POPULATION ECOLOGY - ORIGINAL RESEARCH

The coexistence of acorns with different maturation patterns explains acorn production variability in cork oak

Josep Pons · Juli G. Pausas

Abstract In dry areas such as Mediterranean ecosystems, fluctuations in seed production are typically explained by resource (water) availability. However, acorn production in cork oak (*Quercus suber*) populations shows a very low relationship to weather. Because cork oak trees produce acorns with different maturation patterns (annual and biennial), we hypothesized that acorn production in coexisting individuals with a different dominant acorn maturation type should respond differently to climatic factors and that disaggregating the trees according to their acorn-maturation pattern should provide a more proximal relation to weather factors. We assessed acorn production variability in fragmented cork oak populations of the eastern Iberian Peninsula by counting the total number of acorns in 155 trees during an 8-year period. An initial assessment of acorn production variability in relation to weather parameters yielded very low explained variance (7%). However, after the trees were grouped according to their dominant acorn maturation pattern, weather parameters were found to account for 44% of the variability in acorn crops, with trees with annual acorns exhibiting mast fruiting in years with reduced spring frost and shorter summer droughts and trees with biennial acorns showing the opposite pattern. Thus, conditions that negatively affect annual production could be beneficial for biennial production (and vice versa). The results highlight the importance of the resource-matching hypothesis for explaining acorn production in *Quercus suber* and suggest that different seed maturation types within a population may allow the species to deal with highly variable weather conditions. They also emphasize the importance of understanding acorn maturation patterns for interpreting masting cycles.

Keywords *Quercus suber* · Evergreen oaks · Mediterranean woodlands · Hypothesis · Masting

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Introduction

Understanding variability in seed production is a central issue among ecologists because it is a key component determining offspring success in plants (Venable and Brown 1988). Insight into the factors affecting variability in seed production not only provides valuable information on the potential regeneration capacity of plant populations, but as changes in seed production are linked to changes in wildlife populations (Wolff 1996; Boutin et al. 2006), seed production is also a key ecological step in many food webs. Variability in seed production is especially important in oaks because they are considered to be typical foundation species (Ellison et al. 2005) and dominate many landscapes worldwide (Rodà et al. 1999; McShea and Healy 2002; Logan 2005; Aronson et al. 2009). Indeed, acorns are a crucial component of many food webs, and wildlife population changes often track fluctuations in acorn production (Wolff 1996; Ostfeld et al. 1996; McShea and Healy 2002;
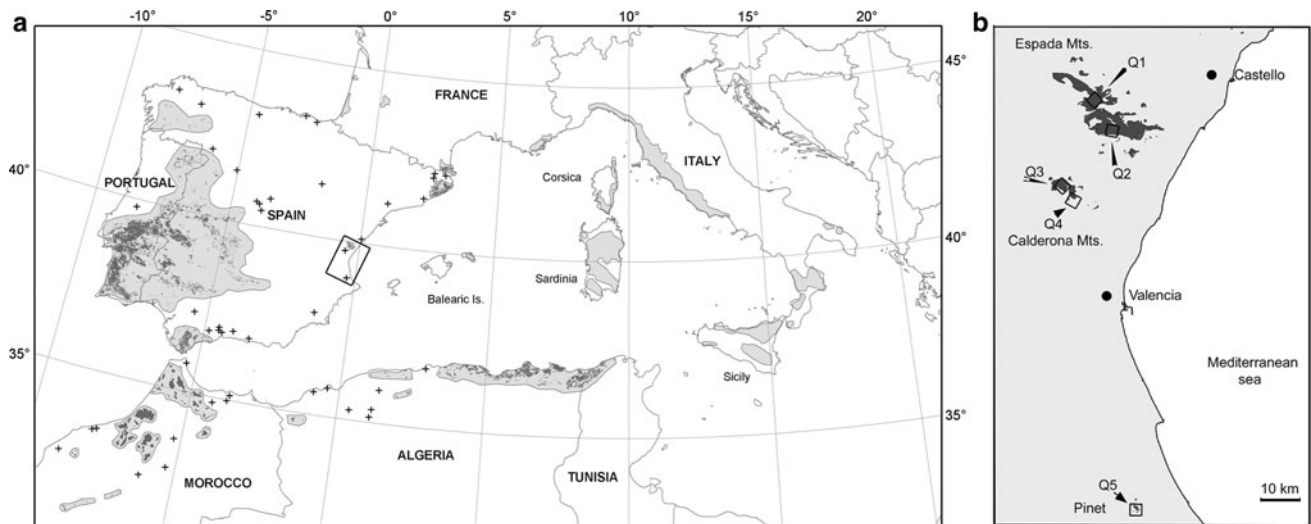
Fig. 1 a Distribution of cork oak (*Quercus suber*) (*gray area and crosses* from Pausas et al. 2009, with permission from Island Press, Washington D.C.); area enclosed by the *square* is the location of the study area in the eastern Iberian Peninsula. **b** Location of the five sam- pled sites within the study area: from north (*top*) to south (*bottom*): two sites in the Espadà mountains (*E1*, *E2*), two in the Calderona moun- tains (*C1*, *C2*), and one site in Pinet (*P1*); *dark gray* indicates *Q. suber* distribution (own data)

Schmidt and Ostfeld 2003; Boutin et al. 2006; Clotfelter et al. 2007). Consequently, considerable attention has been given to understanding oak regeneration processes and acorn production patterns (Koenig and Knops 2000; Kelly and Sork 2002; Liebhold et al. 2004).

