

Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment

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

Key words: abortions; acorn production; economy-of-scale hypothesis; global change; masting cycles; Puéchabon State Forest, southern France; *Quercus ilex*; resource-matching hypothesis; water stress.

INTRODUCTION

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).

Interannual 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 upon 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 of 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 toward reproduction in some years and toward vegeta-

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tive growth in others (Norton and Kelly 1988). In the case that a masting plant species is merely responding to the variable and unpredictable environment ("putative" masting), both reproduction and growth should be favored in good years, whereas both processes would be depleted in years with limiting resources (Monks and Kelly 2006). In nature, cases of "putative" masting are very rare (e.g., Despland and Houle 1997), resource switching being a more frequent event (e.g., Norton and Kelly 1988, Alley et al. 2001, Monks and Kelly 2006). However, there are very few published examples that test strictly resource switching, especially in low-productivity ecosystems such as mediterranean woodlands.

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

Mediterranean-type ecosystems are predicted to be among the most vulnerable to climate change due to an intensification of their already limiting conditions for plant regeneration (Christensen et al. 2007). Global change models predict increasing aridity for the mediterranean area, summer drought being expected to increase in severity (Peñuelas et al. 2004, Christensen et al. 2007). This increasing drought may negatively affect seed production in dominant tree species by reducing the size of the annual seed crop and/or likely by disrupting the environmental cues that synchronize plants for masting (McKone et al. 1998). Other manipulative studies have examined reproductive responses to altered rainfall in herbaceous species (e.g., Kadmon 1993, Fay et al. 2000). However, the impact of increasing drought on initial stages of regeneration such as flowering and seeding has not been experimentally evaluated in tree species, particularly of mediterranean ecosystems.

In this study, we first present the results of a long-term 26-year data set on reproductive and vegetative growth of *Quercus ilex* in a mediterranean woodland located in southern France in order to determine whether mast seeding and flowering are more consistent with the resource-matching hypothesis or the economy-of-scale hypothesis. Based on our initial hypothesis stating water limitation as a key factor that drives masting in the studied species, we also conducted a rainfall exclusion experiment to evaluate the effects of an increasing

drought (anticipating predictions of global change models) on both reproductive processes. Specifically, the main objectives of this ambitious study were: (1) to explore the existence of cyclical patterns in flower and seed production; (2) to identify which environmental factors or resources better explain the interannual variation in both processes; (3) to test the adaptive vs. the nonadaptive hypotheses for masting; (4) to examine the impact of increasing drought on flower and seed production in a manipulative experiment that altered soil water availability under natural conditions; and (5) to discuss the ecological implications of these findings for oak regeneration under current and future environmental scenarios.

MATERIALS AND METHODS

Study area

The study site is located 35 km northwest of Montpellier, southern France, on a flat plateau in the Puéchabon State Forest (3°35'45" E, 43°44'29" N, elevation 270 m). This forest has been managed as a coppice for centuries, but the last clearcut was performed in 1942. Vegetation is largely dominated by a dense overstory of *Quercus ilex* evergreen oak, with a mean canopy height of ~5.5 m. In January 2009, the density of the resprouted stems was 6195 stems/ha, stems with a dbh (measured at 1.3 m above the ground surface) < 4 cm represented 12% of the total, whereas those with dbh > 10 cm represented 12.5%. The understory, dominated by *Buxus sempervirens*, *Phyllirea latifolia*, *Pistacia terebinthus*, and *Juniperus oxycedrus*, composes a sparse shrubby layer with a percent cover <25% and a height <1.5 m.

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

Sample collection over 26 years

In 1983, a total of 26 circular plastic traps (diameter 0.41 m) were randomly distributed beneath the *Quercus ilex* canopy in an area totalling 314 m². Traps were 0.7 m in height to avoid post-dispersal seed removal by mammals (the main acorn predators at the study area; I. M. Pérez-Ramos, J. Rodríguez-Calcerrada, J. M. Ourcival, and S. Rambal, *unpublished data*). Small holes were drilled at the bottom of each trap to facilitate draining of throughfall water. The leaf area index (LAI) over the traps, estimated in 2008 by means of a leaf area meter (LAI 2000; LI-COR, Lincoln, Nebraska, USA),

varied from 1.97 to 3.58 (2.91 ± 0.39 [mean \pm SE]). The minimum distance between traps was 6 m.

