likelihood (Edwards 1992) using a simulating annealing algorithm. Competing models were compared using the Akaike information criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002) as a measure of goodness-of-fit: the lower the AIC value, the better the model. Models with ΔAIC between 0 and 2 were considered to have equivalent and substantial empirical support (Burnham & Anderson 2002). The R^2 of the regression of observed vs. predicted values was used as an additional measure of the goodness-of-fit of each alternative model. This modelling approach is suitable to identify the best environmental factors driving mast-seeding, as previously conducted in other similar studies (Pérez-Ramos *et al.* 2010). In total, 180 models were run for the two oak species. Models were implemented using the 'likelihood' package version 1.1 in R 2.5.0 (R Development Core Team 2006).

Environmental drivers of mast-seeding at the global scale: Mediterranean oak forests

We searched for articles containing the words 'Mediterranean', '*Quercus*' or 'oak', and 'masting' or 'mast-seeding' in the title, keywords or abstract, using the Web of Knowledge (WOK, Thompson Reuters). From the resulting set of articles, we selected those exploring the effects of environmental factors on the process of mast-seeding and

discarded those considering less than six years of seed production data. This resulted in a total of 22 case studies divided equally between evergreen and deciduous species (see Appendix S2 for details). For each case study, we compiled data on (i) the identity of the best environmental predictors of mast-seeding; (ii) the magnitude of the effects of each of these selected predictors (expressed in terms of coefficient of determination, Pearson's or Spearman's rank correlation coefficient); (iii) the magnitude of interannual variability in seed production (expressed in terms of coefficient of variation); (iv) the number of sampling years; (v) the level of temporal synchrony between species in seed production in cases where the study included data on mast-seeding in at least two co-occurring oak species; and (vi) the author's inferences about the role of weather as a proximate cause of masting.

We then grouped weather factors into four different categories according to their relation to water resources (rainfall, water deficit) or temperature (mean, maximum and minimum values) during different periods of time (spring, summer, autumn and winter). Correlation coefficients of the best predictors of mast-seeding were transformed to Fisher's z values (hereafter Z_r values; Fisher 1928) and further classified into one of these eight categories (two groups of weather factors \times four time periods). These Z_r values were then used to calculate the mean effect size of each weather category (hereafter \bar{E}) and their 95% confidence intervals, separating evergreen and deciduous species. When 95% confidence intervals for a particular weather category did not overlap, differences in effect size between evergreen and deciduous species were considered to be significantly different. This approach is commonly used as a meta-analytical tool to compare the overall magnitude of the effect of a particular continuous factor using correlation coefficients derived from studies with different sample sizes (Borenstein *et al.* 2009). The same approach was used to explore significant differences in the effect size of the different weather categories, grouping all case studies independently of leaf habit. Meta-analyses were performed using METAWIN 2.1 software (Rosenberg, Adams & Gueritch 2000).

Results

ENVIRONMENTAL DRIVERS OF MAST-SEEDING AT THE LOCAL SCALE: *Q. CANARIENSIS* AND *Q. SUBER* IN SOUTHERN SPAIN

The two study oak species exhibited variation among years in seed production, with a considerably higher value of CV_p (1.40) for *Q. canariensis* compared with *Q. suber* (0.42). Interestingly, the largest seed crops coincided with years of rainy springs and summers (i.e. with lower water deficit values; Fig. 1a). However, the two species were not synchronous in their patterns of seed production ($r = -0.32$; $P = 0.37$), primarily because acorn crops of *Q. canariensis* were correlated with weather conditions the previous year whereas *Q. suber* responded more strongly to those of the current year (Appendix S1). Within a particular year, the two species were not synchronous either in their patterns of seed fall, *Q. canariensis* dropping nearly all their seeds during October and November whereas seedfall in *Q. suber* continued into at least January (Fig. 1b).