Studies on acorn production in Mediterranean Europe have focused on widespread oaks, such as the Holm oak [*Quercus* ilex; García-Mozo et al. (2007); Espelta et al. (2008); Pérez-Ramos et al. (2010)], and little is known for other species. The aim of our study was to gain an under- standing of acorn production patterns in small and frag- mented cork oak (*Quercus suber* L.) populations of the eastern Iberian Peninsula (Mediterranean Basin; Fig. 1). This Mediterranean oak is important in terms of conserva- tion (species protected by the European Union Habitat Directive) and also for its cultural and socio-economic value (sustainable cork production) (Aronson et al. 2009; Bugalho et al. 2011). Furthermore, there is increasing evi- dence of the conservation and biodiversity value of frag- mented peripheral populations (Lesica and Allendorf 1995; Hampe and Petit 2005; Bridle and Vines 2007), and specifi- cally of *Q. suber*, due to the distinct genetic pools between central and peripheral populations (Jiménez et al. 1999; Magri et al. 2007). Thus, understanding the regeneration capacity and variability of these populations is crucial for inferring their evolutionary potential and their fate in a changing world.

In their review, Kelly and Sork (2002) suggested that in dry conditions, such as Mediterranean ecosystems, fluctua- tions in seed production should be best explained by water availability. There is evidence that summer drought reduces crops through the abortion of immature acorns in the Medi-

terranean Holm oak (*Quercus ilex*; Espelta et al. 2008; Pérez-Ramos et al. 2010). Furthermore, cork oak is consid- ered to be a cold-sensitive species, with cold reducing flower and fruit production (García-Mozo et al. 2001). We therefore hypothesized that cork oak acorn production would also be driven by weather factors, specifically those related to water availability and early frosts. However, while the acorn maturation pattern of most oak species is distinct and fixed, in cork oak it is not constant across indi- viduals of a given population (Elena-Rosello et al. 1993; Díaz-Fernández et al. 2004). Consequently, cork oak can have annual acorns (which ripen in the same year as they are pollinated) or biennial acorns (i.e., acorn development extends to 2 years). There is evidence that differences in maturation timing between species may explain their differ- ent annual acorn production patterns (e.g., Koenig et al. 1991; Fearer et al. 2008) and that these differences may be the consequence of the interaction of environmental param- eters with different phenological stages (Abrahamson and Layne 2003), i.e., adverse climatic conditions may act differently on annual than on biennial acorns because when these conditions occur the different types of acorns are at a different phase in the maturation process (Cecich and Sulli- van 1999). Within this conceptual framework, we predict that acorn production in coexisting individuals with a different dominant acorn maturation type should respond differently to climatic factors in a manner similar to that shown by annual and biennial species. As such, disaggre- gating the trees according to their acorn-maturation pattern should provide a more proximal relation to weather factors. Previous studies have also shown more negative temporal autocorrelations in the acorn production of oak species with

annual crops than in those with biennial crops (Koenig et al. 2003). We therefore predict that this pattern, which has been described among species, should also be reproduced in cork oak (within species) in such a way that cork oak trees with a predominant annual acorn pattern would have a more negative temporal autocorrelation than cork oak trees with predominantly biennial acorns.

In summary, the aim of our study was to describe acorn production in cork oak populations and to test: (1) the relative importance of weather factors (precipitation and temperature) in explaining acorn production patterns, and (2) the importance of discriminating the individual acorn maturation pattern for understanding acorn production variability at the population level.

Methods

Study species

Cork oak (*Quercus suber* L.) is a sclerophyllous evergreen oak that occurs in non-carbonated soils in the western part of the Mediterranean Basin (Fig. 1a; for climatic requirements see Montero and Cañellas 2003; Aronson et al. 2009). The main distinctive feature of this species is its thick insulating bark which evolved as a fire protection mechanism (Pausas 1997; Pausas et al. 2009) and which regrows after extraction (i.e., for cork production; Aronson et al. 2009). *Q. suber* produces both annual and biennial acorns; this heterogeneous acorn maturation pattern is an oddity among oaks. Annual acorns mature the same year as the flowers which produced them, while biennial acorns grow and mature in the autumn of the following year (Elena-Rosello et al. 1993; Díaz-Fernández et al. 2004).

Study areas

This study was conducted in the Valencia region (Spain, Eastern Iberian Peninsula) where *Q. suber* is rare and confined to relatively small patches (Fig. 1). Specifically, in this region there are three main *Q. suber* patches which are located, from north to south, near Espadà (Castelló, latitude 39°52′; approx. 10,000 ha), Calderona (València, latitude 39°44′; approx. 1,000 ha), and Pinet (València, latitude 38°59′; approx. 100 ha). We selected five 3 × 3-km areas (hereafter denoted sites) distributed on the three main patches as follows: two sites at Espadà (E1, E2), two at Calderona (C1, C2), and one at Pinet (P1) (Fig. 1b; see Pons and Pausas 2006, 2008 for further details on these sites). Soils in Calderona and Espadà are mainly acidic on sandstones (Bundsanstein, which is a Triassic bedrock) with soil pH ranging from 4.9 to 6.4 (mean 5.7). At Pinet, *Q. suber* occurs on non-carbonated soils on dolomites, with soil pH
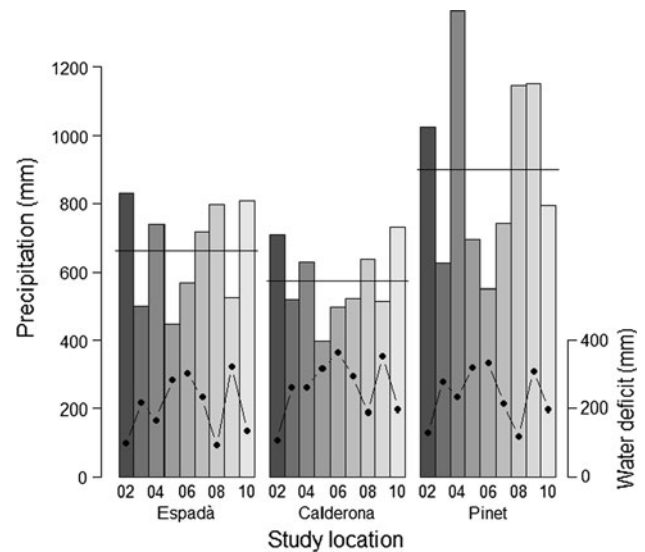
Fig. 2 Precipitation (*bars*) and water deficit (*dots and broken lines*) at the three sampling locations (including 2002, the year previous to the start of the study). Data are for hydrological year (September–August). *Horizontal lines* Mean precipitation value for each site. Monthly climatic variability is shown in Fig. A1 of the ESM

