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1 **Mast seeding and flowering in Mediterranean oak woodlands under increasing drought:**
2 **results from a long-term dataset and from a rainfall exclusion experiment.**

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1 *Abstract.* Mast seeding - the synchronous highly variable seed production among years
 2 - is very common in tree species, but there is no consensus about its main causes and the main
 3 environmental factors affecting it. In this study, we first analyse a long-term dataset on
 4 reproductive and vegetative growth of *Quercus ilex* in a Mediterranean woodland in order to
 5 identify the main environmental drivers of inter-annual variation in flower and seed production,
 6 and contrast the impact of climate *vs.* adaptive factors as main causes of masting. Second, we
 7 conducted an experiment of rainfall exclusion to evaluate the effects of an increasing drought
 8 (simulating predictions of global change models) on both reproductive processes. The annual
 9 seed crop was always affected by environmental factors related to the precipitation pattern,
 10 these abiotic factors disrupting the fruiting process at different periods of time. Seed
 11 production was strongly dependent on water availability for the plant at initial (spring) and
 12 advanced (summer) stages of the acorn maturation cycle, whereas the final step of seed
 13 development was negatively affected by the frequency of torrential-rain events. We also found
 14 clear evidences that seed masting in the study species is not only regulated by selective
 15 endogenous rhythms, but is mainly a physiological response to the variable environment. Our
 16 results from the rainfall exclusion experiment corroborated the conclusions obtained from the
 17 26-year fruiting record and demonstrated that the high inter-annual variation in seed crop was
 18 mainly determined by the success in seed development rather than by the flowering effort.
 19 Under a global change scenario, it could be expected that the drier conditions predicted by
 20 climate models reinforce the negative effects of summer drought on seed production, leading to
 21 negative consequences for tree recruitment and forest dynamics.

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25 *Key words:* Abortions; acorn production; economy-of-scale hypothesis; global change;
 26 masting cycles; *Quercus ilex*; resource-matching hypothesis; water stress

INTRODUCTION

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Mast seeding, the synchronous highly variable seed production among years, is very common in tree species (Silvertown 1980, Kelly 1994, Koenig and Knops 2000). This phenomenon implies several costs for reproduction by reducing recruitment opportunities in years with low seed crops (Waller 1993) and likely by increasing density-dependent seedling mortality during mast years (Hett 1971). Therefore, the evolutionary selection of this reproductive strategy should provide counteracting benefits for the plant (Kelly et al. 2001). Although there is no consensus about these main benefits, the pollination-efficiency (Nilsson and Wästljung 1987, Norton and Kelly 1988, Smith et al. 1990, Kelly et al. 2001) and the predator-satiation hypotheses (Janzen 1971, Silvertown 1980, Kelly and Sullivan 1997) seem to be the most prominent explanations, supported by the results of many studies exploring mast seeding in several tree species (e.g., Kelly 1994, Koenig et al. 1994, Monks and Kelly 2006, Kelly et al. 2008).

Inter-annual variability in resource supply and environmental conditions is clearly involved in mast seeding, but the exact nature of this involvement is not completely understood (Kelly and Sork 2002). On one hand, the resource-matching hypothesis states that plants adapt their reproductive effort to the current available resources (strongly dependent on climate conditions), with no need of adaptive value (Kelly 1994). On the other hand, the authors supporting masting as a selective response to processes such as wind pollination or predator satiation (the economy-of-scale hypothesis) postulate that environmental factors or resources only act as synchronizing cues for individual plants, driving high and low seed crops at regular periods of time (Janzen 1971, Norton and Kelly 1988). The best demonstration that mast seeding is an evolved reproductive strategy and not only the result from the available resources for the plant is the presence of “switching” between growth and reproduction (Kelly and Sork 2002), that is the diversion of resources towards reproduction in some years and towards vegetative

1 growth in others (Norton and Kelly 1988). In the case that a masting plant species is merely
 2 responding to the variable and unpredictable environment (“putative” masting), both
 3 reproduction and growth should be favored in good years, whereas both processes would be
 4 depleted in years with limiting resources (Monks and Kelly 2006). In nature, cases of
 5 “putative” masting are very rare (e.g., Despland and Houle 1977), resource switching being a
 6 more frequent event (e.g., Norton and Kelly 1988, Alley et al. 1998, Monks and Kelly 2006).
 7 However, there are very few published examples that test strictly resource switching,
 8 especially in low productive ecosystems such as Mediterranean woodlands.

9 Among the environmental variables identified as regularizing mast seeding and
 10 flowering, temperature (Sork et al. 1993, Schaubert et al. 2000, Masaka and Sato 2002) and
 11 precipitation (Piovesan and Adams 2001, Abrahamson and Layne 2003) have been the most
 12 thoroughly reported factors. Nevertheless, underlying mechanisms that alter resource allocation
 13 to reproduction in response to inter-annual fluctuations of these key factors are still unknown.
 14 In Mediterranean woodlands, where soil water availability is one of main limiting resources for
 15 plants, we hypothesize that water limitation is the key factor driving inter-annual variability in
 16 seed production of *Quercus* species, as has been recently demonstrated by Espelta et al. (2008)
 17 in a Mediterranean oak forest located in northeast Spain.

18 Mediterranean-type ecosystems are predicted to be among the most vulnerable to
 19 climate change due to an intensification of their already limiting conditions for plant
 20 regeneration (Christensen et al. 2007). Global change models predict increasing aridity for the
 21 Mediterranean area, summer drought being expected to increase in severity (Peñuelas et al.
 22 2004, Christensen et al. 2007). This increasing drought may affect negatively seed production
 23 in dominant tree species, by reducing the size of the annual seed crop and/or likely by
 24 disrupting the environmental cues that synchronize plants for masting (McKone et al. 1998).
 25 Other manipulative studies have examined reproductive responses to altered rainfall in
 26 herbaceous species (e.g., Kadmon 1993, Fay et al. 2000). However, the impact of increasing

1 *DBH* > 10 cm represented 12.5%. The understorey, dominated by *Buxus sempervirens*,
 2 *Phyllirea latifolia*, *Pistacia terebinthus* and *Juniperus oxycedrus*, compose a sparse shrubby
 3 layer with a percent cover lower than 25% and a height < 1.5 m.