The best environmental predictors of both initial and mature acorn production were variables mainly related to water availability and temperature during spring, the period in

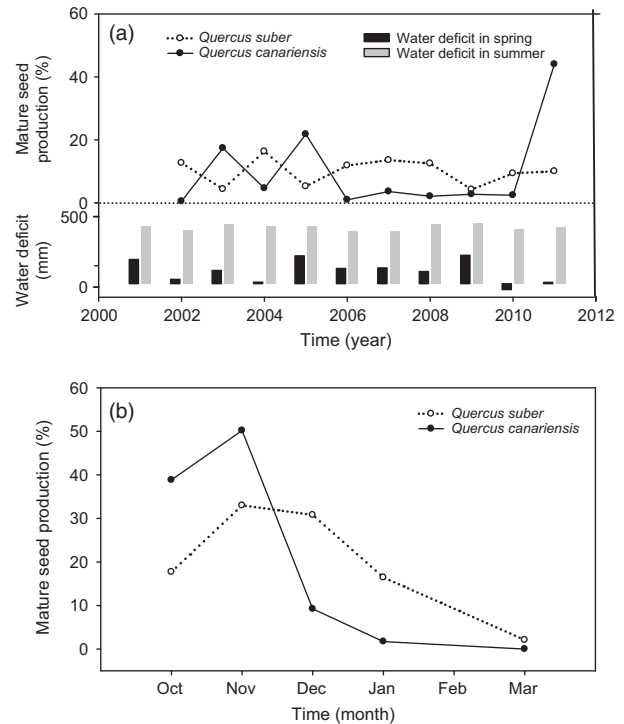


Fig. 1. Variability in seed production for the two oak species (*Quercus canariensis* with solid lines and *Q. suber* with dotted lines) at two different temporal scales (a: interannual; b: intra-annual). Values of seed production are expressed as a per cent of the total number of mature acorns counted for the entire sampling period (a: from 2002 to 2012; b: 2003 to 2004).

which pollination and flower fertilization occur. However, the two species were affected by different variables. In *Q. canariensis*, the production of initial and mature acorns decreased exponentially with water deficit during the spring of the prior year (Fig. 2a) and, to a lesser extent, with summer drought the prior year (Fig. 2b and Appendix S1). In *Q. suber*, seed production was also negatively affected by water deficit in spring (Appendix S1), although not as strongly as for *Q. canariensis* (Fig. 2c).

The best predictors of seed production in *Q. suber* also included temperature in the spring, with the annual seed crop decreasing linearly with the temperature difference in May (ΔT_{May}) as well as with the mean temperature for this month one year earlier (Fig. 3 and Appendix S1). There was also evidence for the effects of temperature in May on the deciduous species (Fig. 3), but with less empirical support than for water deficit (Appendix S1). In contrast to the evergreen species, the effect of temperature in *Q. canariensis* was positive (Fig. 3 and Appendix S1). No models with empirical support better than null were found for the percentage of aborted seeds (Appendix S1).

ENVIRONMENTAL DRIVERS OF MAST-SEEDING AT THE GLOBAL SCALE: MEDITERRANEAN OAK FORESTS

The Mediterranean oak species compiled for the meta-analysis were highly variable in their CV_p values, with marked