ranging from 5.5 to 7.5 (mean: 6.5; Cretaceous bedrock; see Pausas et al. 2006). The three sites are currently protected either as Natural Parks (Espadà and Calderona) or as a regional plant micro-reserve (Pinet). Cork extraction is still ongoing in Espadà and Calderona. The climate at these three locations is typically Mediterranean, with hot dry summers and mild winters, and an annual rainfall ranging from 500 to 800 mm distributed in two peaks, spring and autumn (Pérez Cueva 1994; Millán et al. 2005). Pinet is warmer and wetter than Calderona, while Espadà shows intermediate conditions [Fig. 2; Fig. A1 in the Electronic Supplementary Material (ESM)]. The years 2002, 2004, 2007, 2008, and 2010 had above-average precipitation. In the case of Pinet, 2009 was wetter than 2010, and this site received nearly double the precipitation registered for the other sites in 3 of the study years (2004, 2008, and 2009) (Fig. 2).

Sampling

We randomly selected 172 cork oak trees ≥20 cm DBH (diameter at breast height) distributed over the five sites. Two observers using binoculars and standing on opposite sides of each tree estimated the acorn production by counting the total number of acorns in the crown. The counting was performed in September–October of each year, i.e., immediately prior to acorn fall (October–November), when acorns are large enough to be easily detected, and over an 8-year period (2003–2010). For each sampled tree we measured the DBH, computed the basal area, and recorded the

Table 1 List of weather parameters considered in this study and their biological relevance

Code	Description	Relevance	References
P	Annual precipitation (mm)	General resource availability	Koenig et al. (1996)
Psp, Psu, Pau, Pwi	Spring, summer, autumn and winter precipitation, respectively (mm)	Seasonal resource availability	Koenig et al. (1996), Pérez-Ramos et al. (2010)
P6	June precipitation (mm)	Female flower maturation	Elena-Rosello et al. (1993)
P9	September precipitation (just before acorn crop) (mm)	Acorn maturation	García-Mozo et al. (2007), Montserrat-Martí et al. (2009)
T4, T5	Mean temperature in April and in May, respectively (°C)	Male flowers	Elena-Rosello et al. (1993), Koenig et al. (1996)
T67	Mean June–July temperature	Female flowers	Elena-Rosello et al. (1993)
WD, DI	Annual water deficit (mm, mainly summer drought) and drought index, respectively	Acorn abortion	Koenig et al. (1996), Espelta et al. (2008), Pérez-Ramos et al. (2010)
FD3b	Number of frost days in the second half of March	Catkin frost	García-Mozo et al. (2001)
FDsp	Spring frost days (March–April)	Catkin frost	García-Mozo et al. (2001)

geographical coordinates (GPS). Because our aim was to understand acorn production variability, both trees with very low acorn production (i.e., <20 acorns) during the study period and those sampled for <5 years were excluded from the analysis. Thus, our final data set consisted of 155 trees distributed over the sites as follows: 25 trees at E1, 34 at E2, 45 at C1, 23 at C2, and 28 at P1.

To test the validity of our acorn production estimations, in 2003 and 2004 we selected 25 additional trees with a range of DBH similar to the studied trees. In each of these trees we first counted acorns using the methods described above and then determined the real acorn production by means of the traditional method, namely, climbing the tree and beating down all of the acorns with a pole. Only mature acorns were considered, and abortions were discarded. The relation between the visual estimation and the real acorn production was highly significant ($F_{1,23} = 731$, $R^2 = 0.97$, $p < 0.0001$; ESM Fig. A2), allowing us to be confident about our methodology.

Weather parameters

Climatic data (Table 1) were obtained from 81 meteorological stations in the region. The number of frost days per month and monthly precipitation were interpolated to the center of each sampled site using the spatial module of Arc-View 3.3 (ArcGIS; ESRI, Redlands, CA), and mean monthly temperature was obtained from the weather stations near each site, after correcting for altitude. The number of frost days was considered for the second 2-week period of March (FD3b), and for the spring total (March and April; FDsp). Precipitation data was computed yearly (P) as hydrological years (from September to August) and for seasons (Psp, Psu, Pau, Pwi). Potential and actual

evapotranspiration (PET and AET, respectively) was computed following Thornthwaite and Mather (1957) from monthly climatic data. For AET, we used a bucket model, with the soil holding capacity inferred from available soil analyses (i.e., textures) in the study area (for Pinet, Pausas et al. 2006; for Espadà, Serrasolses et al. 2009; for Calderona, Rubio et al. 1995). The water deficit (WD) was then computed as PET − AET, and the drought index (DI) as DI = 1 − AET/PET. Mean weather values and water balance variables for each site are shown in ESM Table A1.