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

Radial stem growth was used as a representative measure of vegetative growth. This variable was calculated from yearly recorded dbh of 68 *Q. ilex* trees (with dbh > 2 cm), covering a total area of ~ 100 m² at the same study plot where the traps were placed. For comparative purposes between reproductive and vegetative growth, radial stem growth was expressed as the annual increment of dry wood biomass per unit of area, using an allometric equation previously reported at the study area (Rambal et al. 2004).

Environmental factors

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

From each variable, we derived 13 abiotic factors taking into account the critical periods for flower and fruit development: annual mean values for the current and the previous year (following the natural period between two reproductive cycles; from July to June for flowering and from April to March for seeding), mean values for spring, summer, and autumn and mean monthly values during these seasons. For each period of time (annual, seasonal, and monthly), we also calculated four other variables that could have an influence on

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

Rainfall exclusion experiment

In 2003, a rainfall exclusion experiment was established near the 26-year study (<100 m) as part of the European project Mediterranean Terrestrial Ecosystems and Increasing Drought (MIND). The experimental design is comparable, in conception, with the one described by Hanson et al. (2003). The rainfall exclusion experiment was replicated on three plots 200 m from one another and situated on a flat area with no lateral water flow. In each replicate, two treatments were set up on two 140-m² plots (14 \times 10 m). One was a control (farther, control) and the second was subjected to rainfall exclusion (farther, dry). On the dry plot, rainfall exclusion was achieved using 14 m long and 0.19 m wide PVC gutters covering 33% of the ground area under the *Quercus ilex* canopy, with the aim of excluding 33% of throughfall. Taking into account interception losses and stem flow, the rainfall exclusion experiment reduces the net input of precipitation to the soil by 29% compared to the control treatment (Limousin et al. 2008). On the control plot, identical gutters had been placed upside down in order to homogenize, as far as possible, whole-canopy albedo and understory microclimate conditions in both treatments. Total basal area, canopy structure, and density of trees were similar for the two treatments (values [mean \pm SE] for control plots, dbh, 5.5 ± 0.3 cm; tree height, 3.3 ± 0.2 m; number of stems, 85.7 ± 11.8 ; basal area, 27.8 ± 2.6 m²/ha; values for dry plots, dbh,

TABLE 1. Values for the entire sampling period (1983–2008) of the five annual environmental factors measured in the Puéchabon State Forest in southern France, as well as of the best abiotic predictors selected by our modeling approach.

Environmental factor	Mean \pm SD	CV
Annual minimum temperature ($^{\circ}$ C)	8.1 \pm 0.4	0.05
Annual maximum temperature ($^{\circ}$ C)	18.1 \pm 1.0	0.06
Annual mean rainfall (mm)	901.1 \pm 239.5	0.27
Annual net radiation (J/cm^2)	1411 \pm 50.3	0.04
Annual wind velocity (m/s)	3.0 \pm 0.2	0.08
No. days with torrential rain (spring, NTR_{spr})	2.3 \pm 1.6	0.70
No. days with strong rain (summer, NSR_{sum})	3.6 \pm 1.8	0.49
No. days with torrential rain (September, NTR_{sep})	6.5 \pm 2.9	0.46
Water stress index in summer (WSI_{sum} , MPa)	81.2 \pm 11.8	0.14

5.8 \pm 0.1 cm; tree height, 3.5 \pm 0.2 m; number of stems, 94 \pm 8.7; basal area, 35.4 \pm 2.1 m^2/ha).

To test the effectiveness of the rainfall exclusion on plant water status, leaf water potential was measured at predawn with a pressure chamber (model 7000; PMS Instrument Albany, Oregon, USA). In both treatments, 2–3 replicate leaves from four different trees were periodically measured during spring and summer from 2003 to 2006.

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

Data analysis

Masting cycles.—Cyclical patterns of flowering and seeding were explored using single-spectrum Fourier analyses, after subtracting the overall mean from the data series (Bloomfield 1976). Prior to the analyses, series were transformed by means of a process of split-cosine-bell tapering that leads to a reduction of leakage in the spectral density plots (Bloomfield 1976). Interannual variability in flower and seed production was examined using the population-level coefficient of variation (CV_p), calculated as the ratio of the standard deviation to the annual mean of each fraction for the 26 collecting traps. The CV was also calculated for the most explicative environmental factors that were previously selected by our modeling approach.