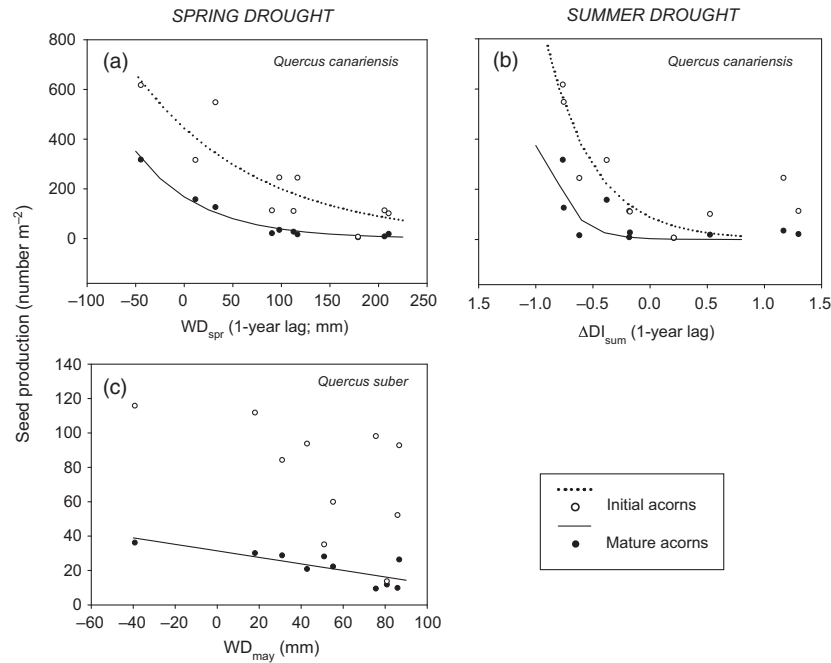


Fig. 2. Impact of drought (in spring, a and c; and summer, b) on the production of initial (i.e. including aborted seeds) and mature acorns. Mature acorn production is represented with black symbols and solid lines, whereas initial acorn production with white symbols and dotted lines. Lines represent the best-fitted models (Appendix S1) for the two oak species. Abbreviations: WD_{spr} (1-year lag) = water deficit in spring one year earlier; ΔDI_{sum} (1-year lag) = difference in summer drought index between the two previous years; WD_{may} = water deficit in May.

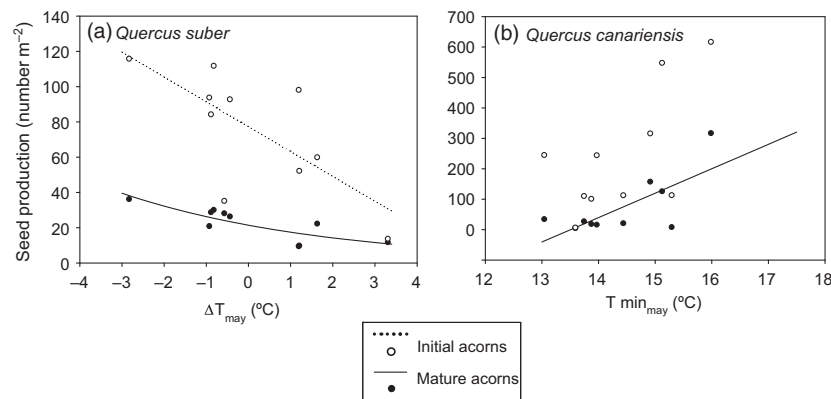


Fig. 3. Impact of temperature (in *Quercus suber*, a; and in *Q. canariensis*, b) on initial seed production (white symbols and dotted lines) and mature seed production (black symbols and solid lines). Lines represent the best-fitted models (Appendix S1). Abbreviations: ΔT_{may} = temperature difference in May regarding the previous year; T_{min}_{may} = minimum temp. in May.

differences not only among oak species but also among populations of a same species inhabiting different sites. For example, *Q. ilex* exhibited CV_p values ranging from 0.54 in open woodlands of southern Spain to 2.01 in forests of north-eastern Spain (Appendix S2). All these studies suggested a significant effect of weather as a proximate driver of interannual variability in seed production. Results from our meta-analysis of these studies indicated that the strongest drivers of mast-seeding were generally related to water resources and temperature, primarily during spring and summer (Appendix S2).

Approximately 70% of the studies found a significant effect of some environmental variable related to precipitation or water deficit in spring or summer. In both time periods,

the effect of a wetter season was mainly positive, with the exception of two cases in which higher humidity in the spring had a significant negative effect on acorn production (Appendix S2). In addition, approximately one-third of the studies detected some effect of precipitation in autumn and winter. Interestingly, the effects of higher precipitation on seed production were primarily negative for the autumn (75% of studies) but positive for the winter (100% of cases). The effect size of water availability on the process of mast-seeding was significantly higher in the summer compared to the spring (combining all species), as indicated by the lack of overlap between their confidence intervals (Fig. 4). No significant difference in \hat{E} values was detected for these