Data analysis

Tree production depends not only on weather and masting cycles, but also on tree size (correlation between total acorn production during the whole period and tree basal area: $r = 0.50$, $P < 0.0001$). Thus, the number of acorns/basal area (cm^2) was used for studying the variability of acorn production among years and trees. However, acorn production may also depend on microsite characteristics (such as tree density, soil depth, bedrock type, topography, etc.). Therefore, to study the relation between weather and acorn production, we first standardized the acorn production of each tree and year by subtracting the long-term mean of the tree (over the 8-year study period) and dividing the product by the standard deviation (SD) over all the years (LaMontagne and Boutin 2007).

Acorn production was first analyzed for all trees ($n = 155$). However, the acorn maturation pattern (annual vs. biennial) in *Q. suber* has been shown to vary greatly (Díaz-Fernández et al. 2004), and coexisting trees may have a dominant annual or biennial pattern. Because mast years are defined as years of exceptional seed production, two consecutive masting years are highly unusual

(LaMontagne and Boutin 2009). However, our preliminary analysis showed that: (1) 2008 and 2009 were years with high acorn production, (2) the year 2008 had the lowest WD during the study period (2003–2010; Fig. 2), and (3) there was a negative relation between trees producing acorns in 2008 and those producing acorns in 2009 ($r = -0.41$, $P < 0.0001$). Thus we considered the trees that masted in 2008 as trees with dominant annual acorns and those that masted in 2009 as trees with biennial acorns (hereafter denoted A and B trees, respectively); a third type of trees (C trees) was assigned to the category of trees that did not show a clear difference between these two years (i.e., masting during the 2 years, or either of the 2 years). For each tree, masting was defined as years in which the annual standardized deviate of acorn production was greater than the absolute magnitude of the variation below the mean (LaMontagne and Boutin 2007, 2009). There were no differences in size (basal area) among these groups of trees ($F_{2,152} = 0.58$, $P = 0.56$). Thus, the statistical analysis was performed for all trees, as well as for A and B trees separately.

Temporal variability in acorn production was evaluated using the following parameters (Herrera et al. 1998; Koenig et al. 2003): mean individual synchrony (heareafter Rp; Buonaccorsi et al. 2001) was calculated as the mean of all pairwise Pearson correlations between individual trees; mean individual acorn-production variability (heareafter CVi) was calculated by averaging across individuals the coefficient of variation for acorn production across years for each individual; mean population acorn-production variability (heareafter CVp) was calculated as the coefficient of variation across individuals of the annual means across years for each tree; the mean (across individuals) of the temporal autocorrelation function of acorn production was calculated at 1-year time lags (heareafter ACF1i). Variability and synchrony parameters (CVi, CVp, Rp) were computed, with values of acorn production expressed as number of acorns per square centimeter of basal area, while the temporal autocorrelation was computed from the standardized acorn production values. All parameters were computed for all trees together, and then for each site and for trees with a different acorn production pattern (A and B trees).

To evaluate the role of weather factors on acorn production variability, we tested the relationship between the standardized acorn production of each year [September (x)–December (x)] where x is the year of acorn production) and the relevant weather factors during the 12 months previous to the acorn production [i.e., September ($x - 1$)–August (x); Table 1]. We also considered the same variables for the previous year [i.e., September ($x - 2$)–August ($x - 1$)] as they could be involved in the formation of biennial acorns.

The test was performed using a mixed-effects (LME) model analysis considering trees nested within site as random factors (i.e., repeated measures analysis), and the best model was selected using a stepwise procedure based on the Akaike Information Criteria (AIC); in each step, the significance was evaluated by a likelihood ratio test (with a change of 1 df).

Results

Acorn production variability

The number of acorns produced by each tree in a given year was quite variable, ranging from 0 to more than 20,000 acorns per tree, but it was strongly biased towards few acorns (median 8 acorns per tree and year; median 28 acorns per tree when excluding trees and years with no acorn production; left skewed distribution). In fact, during the 8-year study period, most of the acorns produced were supplied by only a few trees; for example, about 6% of the trees produced somewhat more than 50% of the acorns, and 20% of the trees produced 80% of the acorns (i.e., acorn production followed the Pareto principle or 80–20 rule). This biased distribution is partially due to the biased distribution in tree sizes because when we divided the number of acorns by the tree's basal area, the distribution became less skewed, with 20% of the trees accounting for about 30% of the acorns/cm^2 of basal area.

The mean annual acorn production between 2003 and 2010 at Pinet and Espadà (0.218 and 0.217 acorns/cm^2 of basal area, respectively) was twofold higher than that at Calderona (0.090 acorns/cm^2 of basal area). For the total of all trees, maximum production was achieved in 2008 (mast year), followed by 2003, 2009, and 2010 (Fig. 3 overall). However, this pattern varied among sites: while trees at Espadà (E1, E2) masted in 2008, at Calderona (C1, C2) the maximum production was achieved in 2009 (Fig. 3). The proportion of A and B trees also varied among sites, decreasing from Pinet to Calderona, with Espadà showing intermediate values (Table 2). This result is in agreement with the gradient from optimal conditions at P1 to xeric conditions at C1, i.e., a shorter spring vegetative growth derived from delayed March warming and early (and longer) summer droughts (Fig. 2; ESM Table A1).