Effects of environmental factors.—To identify individual climate factors that may be useful predictors of annual flowering and seeding, we fitted linear and nonlinear models for each reproductive process, using maximum likelihood techniques. Flower and seed

production were modeled independently as functions of the 156 environmental factors (12 climate variables \times 13 different periods of time) considered in the study (Table 1). We tested three alternative functional forms (linear, exponential, and Michaelis-Menten) that cover a wide range of possible forms (see equations in Appendix A). We first tested models for each factor and functional form independently, and the best of the three models was compared to a null model that assumes no effect of any factor. Second, to test for joint limitation (i.e., more than one factor being limiting at once), we fitted bivariate models using those factors that had an effect on flowering or seeding when evaluated singly. We tried alternative models in which the second environmental factor was added either additively or multiplicatively. Models including more than two factors were not considered due to their lower empirical support. In total, more than 1000 different models were individually run for this study. This modeling approach is suitable for identifying plant responses to abiotic factors at different stages of the regeneration cycle (e.g., Pacala et al. 1996, Kobe 1999, 2006, Gómez-Aparicio et al. 2008, Pérez-Ramos et al. 2008, Urbietta et al. 2008).

Models were parameterized with maximum likelihood (Edwards 1992) using a simulating annealing algorithm. Based on exploratory analyses, we assumed a normal distribution for the dependent variables. Alternative models were compared using the Akaike information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002). The absolute magnitude of the differences in AIC_c (ΔAIC) between alternative models provides an objective measure of the strength of empirical support for the competing models. Models with ΔAIC between 0 and 2 were considered to have equivalent and substantial empirical support (Burnham and Anderson 2002). The R^2 of the regression of observed vs. predicted was used as a measure of the goodness of fit of each alternate model.

We used the same modeling approach to examine the relationships between both reproductive processes (flowering and seeding), as well as between them and the percentage of aborted seeds. All models were implemented using the likelihood package version 1.1

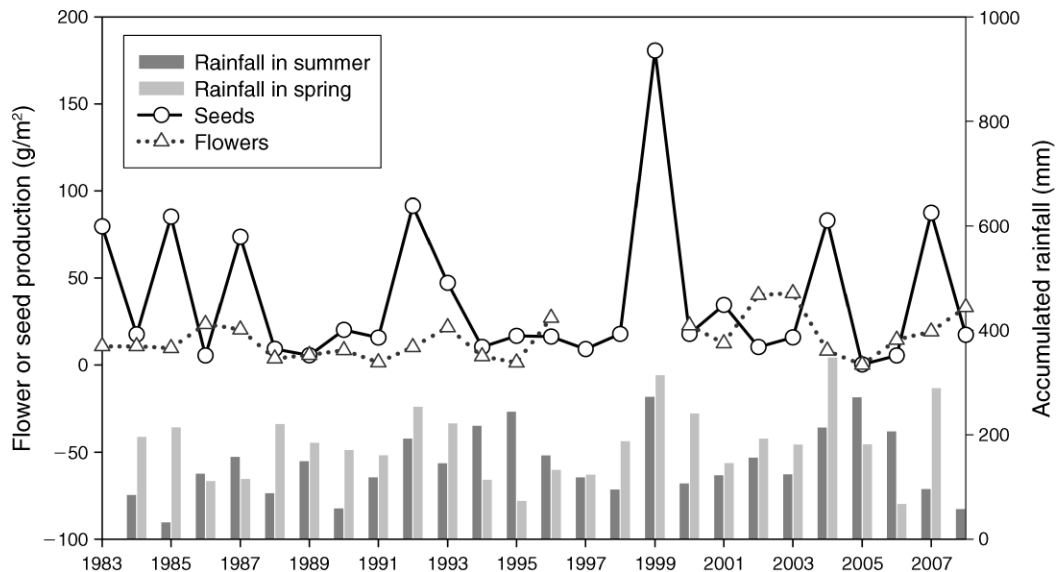


FIG. 1. Flower and seed production of *Quercus ilex* over the 26-year study period (1983–2008) in Puéchabon State Forest in southern France. Values of flower production have not been represented for the period 1997–1999 because no data were available for these years. Temporary dynamics of accumulated rainfall during spring and summer are represented by vertical bars.

for R and software written specifically for this study in R version 2.5.0 (R Development Core Team 2006).