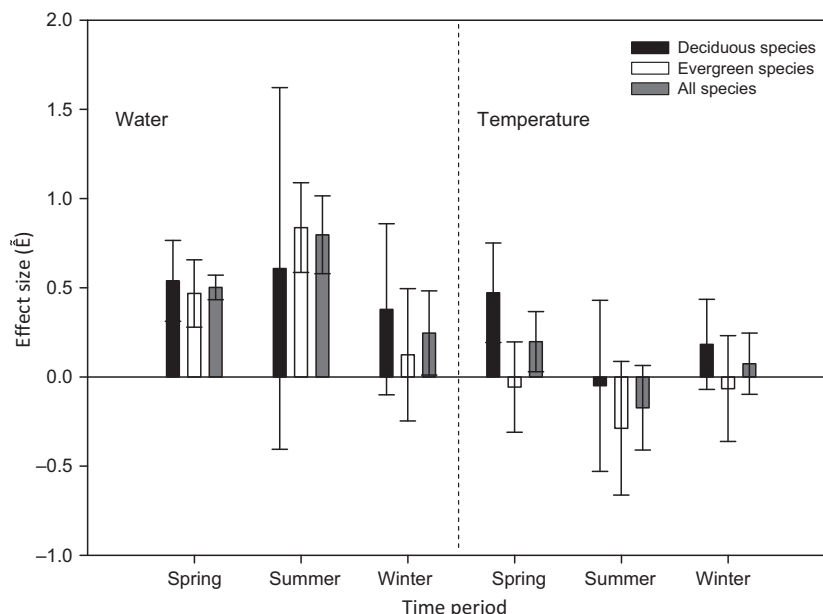


Fig. 4. Comparison of the cumulative effect size (\bar{E}) of different weather variables related to water resources and air temperature on mast-seeding in Mediterranean oaks. Data come from a review of 22 case studies in Mediterranean ecosystems (Appendix S2). Weather variables were grouped into three time categories (spring, summer and winter). Autumn data were excluded from statistical analysis due to the low number of case studies considering this season. \bar{E} values were also separated into evergreen (white bars) and deciduous species (black bars).

weather variables between evergreen and deciduous species (Fig. 4).

Temperature, however, was also identified as a significant driver of mast-seeding in a considerable proportion of studies (from 31% to 59% depending on the season; Appendix S2), although their effect sizes were generally lower compared to the variables related to water resources (Fig. 4). The effect of higher temperatures on acorn production was mostly negative in both winter (71% of cases) and summer (100%), independently of leaf habit (Appendix S2). In spring, however, the effect size of temperature was markedly different between evergreen and deciduous species. Specifically, warmer springs increased seed production in deciduous species, but this effect was variable for the evergreen species (positive for the 60% of studies and negative for 40%, resulting in an \bar{E} value close to zero when all cases were considered; Fig. 4).

Discussion

In general, Mediterranean oak species exhibit strong interannual fluctuations in seed production, but the magnitude of this temporal variability depends on the target oak species and the study site. Interestingly, some of the most dominant oak species, such as *Q. ilex*, exhibit large among-site variability in their CV_p (from 0.54 to 2.01), presumably promoted by the particular environmental conditions of each site. Previous studies have suggested that plants growing in less productive habitats should show higher interannual variability in seed production since resource limitation likely increases the time required to replenish their energy reserves between subsequent large seed crops (Kelly & Sork 2002). The scarcity of

published studies in Mediterranean forests along a broad range of habitat conditions makes it difficult to evaluate whether or not this potential relationship between site quality and mast-seeding fulfils this prediction for a wider spatial scale.

In our local study site in southern Spain, the two coexisting oak species exhibited marked differences in their CV_p , with much lower values for *Q. suber* (0.42) compared with *Q. canariensis* (1.40). The relatively low interannual variability in seed production exhibited by *Q. suber* in our study area, which is comparable to that reported in previous studies for other Mediterranean oaks (Appendix S2), could be attributed to relatively high interindividual variability in this species. For example, in a parallel study in the same area, we found that co-occurring *Q. suber* individuals were highly asynchronous in their temporal patterns of seed production, thus reducing the interannual variability at the population level, mostly due to the large array of soil conditions where they commonly grow (Pérez-Ramos *et al.* 2014).