Synchrony in acorn production in the *Q. suber* populations studied was very low on all sites (Table 3; Fig. 4) but was greatly enhanced when trees were grouped by acorn production type. CVp also increased when the trees were grouped by acorn production type, while mean CVi did not change (Table 3). ACF1i values were lower in A trees than in B trees (Table 3).

Fig. 3 **a** Standardized acorn production for all trees (*overall*), and for each site (**b**–**f**). Years with an *asterisk* are mast years during which the annual standardized deviation of acorn production was greater than the absolute magnitude of the variation below the mean (Lamontagne and Boutin 2007). Data for individual trees is shown in ESM Fig. A3
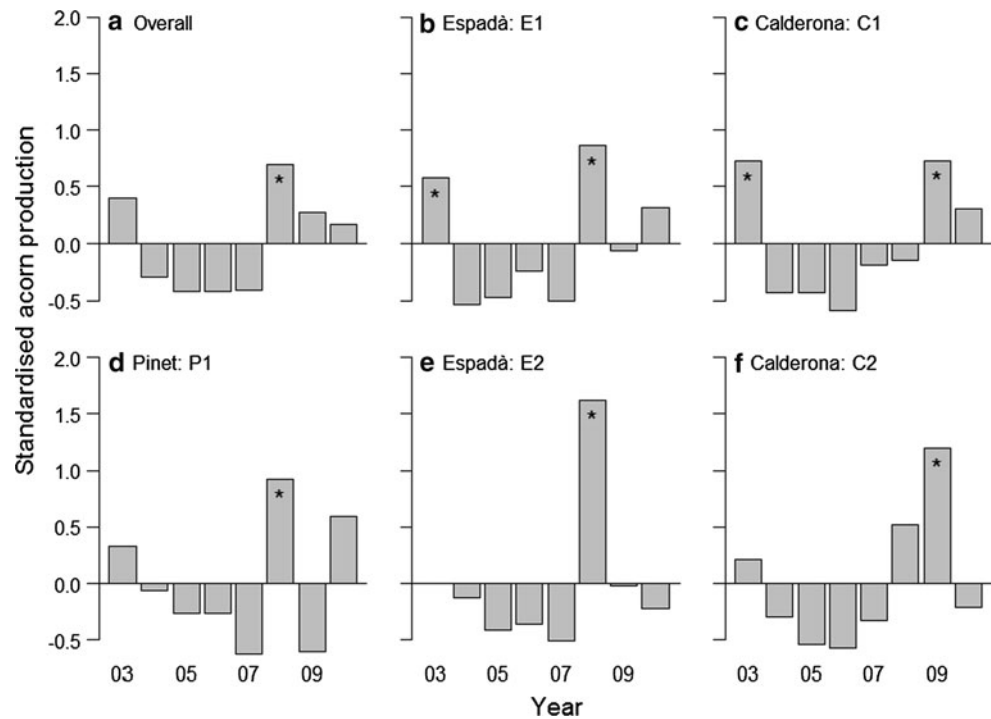
Table 2 Number of trees masting in 2008 (A trees) and in 2009 (B trees) and those with no clear masting pattern (C trees) at the five sites studied

Trees	E1	E2	C1	C2	P1	Total
A trees	11 (44.0)	25 (73.5)	3 (6.7)	6 (26.1)	14 (50.0)	59 (38.1
B trees	3 (12.0)	5 (14.7)	19 (42.2)	12 (52.2)	1 (3.6)	40 (25.8)
C trees	11 (44.0)	4 (11.8)	23 (51.1)	5 (21.7)	13 (46.4)	56 (36.1)
Total	25	34	45	23	28	155
A/B ratio	3.7	5.0	0.2	0.5	14.0	1.5

The proportion of each production group over the total number of trees at each site is given in parenthesis

E1, E2, Espadà site; C1,C2, Calderona; P1, Pinet (see text for details)

Table 3 Variability parameters of acorn production for the different populations studied

Population	n	CVp	CVi	Rp	ACF1i
E1	24	95.5	183.5	0.245	−0.100
E2	33	113.6	183.4	0.484	−0.197
C1	44	106.7	182.1	0.248	−0.061
C2	23	108.0	187.1	0.344	−0.129
P1	28	64.3	143.5	0.333	−0.260
Overall	155	67.9	176.4	0.193	−0.143
A trees	59	139.8	174.7	0.772	−0.256
B trees	40	175.4	186.8	0.730	−0.081
C trees	53	86.0	170.6	0.268	−0.068

CVp Population variability, *CVi* individual variability, *Rp* mean individual synchrony, *ACFi* mean temporal autocorrelation