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

Rainfall exclusion treatment.—Differences between control and dry treatments for leaf water potential (in spring and summer) were tested using one-way ANOVAs. The changes in flower and seed production through the six years of record and in response to the rainfall exclusion treatment were analyzed using a repeated-measures ANOVA. For this type of analysis, data were grouped by plot because the samples were not separated individually (by trap) between June of 2003 and September of 2007. For the last two reproductive cycles (2007–2008 and 2008–2009), when the content of the 72 traps was collected individually, differences between control and dry treatments for flower and seed production (separated into their different categories) were evaluated using one-way ANOVAs. None of the abovementioned variables departed significantly from normality according to the Kolmogorov-Smirnov test.

All these analyses were carried out using Statistica (version 6; StatSoft 2001).

RESULTS

Masting cycles

Seed production was highly variable among years, with mean annual crops ranging from 0.3 to 180.6 g/m² and a relatively high value of CVp (1.18). Remarkably, the largest seed crops mostly coincided with rainy years, especially during spring (Fig. 1). Flower production, however, showed a lower interannual variability, with crop values ranging from 0.1 to 41.3 g/m² and a CVp of 0.80 (Fig. 1). According to single-spectrum Fourier analyses, seed production showed a strong 2.4-year cycle and, to a lesser extent, another cycle of 6 years (Table 2). Remarkably, the 2-year cycle appeared mainly for the first six years (1983–1988), whereas the 6-year cycle was more pronounced during the rest of study years (Fig. 1). Regarding flower production, the most marked cycles matched 3.4 and 4.8 years, appearing more regularly distributed along the whole study period (Table 2, Fig. 1).

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

Effects of environmental factors

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

TABLE 2. Results of single-spectrum Fourier analyses exploring cyclical patterns in seed and flower production of *Quercus ilex* over the entire 26-year period.

Period (yr)	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	12 748.8	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

Notes: The main regular cycles appear in boldface. The periodogram values, which can be interpreted in terms of variance (sums of squares) of the data at the respective frequency or period, were computed as the sum of the squared sine and cosine coefficients at each frequency (times $N/2$). The spectral density estimates were computed by smoothing the periodogram values in order to identify the general frequency “regions” that significantly contribute to the cyclical behavior of the series.

2A). Individually, WSI_{sum} was the factor with the strongest empirical support (within 2 AIC units of the best supported model) and produced an exponential reduction of the annual seed crop (Table 3, Fig. 2B). In

contrast, seed production increased exponentially with NTR_{spr} , though this factor had substantially less empirical support than WSI_{sum} (Table 3, Fig. 2C). There was also evidence for a positive effect of the

TABLE 3. Summary of the models analyzing the effects of environmental factors on flower and seed production and on the percentage of premature seeds (aborted) over the entire 26-year period (1983–2008).

Dependent variable and environmental factor	FF	Relation	R^2	AIC	ΔAIC
Seed production					
$NTR_{spr} + WSI_{sum}$	LIN	+, -	0.65	223.45	0.00
WSI_{sum}	EXP	-	0.59	224.54	1.09
NTR_{spr}	EXP	+	0.49	238.44	14.99
NSR_{sum}	EXP	+	0.40	242.54	19.09
$NTR_{spr} + NSR_{sum}$	LIN	+, +	0.46	243.01	19.56
$NTR_{spr} \times NSR_{sum}$	MM	+, +	0.43	244.19	20.74
Null				252.18	28.73
Flower production					
Null				158.36	0.00
Percentage of aborted seeds					
NTR_{sep}	LIN	+	0.85	52.58	0.00
NTR_{spr}	EXP	-	0.62	58.98	6.40
Null				66.66	14.08

Notes: All the models with better empirical support than null ($2 \leq \Delta AIC$) are shown, ranked from best to poorest fits. Additive (+) and multiplicative (\times) interactions between two factors are noted. The signs of the relationships (positive or negative) between each dependent variable and all the selected environmental predictors are also indicated. Functional form (FF) abbreviations are: LIN, linear model; EXP, exponential model; MM, Michaelis-Menten model; null, null model. See Table 1 for explanations of environmental factor abbreviations.