WHAT ARE THE STRONGEST ENVIRONMENTAL DRIVERS OF MAST-SEEDING IN MEDITERRANEAN OAK SPECIES?

Our results indicate that Mediterranean oak species are sensitive to weather, mast-seeding typically being correlated with variables related to water resources and air temperature. Results from both the local and the global analyses indicated that the time periods during which weather had the strongest influence on subsequent acorn production were spring and summer, the critical periods for flowering and fruiting in Mediterranean regions.

In our local study site in southern Spain, interannual fluctuations in seed production were correlated with weather in spring and summer. The fact that the percentage of variance explained by the models with the best support increased from initial to mature acorn crops might indicate that environmental factors taking place during acorn ripening may also be important in driving the observed interannual fluctuations in seed production (Espelta *et al.* 2008; Pérez-Ramos *et al.* 2010). However, the lack of well-supported weather predictors for the percentage of abortions and the apparent low contribution of this variable to the total seed production ($R^2 = 0.02$, $P = 0.69$) suggest that the final crop size is primarily modulated by environmental conditions that affect the initial number of acorns, as reported by previous studies (Koenig *et al.* 1996; Knapp, Goedde & Rice 2001; Fernández-Martínez, Belmonte & Espelta 2012). Since mast flowering and seeding might be sometimes uncoupled (Montesinos, García-Fayos & Verdú 2012), further studies focused on earlier demographic processes such as flowering, pollination and ovule fertilization are necessary to discern the relative contribution of weather on the reproductive output of the plant via flower abortion.

Results from the global analyses based on Mediterranean oaks corroborate the importance of spring and summer conditions as drivers of mast-seeding. Further, they support the 'weather as a proximate driver' hypothesis (Pearse, Koenig & Knops 2014) stating that weather affects seed output in masting species by mechanisms directly impacting the processes by which seeds are produced, namely flowering, pollination, flower fertilization and/or seed maturation.

Importance of water resources

The strongest environmental drivers of mast-seeding in Mediterranean oaks were weather factors related to water resources (mainly precipitation and water deficit), which exercised a stronger effect than temperature on the annual seed crop in a large proportion of species. The effect of water availability was mainly positive, both in spring and summer. Since water stress decreases transpiration and photosynthesis rates (Sala & Tenhunen 1996), any shortage in resource availability during this crucial time period may lead to a significant reduction of growth and reserve storage with potentially negative consequences for the internal allocation of resources to reproduction (Carevic *et al.* 2010). In addition, the positive effects of increased rainfall on seed production might be explained by the indirect role of soil moisture in facilitating N availability for the plant, as demonstrated by experimental studies of resource supplementation (Smaill *et al.* 2011). Two exceptions to this general tendency were cases in which higher humidity in spring correlated negatively with annual seed output (Garrison, Koenig & Knops 2008; García-Mozo, Domínguez-Vilches & Galán 2012). These apparently contradictory results could be explained by the fact that high-humidity conditions during spring can also adversely affect the aerodynamic properties of pollen flow, thus decreasing the probability of a successful fertilization (Wolgast & Stout 1977; Whitehead 1983).

In addition, one-third of the reviewed studies detected a negative effect of autumn precipitation on seed production, which is potentially attributable to a mechanical effect of torrential rainfalls that likely favoured premature abscission of acorns before having completed the maturation process (Pérez-Ramos *et al.* 2010).

Importance of air temperature

Temperature was found to be a significant driver of mast-seeding in approximately 60% of the studies we reviewed. The effect of this factor on the annual seed crop was variable depending on the season, being primarily negative in summer and winter, but mostly positive in spring.