4 Climate is Mediterranean-type, with cool, wet winters alternating with warm, dry
 5 summers. Rainfall occurs mainly during autumn and winter, with about 80% between
 6 September and April. Mean annual precipitation ranges from 550 to 1549 mm (mean of 901
 7 mm over the previous 26 years). Mean annual temperature varies from 11.5 to 14.1°C (mean of
 8 13.1°C over the same period). Bedrock is dominated by Jurassic limestones, which are covered
 9 by a very shallow soil with a high percentage of clays and a high volumetric rock content: 75%
 10 in the first 50 cm and 90% for the whole soil profile (Rambal et al. 2003).

11 *Sample collection over 26 years*

12 In 1983, a total of 26 circular plastic traps (with 0.41 m of diameter) were randomly
 13 distributed beneath the *Quercus ilex* canopy in an area totalling 314m². Traps were 0.7 m in
 14 height to avoid post-dispersal seed removal by mammals (the main acorn predators at the study
 15 area; Pérez-Ramos et al., *unpublished data*). Small holes were drilled at the bottom of each trap
 16 to facilitate draining of throughfall water. The leaf area index (LAI) over the traps - estimated
 17 in 2008 by means of a leaf area meter (LAI 2000, LiCor Biosciences, USA) - varied from 1.97
 18 to 3.58 (mean of 2.91±0.39). The minimum distance between traps was 6 m.

19 Trap content was periodically collected: at least three times per year from 1983 to 1999,
 20 and monthly from 2000 to 2008. In the laboratory, all samples were sorted into male flower
 21 and acorn fractions. Wood debris and leaf fractions have not been considered for this study.
 22 Each fraction was oven-dried at 60°C for 48h and weighed to the nearest 0.0001 g. Female
 23 flowers and acorns were grouped together due to the difficulty of determining when a female
 24 flower was successfully fertilized. For the last 9-years period, all the collected seeds from the
 25 beginning of July to the end of September were mal- or not completely developed and, thereby,
 26 they were separated from the mature seeds and considered as abortions.

1 Radial stem growth was used as a representative measure of vegetative growth. This
 2 variable was calculated from yearly recorded diameters at breast height (DBH) of 68 *Q. ilex*
 3 trees (with DBH > 2 cm), covering a total area of $\approx 100 \text{ m}^2$ at the same study plot where the
 4 traps were placed. For comparative purposes between reproductive and vegetative growth,
 5 radial stem growth was expressed as the annual increment of dry wood biomass per unit of area,
 6 using an allometric equation previously reported at the study area (Rambal et al. 2004).

7 *Environmental factors*

8 Four environmental variables were daily recorded during the study period: air
 9 temperature (maximum and minimum), rainfall, net radiation and wind velocity. Mean daily
 10 temperature was estimated as the average of maximum and minimum values. Incident
 11 precipitation, air temperature and net radiation were measured in a clearing 300 m apart from
 12 the experiments since 1983. Precipitation was measured with a tipping bucket rain gauge
 13 (ARG100, Environmental Measurements Ltd, Sunderland, UK) calibrated to 0.2 mm per tip
 14 and placed 1 m over the ground; air temperature was recorded with a MP100 sensor (Rotronic,
 15 Bassersdorf, Switzerland) at 2 m in height; and net radiation was measured with a pyranometer
 16 (SKS1110 Skye instruments, UK) at 2 m over the ground. Wind velocity was measured using a
 17 three-dimensional sonic anemometer (Solent Model R3A, Gill Instruments, Lymington,
 18 England) at a height of 11 m from a tall scaffolding tower, located $\approx 5 \text{ m}$ higher than the
 19 dominant trees. Data for the last variable are only available since October of 1998.

20 From each variable, we derived 13 abiotic factors taking into account the critical
 21 periods for flower and fruit development: annual mean values for the current and the previous
 22 year (following the natural period between two reproductive cycles; from July to June for
 23 flowering and from April to March for seeding), mean values for spring, summer and autumn
 24 and mean monthly values during these seasons. For each period of time (annual, seasonal and
 25 monthly), we also calculated other four variables that could have an influence on flowering,
 26 pollination and/or fruit ripening processes: the number of days with frost (air temperature <

1 0°C), the number of days with strong (precipitations > 10 mm) and torrential rainfall
 2 (precipitations > 20 mm), and the number of days with strong wind (wind velocity > 4 m/s). In
 3 addition, we used two variables that quantify soil water limitation for plants: the annual water
 4 deficit ($WD = PCP - PET$, where PCP is the precipitation value and PET is the potential
 5 evapotranspiration, see Espelta et al. 2008); and the water stress index during summer (WSI_{sum}),
 6 that was estimated from discrete measurements of soil water storage integrated over the rooting
 7 depth and predawn leaf water potential. Soil water storage was measured monthly with a
 8 neutron moisture gauge, and predawn leaf water potential with a Scholander-type pressure
 9 chamber. These discrete measurements of soil water storage were interpolated at a daily time
 10 scale using a soil water balance model (Rambal 1993) and further transformed in predawn leaf
 11 water potential across the Campbell-type retention curve proposed by Rambal et al. (2003).
 12 The goodness of fit between measured and estimated values was very high for both types of
 13 measurements ($R^2 = 0.91$, $n = 89$ and $R^2 = 0.88$, $n = 54$ for soil water storage and leaf water
 14 potential, respectively). The water stress index during summer (WSI_{sum}) was calculated
 15 following the approach proposed by Myers (1988), by cumulating daily values of predawn leaf
 16 water potential over the summer period.