Weather parameters as determinants of acorn production

Quercus suber acorn production was correlated with weather variables, but the variability explained by these variables was very low (7.6%; Table 4), making the interpretation difficult. The variance remained low even when the regressions were performed separately for each site (not shown). However, when the trees were disaggregated according to their acorn production pattern (A trees, B trees), the total variance explained increased sixfold and the weather variables were easier to interpret (Table 4). In both A and B trees, acorn production was related mainly to precipitation and secondarily to temperature. For A trees, production increased with June precipitation (explained 23.3% of the variation) and April temperatures and decreased with
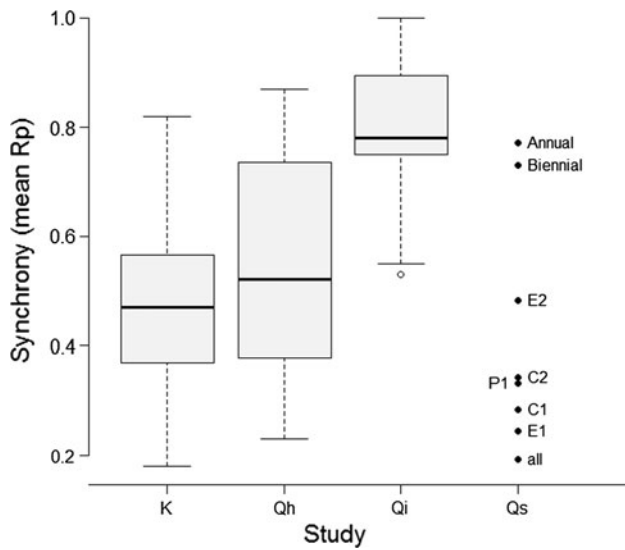
Fig. 4 Synchrony values for different *Quercus* species. *K* North American oaks (Koenig et al. 2003), *Qh*, *Qi Q. humilis* and *Q. ilex*, respectively (Espelta et al. 2008), *Qs* data from the *Q. suber* locations in this study, including the aggregation of trees by annual and biennial acorn production pattern [A (*Annual*) and B (*Biannual*) trees]. In all cases, synchrony is expressed as a mean of the pairwise Pearson correlation between all individuals. Variability in K, Qs, and Qi refers to different sites (for site identification, see Fig. 1)

high June–July temperatures in the previous year, summer WD, and number of frost days in March (Table 4). For B trees, production increased mainly with September precipitation (i.e., during acorn ripening; explained 22.7% of the variation) and number of frost days in March, and decreased with high June–July temperatures in the previous year, April temperatures, and June precipitation (Table 4). For the two models, the explained deviance was >44% for both A trees and B trees (Table 3).

Discussion

Acorn production variability in cork oak was found to be related to water availability in general and to summer drought in particular. This result is in agreement with results obtained on other Mediterranean oaks (García-Mozo et al. 2007; Espelta et al. 2008; Carevic FS et al. 2010; Pérez-Ramos et al. 2010). Our variability values also fell within the range observed for other oaks (Koenig et al. 2003; Espelta et al. 2008), with mean individual (temporal) variability (CVi) higher than population (spatial) variability (CVp). Nevertheless, in *Q. suber*, the effect of climate on acorn production was masked by the coexistence of acorns with different maturation patterns (annual and biennial acorns). When all trees or all the trees from a given geographical location were considered, synchrony in acorn production was very low compared to that in other oaks

Table 4 Summary of the stepwise selection for the regressions of the standardized acorn production against weather variables, for all trees, A trees (presumably annual), and B (presumably biennial) trees

Trees[a]	AIC	LogLik	LR	*p* value	Coefficient
All trees					
Null	3,324.37	−1,658.19	–	–	–
+T67(−1)	3,221.68	−1,605.84	104.70	<0.0001	−0.302
+WD	3,106.94	−1,547.47	116.73	<0.0001	−0.004
+FD3b	3,083.89	−1,534.94	25.06	<0.0001	−0.265
+T4	3,081.35	−1,532.68	4.54	0.0332	0.060
A trees					
Null	1,270.21	−631.11	–	–	–
+P6	978.47	−484.24	293.74	<0.0001	0.007
+T4	892.90	−440.45	87.58	<0.0001	0.316
+T67(-1)	821.99	−403.99	72.91	<0.0001	−0.245
+WD	746.74	−365.37	77.25	<0.0001	−0.007
+FD3b	723.12	−352.56	25.62	<0.0001	−0.338
B trees					
Null	867.70	−429.85	–	–	–
+P9	674.35	−332.17	195.35	<0.0001	0.007
+T67(-1)	562.58	−275.29	113.76	<0.0001	−0.365
+FD3b	512.92	−249.46	51.66	<0.0001	0.731
+T4	501.07	−242.54	13.85	0.0002	−0.145
+P6	494.43	−238.21	8.64	0.0033	−0.005

AIC Akaike Information Criteria, *LogLik* the log-likelihood, *LR* likelihood ratio test with a change of 1 *df*, *p value* *p* value associated for the mixed-effects model, *Coefficient* coefficients of the final model (all coefficients are significant at *p* < 0.05)

The explained deviance of each model is: 7.57% (all trees), 44.14 (A trees), and 44.58 (B trees)

[a] The Null model refers to the model with only random effects, and no fixed effects. For weather parameters, see Table 1

(Table 3; Fig. 4), and all of the regressions tested with weather parameters led to very low explained variance (Table 4). However, both the temporal synchrony in acorn production and the explained variance of the weather regression increased drastically when the trees with annual acorns were disaggregated from those with biennial acorns (A and B trees; Table 4; Fig. 4). In general, the most important factors for acorn production in our oak populations were water-related parameters (for other Mediterranean oaks, see Espelta et al. 2008 and Pérez-Ramos et al. 2010), namely, summer precipitation for annual trees and September precipitation (i.e., when acorns start to grow) for biennial trees. More specifically, trees with annual acorns responded to favorable conditions during leaf renewal and female fertilizations (high June precipitation; low water deficit) and to mild temperatures (low number of frost days in spring; elevated temperatures in April). In contrast, trees with biennial acorns responded positively to water availability at the end of summer and to spring frosts. Indeed,

some variables showed an opposite effect on each group of trees (Table 4), suggesting an interaction effect between the two types of acorns, i.e., conditions that negatively affect annual production could be beneficial for biennial production (and vice versa). This interaction may suggest the existence of a trade-off at branch level that resembles the trade-off between vegetative growth and acorn production described in other oaks (Sánchez-Humanes et al. 2011). For example, late March frost shortens the time window for acorn maturation (García-Mozo et al. 2001) before the summer drought and thus decreases the annual acorn production. However, the incipient acorns may mature the following year, thus increasing biennial acorns. In fact, maximum acorn production would be expected in a year with good conditions for annual acorn production, preceded by a year that was inappropriate for annual production. A detailed monitoring of individual acorns would be needed for a deeper understanding of acorn dynamics and the processes behind acorn production variability in *Q. suber*.