Higher temperatures during the period of resource accumulation for evergreen species (winter) or seed development (summer) could have both direct (increasing respiratory costs) and indirect effects (increasing water stress) on the internal storage of carbohydrates of the tree (Adams *et al.* 2009; Redmond, Forcella & Barger 2012), potentially leading to decreased seed production (Isagi *et al.* 1997; Sala *et al.* 2012). Alternatively, warmer conditions during the flowering period (spring) may favour ovule development and fertilization (Sork, Bramble & Sexton 1993), promote pollination and pollen dehiscence by stimulating the growth and maturation of catkins (Sharp & Chisman 1961), or increase pollen availability by enhancing flowering synchrony within the population (Koenig *et al.* 2015).

Interestingly, the results from our study in southern Spain indicated a stronger influence of the temperature difference between the prior two springs (ΔT_{spr}) than of the absolute values for either of these periods. Thus, at least for these species, we found support for the hypothesis recently proposed by Kelly *et al.* (2013) that identifies the temperature difference as a strong synchronizing cue for masting. Parallel studies in this area, however, indicate the importance of other proximate factors as well, including soil resource availability, which affects the magnitude and the interannual variability of seed production at the individual level (Pérez-Ramos *et al.* 2014).

IS MAST-SEEDING AFFECTED DIFFERENTLY BY WEATHER IN EVERGREEN AND DECIDUOUS SPECIES?

The two oak species we studied were affected by weather in quite different ways, most likely because of their different abiotic requirements as well as by their different strategies of resource use and biomass allocation stemming from their contrasting leaf habits. On the one hand, annual seed production in *Q. canariensis* was more severely limited by drought than in *Q. suber*, most likely because of its lower efficiency of water and mineral resource use (Kloeppel *et al.* 2000; Montserrat-Martí *et al.* 2009). Results from our global analysis of Mediterranean oak species, however, did not detect any difference between deciduous and evergreen species in the overall effect of water resources on mast-seeding. The higher sensitivity to drought of *Q. canariensis* is most likely related to its strong dependence on water, as indicated by its more

restricted geographical distribution to wetter sites (such as our study area) in comparison with other deciduous species and its local association to water sources such as streams (Urbieto, Zavala & Marañón 2008).

On the other hand, the two oak species we studied also exhibited contrasting responses to spring temperature. Annual seed crop size increased with warmer temperatures in May for *Q. canariensis*, whereas it decreased with higher values of Δt in May for *Q. suber*, likely as a consequence of the negative effect of higher temperatures for the current year and the positive effect of that for the previous year (as indicated by the selection of these weather variables as good predictors in our modelling approach). This result may be a consequence of the different functional strategies of the two oak species in the use and allocation of resources to reproduction, being more conservative in *Q. suber* and predominantly acquisitive (i.e. with a more wasteful use of resources to maintain higher growth rates) in *Q. canariensis* (De la Riva *et al.* 2014). We hypothesize that *Q. suber*, which appears to invest a similarly low amount of energy to reproduction every year, diverts more internal resources towards vegetative growth and slightly less to seed production during warmer springs, years with larger crop sizes being mainly restricted to colder and wetter springs. This hypothesis is supported by a previous study with California oaks reporting that growth and reproduction in these species are frequently governed by environmental conditions in opposite ways (Knops, Koenig & Carmen 2007). In contrast, in *Q. canariensis*, which should renew all its leaves every year, the enhanced rates of photosynthesis and reserve accumulation derived from higher temperatures over the growth season may permit higher resource investment in reproduction during warmer years. Further physiological studies will be necessary, however, in order to discern whether evergreen and deciduous species have different functional strategies regulating the process of mast-seeding, and how their patterns of biomass allocation differ in response to changing environmental conditions.

HOW TEMPORALLY CONCORDANT ARE CO-OCCURRING OAK SPECIES IN THEIR PATTERNS OF SEED PRODUCTION?

The two oak species we studied in southern Spain exhibited a low level of temporal synchrony in their seed production patterns. This temporal discordance between co-occurring species may be due not only to their potentially different strategies in resource use and biomass allocation, as suggested above, but also to phenological differences in the process of seed production.