17 *Rainfall exclusion experiment*

18 In 2003, a rainfall exclusion experiment was established near the 26-year study (<100
 19 m) as part of the European project MIND (Mediterranean Terrestrial Ecosystems and
 20 Increasing Drought). The experimental design is comparable, in conception, with the one
 21 described by Hanson et al. (2003). The rainfall exclusion experiment was replicated on three
 22 plots 200 m away one from the other, and situated on a flat area with no lateral water flow. On
 23 each replication, two treatments were set up on two 140 m² plots (14 x 10 m). One was a
 24 control (further, control) and the second was subjected to rainfall exclusion (further, dry). On
 25 the dry plot, rainfall exclusion was achieved using 14 m long and 0.19 m wide PVC gutters
 26 covering 33% of the ground area under the *Quercus ilex* canopy, with the aim of excluding

1 33% of throughfall. Taking into account interception losses and stemflow, the rainfall
 2 exclusion experiment reduces the net input of precipitation to the soil by 29% compared to the
 3 control treatment (Limousin et al. 2008). On the control plot, identical gutters had been set up
 4 upside down in order to homogenize, as far as possible, whole-canopy albedo and understorey
 5 microclimate conditions in both treatments. Total basal area, canopy structure and density of
 6 trees were similar for the two treatments (mean values \pm std. errors for control plots: DBH =
 7 5.5 ± 0.3 cm, tree height = 3.3 ± 0.2 m, number of stems = 85.7 ± 11.8 and basal area = $27.8 \pm$
 8 2.6 m²/ha; mean values \pm std. errors for dry plots: DBH = 5.8 ± 0.1 cm, tree height = 3.5 ± 0.2
 9 m, number of stems = 94 ± 8.7 and basal area = 35.4 ± 2.1 m²/ha).

10 To test the effectiveness of the rainfall exclusion on plant water status, leaf water
 11 potential was measured at predawn with a pressure chamber (PMS Instrument Co. 7000
 12 Albany USA). Two-three replicate leaves from four different trees were periodically measured
 13 in both treatments during spring and summer from 2003 to 2006.

14 In each plot, 24 circular plastic traps (of 0.35 m of diameter) were randomly distributed
 15 beneath the *Quercus ilex* canopy, at ≈ 1.5 m above the ground. Trap content was collected
 16 monthly and divided into male flower and acorn fractions. Wood debris and leaf fractions have
 17 not been considered for this study. Acorns were further categorized into three different
 18 categories: (1) aborted (not completely or mal-developed seeds, with length < 13 mm or
 19 diameter < 7 mm), (2) insect infested (having signs of larvae predation, such as gnaw marks or
 20 holes), and (3) sound (attaining mature seed size). For each fraction, all seeds were counted
 21 and the entire sample was oven-dried at 60°C for 48h and weighed to the nearest 0.0001 g.

22 *Data analysis*

23 *Masting cycles.*- Cyclical patterns of flowering and seeding were explored using Single
 24 Spectrum Fourier analyses, after subtracting the overall mean from the data series (Bloomfield
 25 1976). Prior to the analyses, series were transformed by means of a process of split-cosine-bell
 26 tapering that leads to a reduction of leakage in the spectral density plots (Bloomfield 1976).

1 Inter-annual variability in flower and seed production was examined using the population-level
 2 coefficient of variation (CVp), calculated as the ratio of the standard deviation to the annual
 3 mean of each fraction for the 26 collecting traps. CV was also calculated for the most
 4 explicative environmental factors that were previously selected by our modelling approach (see
 5 details below).

6 *Effects of environmental factors.*- To identify individual climate factors that may be
 7 useful predictors of annual flowering and seeding, we fitted linear and non-linear models for
 8 each reproductive process, using maximum likelihood techniques. Flower and seed production
 9 were modeled independently as functions of the 156 environmental factors (12 climate
 10 variables x 13 different periods of time) considered in the study (Table 1). We tested three
 11 alternative functional forms (linear, exponential and Michaelis-Menten), that cover a wide
 12 range of possible forms (see equations in Appendix 1). We first tested models for each factor
 13 and functional form independently, and the best of the three models was compared to a null
 14 model which assumes no effect of any factor. Second, to test for joint limitation (i.e. more than
 15 one factor being limiting at once), we fitted bivariate models using those factors that had an
 16 effect on flowering or seeding when evaluated singly. We tried alternative models in which the
 17 second environmental factor was added either additively or multiplicatively. Models including
 18 more than two factors were not considered due to their lower empirical support. In total, more
 19 than 1000 different models were individually run for this study. This modelling approach is
 20 suitable to identify plant responses to abiotic factors at different stages of the regeneration
 21 cycle (e.g., Pacala et al. 1996, Kobe 1999, 2006, Gómez-Aparicio et al. 2008, Pérez-Ramos et
 22 al. 2008, Urbieta et al. 2008).

23 Models were parameterised with maximum likelihood (Edwards 1992), using a
 24 simulating annealing algorithm. Based on exploratory analyses, we assumed a normal
 25 distribution for the dependent variables. Alternative models were compared using the Akaike

1 Information Criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002).
 2 The absolute magnitude of the differences in AIC_c (ΔAIC) between alternative models
 3 provides an objective measure of the strength of empirical support for the competing models.
 4 Models with ΔAIC between 0-2 were considered to have equivalent and substantial empirical
 5 support (Burnham and Anderson 2002). The R^2 of the regression of observed vs. predicted was
 6 used as a measure of the goodness of fit of each alternate model.

7 We used the same modeling approach to examine the relationships between both
 8 reproductive processes (flowering and seeding), as well as between them and the percentage of
 9 aborted seeds. All models were implemented using the *likelihood* package version 1.1 for R
 10 and software written specifically for this study in R v 2.5.0 (R Development Core Team 2006).

11 *Resource-matching versus economy-of-scale hypothesis.*- To test whether mast seeding
 12 is an evolved reproductive strategy (economy-of-scale hypothesis) or only results from the
 13 available resources for the plant (resource-matching hypothesis), we used two different
 14 approaches. First, we explored the presence of switching by examining the relationship
 15 between the reproductive effort (flower and seed production) and the radial stem growth (used
 16 as a measure of vegetative growth) using maximum likelihood techniques. Second, we used the
 17 Cross-spectrum Fourier analysis to evaluate the level of synchrony between the two
 18 reproductive variables and the best environmental predictors (selected by our modeling
 19 approach).