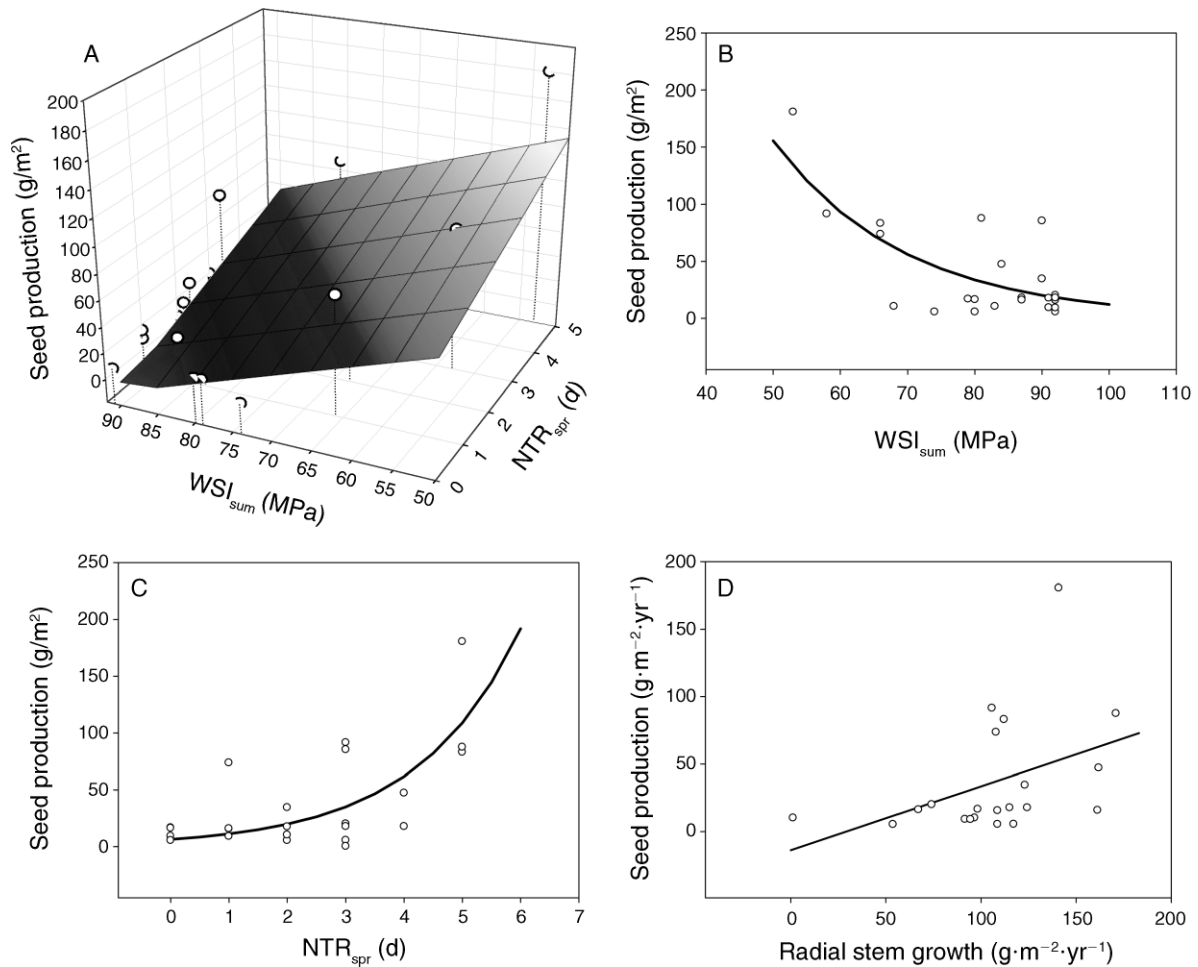


FIG. 2. Seed production as a function of the best environmental predictors: additive bivariate model including (A) water stress index in summer (WSI_{sum}) and number of days with torrential rain in spring (NTR_{spr}), (B) WSI_{sum} , and (C) NTR_{spr} . (D) Relationship between seed production and radial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

number of days with strong rain during summer (NSR_{sum}), which also interacted with NTR_{spr} (as indicated by the selected bivariate models), but with less empirical support than the other two predictors (Table 3).