All of the populations studied had trees with annual acorns as well as trees with biennial acorns, although the proportions of each type were different among the different populations. Annual acorn types were more frequent at the E2 and P1 sites than at the other sites. The location of these two sites closer to the Mediterranean Sea and at lower altitudes (ESM Table A1) implies more mesic conditions derived from warmer winters, higher precipitation, more frequent fogs (and thus enhanced summer water availability; Estrela et al. 2008), and shorter summer droughts. Thus, a biennial acorn production seems to be a response to harsher climatic conditions (Elena-Rosello et al. 1993), as in the case of our Calderona site.

Our classification of annual and biennial trees was indirect and made a posteriori because of the difficulties encountered in differentiating annual and biennial acorns in the field. Nevertheless, we have confidence in this classification for several reasons: (1) the explained variance in the regressions with weather variables increased extraordinarily, and this increase cannot be expected by chance alone; (2) it is consistent with the expected differences in temporal autocorrelation in most of the oak species analyzed (Koenig et al. 2003); (3) it is supported by previous (although limited) observations of marked acorns in the study area (on the basis of 27 trees marked in 2003 at the three locations studied, 12 out of 15 trees in Calderona showed an annual/biennial acorn ratio <0.25, while three of 12 trees showed this value in Espadà and Pinet; unpublished data from the authors).

An open question is why trees with annual acorn production coexist with trees with biennial production. The microclimatic conditions of each tree (e.g., soil depth, slope, stoniness) may enhance or smooth stressful conditions and drive variations in acorn maturation. Other conditions, such as age, time since cork harvesting, or the number of previous harvests, may also contribute to shaping individual responses to climatic conditions. The ability to modulate the acorn production pattern of a given year according to the environmental conditions could be regarded as an example of phenotypic plasticity for facing variable and uncertain climatic conditions (Rehfeldt et al. 2001; Nicotra et al. 2010). This ability may not be exclusive to *Q. suber*; for example, *Q. coccifera* also shows a complex and diverse phenological pattern (Bianco and Schirone 1985). To what extent other oaks living under variable and stressful conditions behave similarly remains to be explored.

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Electronic Supplementary Material (ESM)

Table A1. Weather and site variables (mean values) for the five sites studied. Weather information is based on the period 2002-2010 (hydrological years).

|	Location:	Espadà		Calderona		Pinet
	Sites:	E1	E2	C1	C2	P1
Site variables						
Basal area (cm^2/tree)		1017	1671	1439	879	1047
Distance to coast (km)		26.8	18.9	25.8	21.7	12.1
Altitude (m.a.s.l.)		689	550	637	764	599
Slope (%)		18.4	18.9	11.3	10.7	13.7
Climatic variables						
Annual precipitation		652.4	665.2	565.6	580.8	898.9
Spring precipitation		212.2	225.6	194.5	193.2	253.8
Summer precipitation		71.1	52.6	63.1	63.5	59.5
Drought Index		186.2	225.9	266.4	255.2	237.2
September precipitation		95.7	98.0	76.2	78.9	106.8
Frost days in late march		0.1	0.1	0.1	0.0	0.2
Spring frost days		1.7	1.3	2.1	1.9	1.8
Mean April temperature		12.5	13.3	12.6	12.3	13.0
Mean May temperature		16.1	16.9	16.1	15.8	16.4
Mean June-July temperature		22.3	23.0	22.3	21.9	22.4
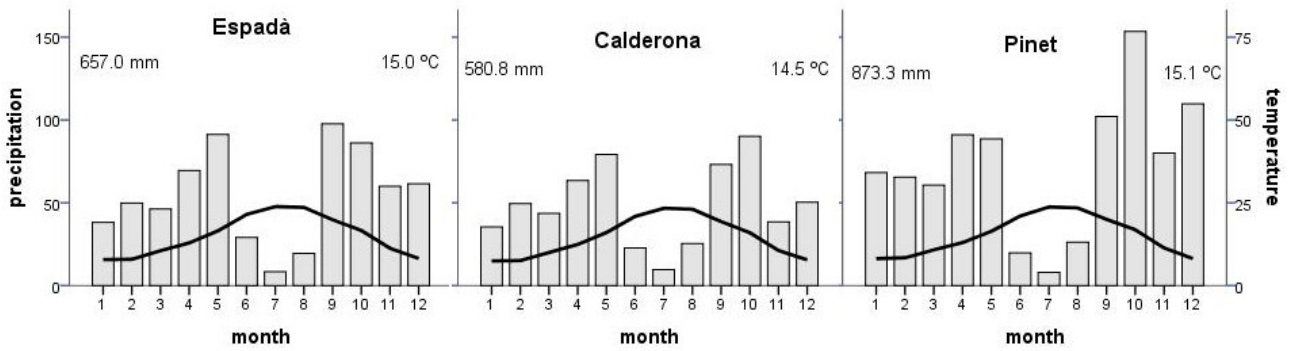
Fig. A1. Climatic diagram for the three areas studied during the study period (2002-2010). Bars and left axis: mean annual precipitation (2001-2010); lines and right axis: mean annual temperature.
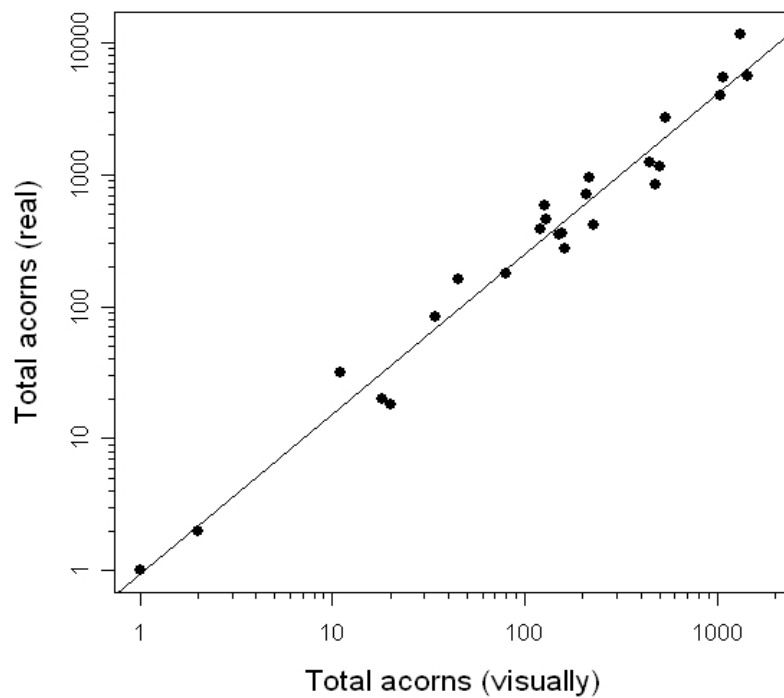