20 *Rainfall exclusion treatment.*- Differences between control and dry treatments for leaf
 21 water potential (in spring and summer) were tested using one-way ANOVAs. The changes in
 22 flower and seed production through the 6 years of record and in response to the rainfall
 23 exclusion treatment were analysed using a repeated measures ANOVA. For this type of
 24 analysis, data were grouped by plot because the samples were not separated individually (by
 25 trap) between June of 2003 and September of 2007. For the last two reproductive cycles (07/08

1 and 08/09), when the content of the 72 traps was collected individually, differences between
 2 control and dry treatments for flower and seed production (separated into their different
 3 categories) were evaluated using one-way ANOVAs. None of the abovementioned variables
 4 departed significantly from normality according to the Kolmogorov-Smirnov test. All these
 5 analyses were carried out using Statistica (v. 6, Statsoft Inc. 2001).

6
 7 **RESULTS**

8 *Masting cycles*

9 Seed production was highly variable among years, with average annual crops ranging
 10 from 0.3 to 180.6 g m⁻², and a relatively high value of CV_p (1.18). Remarkably, the largest
 11 seed crops mostly coincided with rainy years, especially during spring (Fig. 1). Flower
 12 production, however, showed a lower inter-annual variability, with crop values ranging from
 13 0.1 to 41.3 g m⁻², and a CV_p of 0.80 (Fig. 1). According to Single Spectrum Fourier analyses,
 14 seed production showed a strong 2.4-years cycle and, to a lesser extent, other cycle of 6 years
 15 (Table 2). Remarkably, the 2-year cycle appeared mainly for the first six years (1983-1988),
 16 whereas the second 6-year cycle was more pronounced during the rest of study years (Fig. 1).
 17 Regarding flower production, the most marked cycles matched 3.4 and 4.8 years, appearing
 18 more regularly distributed along the study whole period (Table 2 and Fig. 1).

19 The environmental factors showed a lower year-to-year variability, with values of CV
 20 ranging from 0.04 to 0.70, depending on the variable considered (Table 1).

21 *Effects of environmental factors*

22 The main abiotic factors affecting annual seed production in *Q. ilex* were all related to
 23 water resource. The water stress index during summer (WSI_{sum}) and the number of days with
 24 torrential rain during spring (NTR_{spr}) were the best predictors of seed production, as indicated
 25 by the best-supported bivariate model including both environmental variables (Table 3 and Fig.

1 2a). Individually, WSI_{sum} was the factor with the strongest empirical support (within 2 AIC
 2 units of the best supported model), and produced an exponential reduction of the annual seed
 3 crop (Table 3 and Fig. 2b). In contrast, seed production increased exponentially with NTR_{spr} ,
 4 though this factor had substantially less empirical support than WSI_{sum} (Table 3 and Fig. 2c).
 5 There was also evidence for a positive effect of the number of days with strong rain during
 6 summer (NSR_{sum}), that also interacted with NTR_{spr} (as indicated by the selected bivariate
 7 models), but with less empirical support than the other two predictors (Table 3).

8 NTR_{spr} also affected the percentage of premature acorns, with higher proportion of
 9 aborted seeds being associated with drier springs (Table 3 and Fig. 3a). However, the number
 10 of days with torrential rain in September (NTR_{sep}) was the factor with the strongest empirical
 11 support, increasing linearly the percentage of aborted seeds (Table 3 and Fig. 3b). Remarkably,
 12 the proportion of premature (aborted) seeds was negatively correlated with the annual seed
 13 crop ($R^2=0.70$ and $\Delta AIC=9.43$ with regard to the null model; Fig. 3c).

14 Regarding flower production, no environmental factors were found with stronger
 15 empirical support than the null model (Table 3). This reproductive variable was not correlated
 16 with the annual seed production ($R^2=0.01$ and $\Delta AIC=-5.72$ with regard to the null model).

17 *Resource-matching versus economy-of-scale hypothesis*

18 A positive linear relationship was found between seed production and the average radial
 19 stem growth ($R^2=0.17$ and $\Delta AIC=2.01$ with regard to the null model), that indicates the
 20 absence of switching and, thereby, supports the resource-matching hypothesis as a possible
 21 explanation for mast seeding in *Q. ilex* (Fig. 2d). On the contrary, no good correlation was
 22 found between radial stem growth and flower production ($R^2=0.003$ and $\Delta AIC=-1.95$ with
 23 regard to the null model).

24 Results of Cross-Spectrum Fourier analysis showed that the main regular cycles of seed
 25 and flower production were highly correlated with the temporal series of the most explicative
 26 environmental factors predicted by our modeling approach. On one hand, seed production was

1 correlated with WSI_{sum} at the 2.4-year cycle and with NTR_{spr} at the 6-year cycle, as indicated
 2 by the highest values of cross-amplitude for these two periods (Appendix 2). On other hand,
 3 flower production showed a high level of synchrony with WSI_{sum} for a periodicity of 3.4 years
 4 and, to a lesser extent, with NTR_{spr} for 4.8 years (Appendix 2).

5 *Rainfall exclusion experiment*

6 As expected, rainfall exclusion decreased leaf water potential during summer for all the
 7 sampling years (Appendix 3). In spring, however, this reduction was only significant for 2005
 8 (Appendix 3).

9 Rainfall exclusion induced a double effect on the seeding process: i) a significant reduction in
 10 the production of sound acorns, in terms of biomass, and ii) a significant increase in the
 11 number of premature (aborted) seeds (Fig. 4). Thereby, *Q. ilex* trees produced a similar number
 12 of acorns ($F=0.04$ and $p=0.84$ for differences between treatments in the total number of acorns),
 13 but with a different proportion of aborted seeds depending on the available water resource. No
 14 significant differences between treatments were found neither for the flower production
 15 ($F=0.25$ and $p=0.62$) nor for the infested acorn fraction (both in number of seeds and in
 16 biomass; Fig. 4).

17 Interestingly, differences caused by rainfall exclusion were significant for the
 18 2007/2008 period, considered as a masting year, but not for the 2008/2009 period when the
 19 seed crop was substantially smaller (Fig. 4). The same observation holds when the complete 6-
 20 year cycle is examined, the highest differences appearing in years with high seed crops
 21 (2004/2005 and 2007/2008; Appendix 4). However, these differences between treatments were
 22 not statistically significant, likely because of the very low number of replicates considered in
 23 the analyses when samples were grouped per plot.