The number of days with torrential rain during spring also affected the percentage of premature acorns, with higher proportion of aborted seeds being associated with drier springs (Table 3, Fig. 3A). However, the number of days with torrential rain in September (NTR_{sep}) was the factor with the strongest empirical support, increasing linearly with the percentage of aborted seeds (Table 3, Fig. 3B). Remarkably, the proportion of premature (aborted) seeds was negatively correlated with the annual seed crop ($R^2 = 0.70$ and $\Delta AIC = 9.43$ with regard to the null model; Fig. 3C).

Regarding flower production, no environmental factors were found with stronger empirical support than the null model (Table 3). This reproductive

variable was not correlated with the annual seed production ($R^2 = 0.01$ and $\Delta AIC = -5.72$ with regard to the null model).

Resource-matching hypothesis vs. economy-of-scale hypothesis

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

Results of cross-spectrum Fourier analysis showed that the main regular cycles of seed and flower production were highly correlated with the temporal series of the most explicative environmental factors

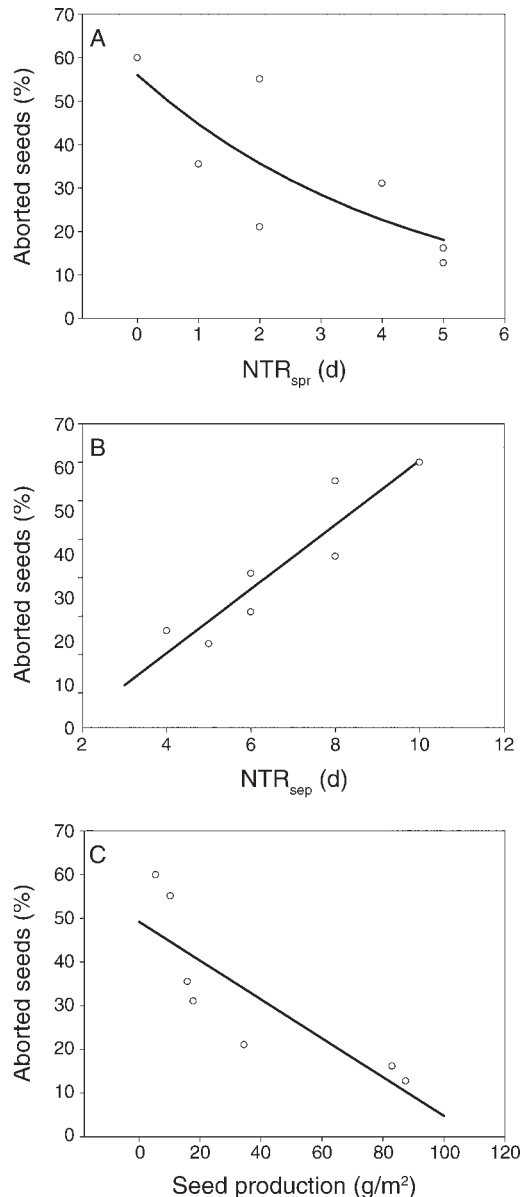


FIG. 3. Percentage of premature (aborted) seeds as a function of the best environmental predictors: (A) number of days with torrential rainfall during spring (NTR_{spr}); (B) number of days with torrential rainfall in September (NTR_{sep}); and (C) relationship between the percentage of premature (aborted)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

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

Rainfall exclusion experiment

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

Rainfall exclusion induced a double effect on the seeding process: (1) a significant reduction in the production of sound acorns, in terms of biomass, and (2) a significant increase in the number of premature (aborted) seeds (Fig. 4). Therefore, *Q. ilex* trees produced a similar number of acorns ($F_{1,23} = 0.04$ and $P = 0.84$ for differences between treatments in the total number of acorns), but with a different proportion of aborted seeds, depending on the available water resource. No significant differences between treatments were found either for the flower production ($F_{1,23} = 0.25$ and $P = 0.62$) or for the infested acorn fraction (both in number of seeds and in biomass; Fig. 4).

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

DISCUSSION

Effects of environmental factors on mast seeding and flowering

Quercus ilex showed strong among-year variation in seed production, with a high CVp value (1.5) that is comparable with other studies of oak species (e.g., Kelly et al. 2000, Kelly and Sork 2002, Espelta et al. 2008). The high interannual 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), which 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 appeared in years with the lowest seed crops, coinciding with those that showed the driest summers.