Fig. A2. Relation between the number of acorns estimated visually (by counting acorns with binoculars) and the number of acorns counted by climbing the tree and beating down all the acorns (real). The fitted line represents the following function: $\log_{10}(\text{real } \#\text{acorns} + 1) = -0.02536 + 1.21336 \cdot \log_{10}(\text{visual } \#\text{acorns} + 1)$; n= 25, $F_{1,23}$= 731, R^2= 0.9695, p<0.0001.
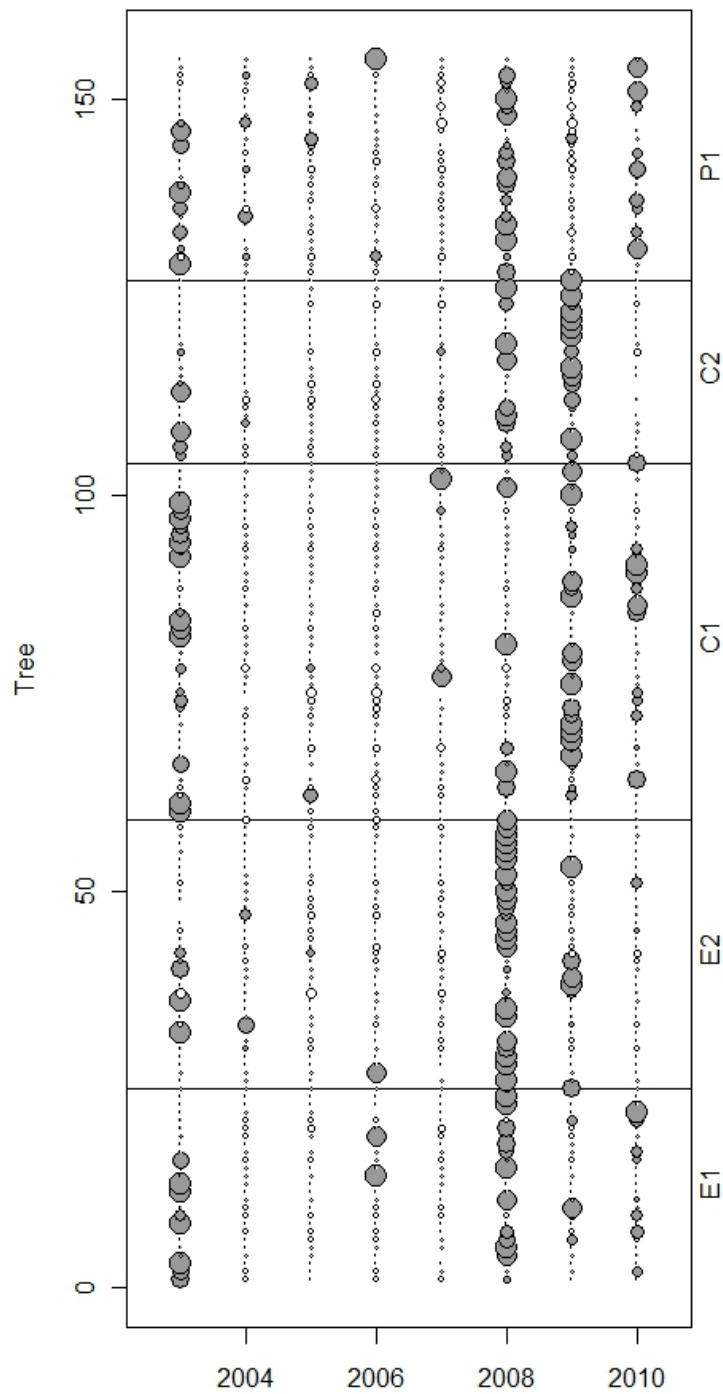
Fig. A3. Standardised acorn production for each of the trees on the five sites (E1, E2, C1, C2, P1) during the study period (2003 to 2010). The size of the symbols is proportional to the absolute value of the standardised acorn production; white and grey colour correspond to negative and positive values, respectively.