First, the two species were not synchronous in their patterns of seed fall, *Q. suber* requiring a longer period of time to drop all its seeds than *Q. canariensis*. This low level of temporal synchrony between species, likely derived from differences in their reproductive phenologies of fruit ripening, potentially results in different interactions of weather with subsequent reproductive stages for the two species, as reported earlier by Espelta *et al.* (2008). An advanced seed

fall, likely derived from earlier bud burst and seed development, has been identified as an effective strategy in deciduous species to compensate for their shorter time window for growth before the arrival of the dry season (Peñuelas & Filella 2001).

Secondly, the fact that *Q. canariensis* was mostly affected by weather conditions during the prior year supports our hypothesis that this species requires two years for seed maturation. Previous studies with North American oaks (Koenig *et al.* 1994; Abrahamson & Layne 2003; Liebhold *et al.* 2004) have reported low levels of temporal synchrony between co-occurring species that differ in the number of years required for acorn maturation. In addition, Espelta *et al.* (2008) detected relatively high synchrony between two co-occurring species requiring a single year to mature acorns despite their contrasting leaf habit, which they attributed to similar endogenous dynamics of seed development. The importance of seed maturation timing for interpreting mast seeding cycles has also been demonstrated at the intraspecific level by Pons & Pausas (2012), who reported asynchronous patterns of seed production between co-occurring *Q. suber* individuals, some of which matured acorns in one year and others in two years.

Although these studies indicate that seed maturation timing plays a crucial role as a synchronizing mechanism for mast seeding between species and within species, further studies including coexisting species that differ only in leaf habit or reproductive phenology will be necessary in order to discern the proximate causes triggering asynchronous reproduction in co-occurring species. Furthermore, understanding how temporally concordant coexisting species are in fruiting may be relevant for a better understanding of plant recruitment patterns and dynamics in multispecies communities dominated by trees sharing the same seed predators and dispersers (Janzen 1971; Silvertown 1980).

ECOLOGICAL IMPLICATIONS FOR OAK RECRUITMENT AND FOREST DYNAMICS UNDER FUTURE CLIMATE CHANGE SCENARIOS

Understanding how different species adjust their reproductive abilities to weather may enable us to infer the effects of ongoing environmental changes on recruitment and persistence of their populations. This is particularly relevant in mixed forests consisting of species with different leaf habit and/or reproductive phenology, where the current species composition could be altered under future climate change scenarios.

In our study area in southern Spain, for example, the future drier and warmer conditions predicted by climate change models (IPCC 2007) could generate different prediction for future seed output, and thus for recruitment, of the two coexisting oak species. On the one hand, it could be expected that longer and more recurrent drought periods will reinforce the negative effects of water limitation on seed production. This would potentially have negative consequences for the recruitment of both oak species, which already suffer regeneration problems at the study site (Pérez-Ramos & Marañón 2012; Pérez-Ramos *et al.* 2012). This could be particularly alarming

for *Q. suber*, which produced a very small acorn crop during the overall sampling period (especially in dry years), but may also be relevant for *Q. canariensis*, which was more severely limited by drought than *Q. suber*. However, these differing responses between deciduous and evergreen species may be restricted to communities inhabiting wetter sites such as found in our study area, given that we found no significant differences between functional groups for this weather factor in our global analyses.

On the other hand, results from our study in southern Spain suggest that the expected warmer temperatures due to climate change could negatively affect evergreen species as a consequence of their more conservative strategy of biomass allocation. However, this inference should be taken with caution given the peculiarities of the study species. To what extent these contrasting responses to ongoing environmental changes influence seed output in co-occurring species constitutes an exciting question to be further investigated not only in Mediterranean but in other plant communities world-wide. Long-term studies involving both observational and experimental studies on successive stages of regeneration, not only in seed production but also seed predation, seedling establishment and survival (Pérez-Ramos *et al.* 2013b), will be necessary in order to draw a full picture of the ecological consequences of climate change on plant recruitment and forest dynamics in Mediterranean communities composed by functionally dissimilar species.

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Data accessibility

The whole data set of this study is publicly available in the Dryad Digital Repository (Pérez-Ramos *et al.* 2015).