24
 25

DISCUSSION

Effects of environmental factors on mast seeding and flowering

Q. ilex showed strong among-year variation in seed production, with a high CV_p value (1.5) that is comparable with other studies on oak species (e.g., Kelly et al. 2000, Kelly and Sork 2002, Espelta et al. 2008). The high inter-annual variation in seed production was largely explained by the variation of some abiotic variables related to water resource. The water stress in summer was the best predictor of seed production, supporting previous studies in other Mediterranean oak forests (Espelta et al. 2008) and confirming our initial hypothesis stating water limitation as the key driver for mast seeding in the studied species. In Mediterranean-type ecosystems, the process of acorn maturation occurs under water limited conditions in summer, and oaks usually exhibit high abortion rates during this period (e.g., Siscart et al. 1999, Espelta et al. 2008), that likely reflect the excess fruit that the tree is not able to keep as a function of the available resources (Lloyd 1980). Results from our observational study confirm this fact, the highest proportion of premature (aborted) acorns appearing in years with the lowest seed crops, coinciding with those that showed the driest summers.

The water availability for the plant during spring, when flowering and fertilization processes occur, also affected the annual seed crop. Remarkably, the number of days with torrential rainfall in spring (NTR_{spr}), instead of mean values of precipitation, was the only selected variable during this period. This result might be explained by the low depth of the soils at the study area, which probably dry up very fast and need to receive high sporadic amounts of water to be well-soaked. Previous studies on *Quercus* species have reported positive effects of high levels of precipitation during spring on the flowering effort (e.g., Cecich and Sullivan 1999, Abrahamson and Layne 2003). In our study, NTR_{spr} did not influence the annual production of male flowers, but it had an important effect on the percentage of aborted acorns (i.e., unfertilized flowers or not completely developed seeds).

1 Since the production of male flowers - and consequently the pollen production - was relatively
 2 constant among years and was not limited by drought, the most plausible explanation is that the
 3 higher abortion rates during drier springs were rather due to an early-abscission of recently
 4 pollinated flowers than to fertilization failures.

5 In addition to the effects of WSI_{sum} and NTR_{spr} on the proportion of aborted seeds, that
 6 emphasize the role of water as a limiting resource for the plant, we detected a negative effect of
 7 the frequency of intense precipitations at the end of summer. The mechanical effect produced
 8 by frequent torrential rainfalls during September likely favoured the premature-abscission of
 9 acorns before they had completed their maturation process. Such a pattern of mechanical
 10 premature-abscission of acorns has already been documented in other previous studies (Feret et
 11 al. 1982).

12 In summary, precipitation pattern determined the seed crop size by disrupting the
 13 fruiting process at different periods of time. The acorn ripening process was strongly
 14 dependent on water availability for the plant at initial (spring) and advanced (summer) stages
 15 of the maturation cycle, whereas the final step of seed development was negatively affected by
 16 the frequency of torrential-rain events.

17 *Resource-matching versus economy-of-scale hypothesis*

18 Our results from the long-term dataset demonstrated that the masting phenomenon for
 19 *Q. ilex* populations in southern France is not simply an evolved reproductive strategy, but is
 20 strongly dependent on the available resources for the plant. On one hand, the positive
 21 correlation between seed production and radial stem growth refutes the existence of switching
 22 and, thereby, supports the resource-matching hypothesis (Norton and Kelly 1988, Kelly and
 23 Sork 2002). According to this hypothesis, plants invest more internal resources in everything
 24 (vegetative growth and reproduction) during good years, whereas both processes are depleted
 25 in years with limiting resources (Monks and Kelly 2006). On other hand, the high level of
 26 synchrony between the masting cycles and the temporal series of certain environmental factors

1 such as WSI_{sum} and NTR_{spr} suggests that the inter-annual variation in seed crop is not regulated
 2 simply by selective endogenous rhythms, but is mainly a physiological response to the variable
 3 environment.

4 Although our findings agree most closely with the resource-matching hypothesis, we
 5 can not conclude that climate is the only responsible for masting. The relatively low correlation
 6 ($R^2=0.17$) between vegetative growth and seed production, and the higher variability for seed
 7 crop than for abiotic factors, suggest that our study case is not probably a pure example of
 8 “putative” masting. Among the possible selective benefits that could favour a highly variable
 9 reproduction in *Q. ilex*, the predator-satiation (Janzen 1971, Silvertown 1980, Kelly and
 10 Sullivan 1997) seems to be the best hypothesis supporting our results. Thus, the lowest
 11 probabilities of seed predation at the study site were quantified in years with the highest seed
 12 crops (Pérez-Ramos et al., *unpublished data*), probably due to a satiating effect on seed
 13 predators. This temporal pattern of lower consumption rates in more productive years has been
 14 documented in other forest types (e.g., Shaw 1968, Pérez-Ramos and Marañón 2008). In
 15 addition, the seeding pattern observed in this study (with alternating 2- and 6-year cycles) is
 16 consistent with a chaotic driver (Rees et al. 2002). Such a temporal sequence of seeding
 17 production has been described by Kelly et al. (2008), and was interpreted as an effective
 18 mechanism for satiating predators in ecological time. On the other hand, the fact that a higher
 19 flowering effort does not imply a higher size of the annual seed crop (since no significant
 20 correlations were found between both reproductive variables), disproves the pollination-
 21 efficiency hypothesis (Nilsson and Wästljung 1987, Norton and Kelly 1988, Smith et al. 1990,
 22 Kelly et al. 2001) as a possible selective force that drives masting in the study species. Similar
 23 evidences refuting this hypothesis have been documented for other temperate oaks (Shibata et
 24 al. 2002, Sork et al. 2003, Espelta et al. 2008).

25

1 *Rainfall exclusion experiment: implications for *Q. ilex* regeneration under increasing drought*
 2 *scenarios*

3 Our results from the manipulative experiment of rainfall exclusion are interesting for
 4 several reasons. First, they allowed us to corroborate the conclusions obtained from the 26-year
 5 fruiting record highlighting the importance of abiotic variables linked to soil water availability
 6 as key factors driving the annual fluctuations in seed production of *Q. ilex*.