The water availability for the plants during spring, when flowering and fertilization processes occur, also

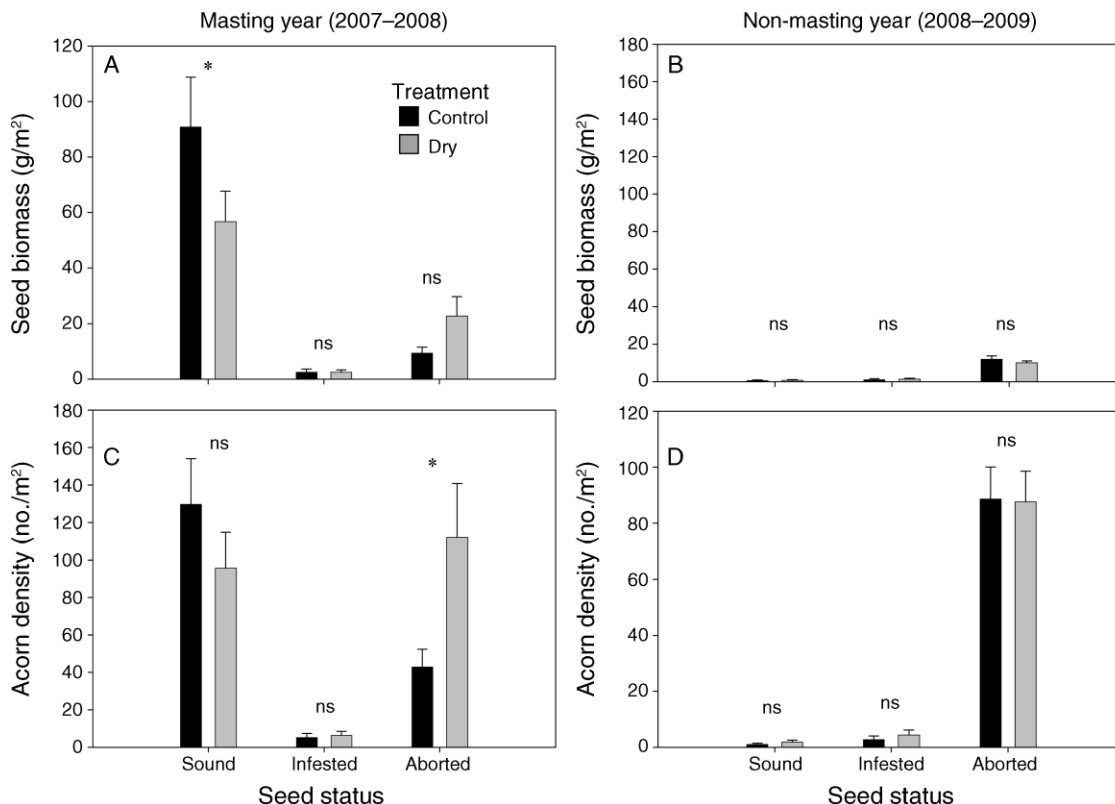


FIG. 4. Differences between rainfall exclusion treatments on seed production (both in terms of number of acorns and in seed biomass; mean + SE) for the two studied cycles. The dry treatment was achieved experimentally by excluding 33% of throughfall, while the control treatment consisted of ambient rainfall. Seeds were sorted at the laboratory into three different categories: premature (aborted), depredated by larvae (infested), and sound.

* $P < 0.05$; ns, not significant.

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

In addition to the effects of WSI_{sum} and NTR_{spr} on the proportion of aborted seeds, which emphasize the role of water as a limiting resource for the plant, we

detected a negative effect of the frequency of intense precipitation at the end of summer. The mechanical effect produced by frequent torrential rainfalls during September likely favored the premature abscission of acorns before they had completed the maturation process. Such a pattern of mechanical premature abscission of acorns has already been documented in other previous studies (Feret et al. 1982).

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

Resource-matching hypothesis vs. economy-of-scale hypothesis

Our results from the long-term data set demonstrated that the masting phenomenon for *Q. ilex* populations in southern France is not simply an evolved reproductive strategy, but is strongly dependent upon the available resources for the plant. On one hand, the positive

correlation between seed production and radial stem growth refutes the existence of switching and, thereby, supports the resource-matching hypothesis (Norton and Kelly 1988, Kelly and Sork 2002). According to this hypothesis, plants invest more internal resources in everything (vegetative growth and reproduction) during good years, whereas both processes are depleted in years with limiting resources (Monks and Kelly 2006). On the other hand, the high level of synchrony between the masting cycles and the temporal series of certain environmental factors such as WSI_{sum} and NTR_{spr} suggests that the interannual variation in seed crop is not regulated simply by selective endogenous rhythms, but is mainly a physiological response to the variable environment.