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Supporting Information

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

Appendix S1. Summary of the best-fitted models analyzing the impact of weather on the production of initial (i.e. including the abortions) and mature acorns as well as on the frequency of abortions, for the two studied oak species.

Appendix S2. Summary of compiled studies analyzing the effects of environmental factors on mast-seeding in Mediterranean oak species.

1 **Supporting information**

2 **Appendix S1.** Summary of the best-fitted models analyzing the impact of weather on the
3 production of initial (i.e. including the abortions) and mature acorns as well as on the
4 frequency of abortions, for the two studied oak species. Only the models with better empirical
5 support than null are shown, ranked from best to poorest fits. The best-supported model and
6 their equivalents ($\Delta AIC < 2$) have been highlighted with bold letters for each component. The
7 signs of the relationships (positive or negative) between each dependent variable and the
8 selected soil predictors are also indicated. Model Forms: LIN, linear model; EXP, exponential
9 model; null, null model.

10

11 Note: The equations of the different functions fitted in the models calibrated for this study are:

12 (1) Linear additive: $a + bFactorAi + cFactorBi$

13 (2) Linear multiplicative: $a + bFactorAi * cFactorBi$

14 (3) Exponential additive: $ae^{(bFactorAi + cFactorBi)}$

15 (4) Exponential multiplicative: $ae^{(bFactorAi * cFactorBi)}$

16 (5) Michaelis- Menten multiplicative:

$$\frac{aFactorAi * FactorBi}{(a/b + FactorAi) * (a/c + FactorBi)}$$

21 where a, b, and c are parameter estimates that maximized the likelihood function, and *Factors*

22 *Ai* and *Bi* are the selected weather variables for each year “*i*”.

Species	Dependent variable	Abiotic factors	Abbreviation	Model	Relation	R ²	AICc	ΔAICc	
QUERCUS CANARIENSIS	Initial acorn production (nb m ⁻² BA)	Water Deficit in Spring (1 year earlier)	WD_{spr} (1-yr lag)	EXP	-	0.77	128.64	0.00	
		Δ Summer Drought Index (1 year earlier)	ΔDI _{sum} (1-yr lag)	EXP	-	0.69	131.65	3.01	
		Δ Spring Drought Index (1 year earlier)	ΔDI _{spr} (1-yr lag)	LIN	-	0.48	136.81	8.17	
				null			139.15	10.51	
	Mature acorn production (nb m ⁻² BA)	Water Deficit in Spring (1 year earlier)	WD_{spr} (1-yr lag)	EXP	-	0.98	90.19	0.00	
		Δ Summer Drought Index (1 year earlier)	ΔDI _{sum} (1-yr lag)	EXP	-	0.55	121.61	31.42	
		Minimum Temperature in May	T _{min} _{may}	LIN	+	0.53	122.02	31.82	
				null			125.25	35.05	
	Percentage of abortions (%)			null			94.10		
	QUERCUS SUBER	Initial acorn production (nb m ⁻² BA)	Temperature in May (1 year earlier)	T_{mean}_{may} (1-yr lag)	LIN	+	0.52	100.40	0.00
			Δ Temperature in May	ΔT _{may}	LIN	-	0.52	100.48	0.08
			Δ Precipitation in May	ΔP _{may}	EXP	+	0.50	100.90	0.49
				null			103.56	3.15	
Mature acorn production (nb m ⁻² BA)		Δ Temperature in May	ΔT _{may}	EXP	-	0.70	69.88	0.00	
		Δ Spring Drought Index	ΔDispr	EXP	-	0.62	72.31	2.44	
		Water Deficit in May	WD _{may}	LIN	-	0.61	72.49	2.62	
		Precipitation in May	P _{May}	LIN	+	0.59	73.04	3.17	
		Temperature in May (1 year earlier)	T _{mean} _{may}	LIN	+	0.54	74.15	4.27	
		Maximum Temperature in May	T _{max} _{may}	LIN	-	0.50	74.95	5.08	
		Δ Precipitation in May	ΔP _{may}	EXP	+	0.49	75.14	5.27	
				null			77.64	7.77	
Percentage of abortions (%)			null			94.03			