7 Second, we could describe the underlying mechanisms (proximate causes) of masting.
 8 The high year-to-year variation in seed production was mainly determined by the success in
 9 seed development rather than by the annual fluctuations in flowering effort. Thus, *Q. ilex* trees
 10 produced a similar number of male flowers and seeds in both treatments, but the number of
 11 abortions increased and, the production of sound acorns was reduced when drought was
 12 experimentally intensified. These results stating seed survival as the proximate cause of
 13 masting are in accordance with some studies on oak species (Williamson 1966, Farmer 1981,
 14 Espelta et al. 2008), but contrast with others that identified the number of flowers (Feret et al.
 15 1982, Cecih and Sullivan 1999, Masaka and Sato 2002) or even both processes (Sork et al.
 16 1993) as the main determinants of the final seed crop. Remarkably, the alteration of water
 17 availability by the rainfall exclusion did not produce any effect on the seed production pattern
 18 in years of low seed crop. In low-productive habitats such as Mediterranean woodlands, where
 19 the large seed crops are mainly restricted to wetter years, an additional increase in drought
 20 severity was probably not able to aggravate the already limiting conditions of extremely dry
 21 years.

22 Finally, these findings enable us to accurately predict global change effects in future
 23 environmental scenarios. Under a global change scenario, summer rainfall is expected to
 24 decline in the Mediterranean region (Christensen et al. 2005, Giorgi 2006). At the study site,
 25 where the annual seed crop is largely driven by water availability during summer, it could be
 26 expected that the drier conditions predicted by climate models reinforce the negative effects of

1 summer drought on seed production. A collapse during this early stage could have important
 2 negative consequences for the recruitment of the study species, which already suffers serious
 3 regeneration problems at the study site (*personal observation*). In general, natural recruitment
 4 of Mediterranean tree species is usually restricted to sporadic ‘wet’ years (e.g., Traveset et al.
 5 2003, Gómez-Aparicio et al. 2005), and could be even more dependent on such years in future
 6 environmental scenarios (Gómez-Aparicio et al. 2008). The information provided by our
 7 experimental approach constitutes a crucial step to evaluate the impact of increasing drought
 8 due to climate change on the early stages of regeneration in Mediterranean tree species, taking
 9 as example one of the most dominant oak species in temperate woodlands. In the future, it
 10 would be interesting to investigate the effects of increasing drought on the successive
 11 regeneration stages (such as seed germination, seedling emergence, survival and growth) to
 12 draw a full picture of the ecological consequences of the decline in water resource on tree
 13 recruitment and forest dynamics under Mediterranean conditions.

14
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 18 Rainfall exclusion experiment was performed within the framework of the European project
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TABLES

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Table 1. Mean, standard deviation and coefficient of variation (CV) of the five annual environmental factors measured in the study, and of the best abiotic predictors selected by our modeling approach.

Environmental factor	Mean±SD	CV
Annual minimum temperature (°C)	8,1 ± 0,4	0,05
Annual maximum temperature (°C)	18,1 ± 1,0	0,06
Annual mean rainfall (mm)	901,1 ± 239,5	0,27
Annual net radiation (j cm ⁻²)	1411 ± 50,3	0,04
Annual wind velocity (m s ⁻¹)	3,0 ± 0,2	0,08
Nb days with torrential rain (spring, NTR _{spr})	2,3 ± 1,6	0,70
Nb days with strong rain (summer, NSR _{sum})	3,6 ± 1,8	0,49
Nb days with torrential rain (september, NTR _{sep})	6,5 ± 2,9	0,46
Water stress index in summer (Mpa, WSI _{sum})	81,2 ± 11,8	0,14

1 **Table 2.** Results of Single Spectrum Fourier Analyses exploring cyclical patterns in seed and
 2 flower production of *Q. ilex* over the entire 26-years period. The main regular cycles have been
 3 highlighted with bold letters. The period has been expressed in years. The periodogram values,
 4 that can be interpreted in terms of variance (sums of squares) of the data at the respective
 5 frequency or period, were computed as the sum of the squared sine and cosine coefficients at
 6 each frequency (times N/2). The spectral density estimates were computed by smoothing the
 7 periodogram values in order to identify the general frequency "regions" that significantly
 8 contribute to the cyclical behaviour of the series.

9

	Period	Frequency	Cosine	Sine	Periodogram	Spectral Density
Seed production	2,0	0,5	16,5	0,0	3279,4	2503,2
	2,2	0,5	-0,2	4,7	266,7	4094,7
	2,4	0,4	-5,7	-32,1	12748,8	6634,0
	2,7	0,4	7,3	-13,6	2861,9	4908,3
	3,0	0,3	1,1	12,8	1993,8	2623,3
	3,4	0,3	-5,0	-11,5	1880,1	2374,4
	4,0	0,3	13,3	11,8	3773,9	2750,0
	4,8	0,2	-4,3	9,0	1189,4	3370,4
	6,0	0,2	-20,4	-13,3	7112,3	4613,4
	8,0	0,1	15,1	10,8	4143,5	3742,4
	12,0	0,1	-2,3	6,0	501,5	1583,0
	24,0	0,0	1,0	-5,8	412,1	513,9
Flower production	2,0	0,5	1,7	0,0	34,4	25,0
	2,2	0,5	-0,7	1,0	16,9	22,0
	2,4	0,4	0,8	-1,1	20,7	24,5
	2,7	0,4	1,1	0,2	15,6	76,1
	3,0	0,3	3,4	1,6	172,1	235,2
	3,4	0,3	-6,7	-2,7	617,9	369,0
	4,0	0,3	-2,4	-2,3	137,2	351,3
	4,8	0,2	1,8	-6,2	504,7	378,6
	6,0	0,2	2,4	5,0	370,7	365,9
	8,0	0,1	0,6	4,5	246,5	323,4
	12,0	0,1	0,4	5,8	403,3	311,6
	24,0	0,0	-1,6	-4,2	244,3	224,0

1 **Table 3.** Summary of the models analyzing the effects of environmental factors on flower and seed production, and on the percentage of
 2 premature seeds (aborted), over the entire 26-years period (1983-2008). All the models with better empirical support than null ($2 \leq \Delta AIC$) are
 3 shown, ranked from best to poorest fits. Additive interactions between two factors are noted as (+) and multiplicative as (X). The signs of the
 4 relationships (positive or negative) between each dependent variable and all the selected environmental predictors are also indicated, separated by
 5 commas. Functional Forms (FF): LIN, Linear model; EXP, Exponential model; MM, Michaelis-Menten model; null, Null model.