Although our findings agree most closely with the resource-matching hypothesis, we cannot conclude that climate is the only factor responsible for masting. The relatively low correlation ($R^2 = 0.17$) between vegetative growth and seed production and the higher variability for seed crop than for abiotic factors suggest that our study case is probably not a pure example of "putative" masting. Among the possible selective benefits that could favor a highly variable reproduction in *Q. ilex*, predator satiation (Janzen 1971, Silvertown 1980, Kelly and Sullivan 1997) seems to be the best hypothesis supporting our results. Thus, the lowest probabilities of seed predation at the study site were quantified in years with the highest seed crops (I. M. Pérez-Ramos, J. Rodríguez-Calcerrada, J. M. Ourcival, and S. Rambal, *unpublished data*), probably due to a satiating effect on seed predators. This temporal pattern of lower consumption rates in more productive years has been documented in other forest types (e.g., Shaw 1968, Pérez-Ramos and Marañón 2008). In addition, the seeding pattern observed in this study (with alternating two- and six-year cycles) is consistent with a chaotic driver (Rees et al. 2002). Such a temporal sequence of seeding production has been described by Kelly et al. (2008) and was interpreted as an effective mechanism for satiating predators in ecological time. On the other hand, the fact that a higher flowering effort does not imply a higher size of the annual seed crop (since no significant correlations were found between both reproductive variables) disproves the pollination efficiency hypothesis (Nilsson and Wästljung 1987, Norton and Kelly 1988, Smith et al. 1990, Kelly et al. 2001) as a possible selective force that drives masting in the study species. Similar evidence refuting this hypothesis has been documented for other temperate oaks (Sork et al. 1993, Shibata et al. 2002, Espelta et al. 2008).

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

Our results from the manipulative experiment of rainfall exclusion are interesting for several reasons. First, they allowed us to corroborate the conclusions obtained from the 26-year fruiting record, highlighting

the importance of abiotic variables linked to soil water availability as key factors driving the annual fluctuations in seed production of *Q. ilex*.

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

Finally, these findings enable us to accurately predict global change effects in future environmental scenarios. Under a global change scenario, summer rainfall is expected to decline in the mediterranean region (Giorgi 2006, Christensen et al. 2007). At the study site, where the annual seed crop is largely driven by water availability during summer, it could be expected that the drier conditions predicted by climate models reinforce the negative effects of summer drought on seed production. A collapse during this early stage could have important negative consequences for the recruitment of the study species, which already suffers serious regeneration problems at the study site (I. M. Pérez-Ramos, *personal observation*). In general, natural recruitment of mediterranean tree species is usually restricted to sporadic "wet" years (e.g., Traveset et al. 2003, Gómez-Aparicio et al. 2005) and could be even more dependent on such years in future environmental scenarios (Gómez-Aparicio et al. 2008). The information provided by our experimental approach constitutes a crucial step to evaluate the impact of increasing drought due to climate change on the early stages of regeneration in mediterranean tree species, taking as example one of the most dominant oak species in temperate woodlands. In the future, it would be interesting to investigate the effects of increasing drought on the successive regeneration stages (such as seed germination, seedling emergence, survival, and growth) to draw a full picture of the ecological consequences of the decline in water resource on tree recruitment and forest dynamics under mediterranean conditions.

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APPENDIX A

Equations of the different functions fitted in the models calibrated for this study (*Ecological Archives* E091-212-A1).

APPENDIX B

Results of cross-spectrum Fourier analyses evaluating the level of synchrony, at different frequencies of time, between the two reproductive variables and the best environmental predictors selected by our modeling approach (*Ecological Archives* E091-212-A2).

APPENDIX C

Seasonal variation in predawn leaf water potential from 2003 to 2006 in dry and control plots (*Ecological Archives* E091-212-A3).

APPENDIX D

Differences between rainfall exclusion treatments on seed production for the 2003–2008 period (*Ecological Archives* E091-212-A4).