6

Dependent variable	Environmental factor	FF	Relation	R ²	AIC	ΔAIC
<i>Seed production (g m⁻²)</i>	NTR _{spr} + WSI _{sum}	LIN	+, -	0,65	223,45	0,00
	Water stress index (summer, WSI _{sum})	EXP	-	0,59	224,54	1,09
	Nb days with torrential rain (spring, NTR _{spr})	EXP	+	0,49	238,44	14,99
	Nb days with strong rain (summer, NSR _{sum})	EXP	+	0,40	242,54	19,09
	NTR _{spr} + NSR _{sum}	LIN	+, +	0,46	243,01	19,56
	NTR _{spr} x NSR _{sum}	MM	+, +	0,43	244,19	20,74
	null				252,18	28,73
<i>Flower production (g m⁻²)</i>	null				158,36	0,00
<i>Percentage of aborted seeds (%)</i>	Nb days with torrential rain (september, NTR _{sep})	LIN	+	0,85	52,58	0,00
	Nb days with torrential rain (spring, NTR _{spr})	EXP	-	0,62	58,98	6,40
	null				66,66	14,08

FIGURE LEGENDS

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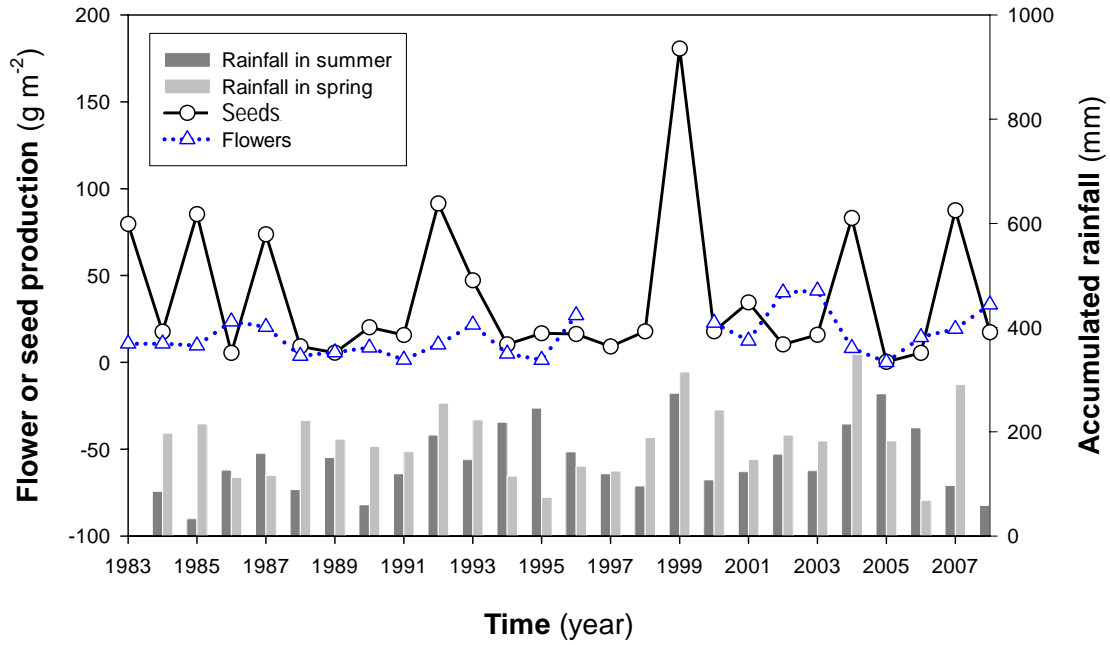
Figure 1. Flower and seed production of *Quercus ilex* over the 26-years study period (1983-2008). Values of flower production have not been represented for the period 1997-1999 because no data were available for these years. Temporary dynamics of accumulated rainfall during spring and summer has been represented with vertical bars.

Figure 2. Seed production as a function of the best environmental predictors: additive bivariate-model including WSI_{sum} and NTR_{spr} (A); water stress index in summer (WSI_{sum} , B); and number of days with torrential rainfall during spring (NTR_{spr} , C). Relationship between seed production and radial stem growth over the 26-years study period (1983-2008, D). Lines represent the predicted models with the best empirical support (see Table 3).

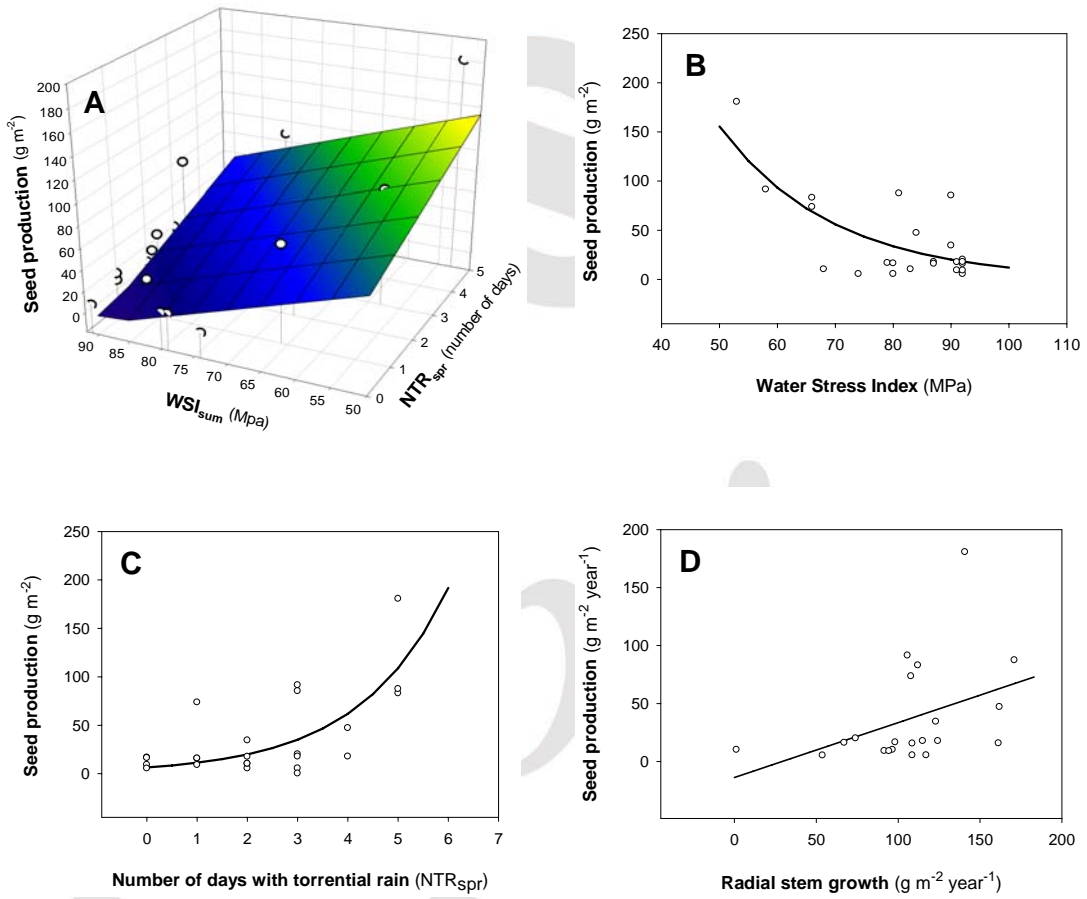
Figure 3. Percentage of premature (aborted) seeds as a function of the best environmental predictors: number of days with torrential rainfall during spring (NTR_{spr} , A); number of days with torrential rainfall in September (NTR_{sep} , B); and relationship between the annual seed production and the percentage of premature (aborted) seeds for the 2000-2007 period (C). Lines represent the predicted models with the best empirical support (see Table 3).

Figure 4. Differences between rainfall exclusion treatments (control as black bars and dry as grey bars) on seed production (both in number of acorns and in seed biomass), for the two studied cycles. Seeds were sorted at laboratory in three different categories: premature (aborted), predated by larvae (infested) and sounds. The significance level is expressed as: ns, not significant; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Vertical lines denote standard error values.

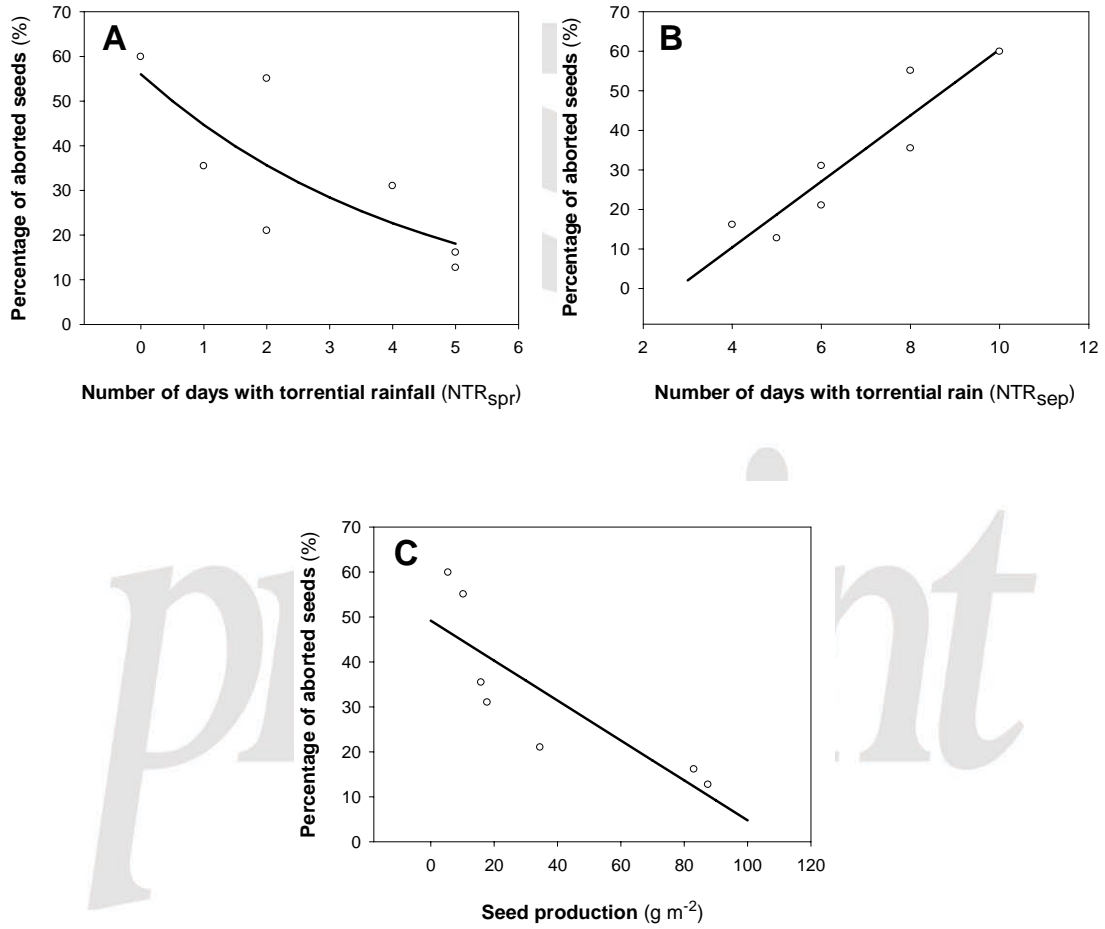
1 **Figure 1.**



1 **Figure 2.**



1 **Figure 3.**



1 **Figure 4.**

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