*Ecology*, 00(0), 0000, pp. 000–000

# MASTING MEDIATED BY SUMMER DROUGHT REDUCES ACORN PREDATION IN MEDITERRANEAN OAK FORESTS

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*Abstract*. Temporally variable production of seed crops by perennial plants (masting) has been hypothesized to be a valuable mechanism in the reduction of seed predation by satiating and starving seed consumers. To achieve these benefits, coexisting species subjected to the same predator would benefit from a similar pattern of seeding fluctuation over time that could lead to a reduction in predation at the within-species level. We tested for the existence of an environmental factor enforcing synchrony in acorn production in two Mediterranean sympatric oaks (*Quercus ilex* and *Q. humilis*) and the consequences on within-species and between-species acorn predation, by monitoring 15 mixed forests (450 trees) over seven years. Acorn production in *Q. ilex* and *Q. humilis* was highly variable among years, with high population variability (CVp) values. The two species exhibited a very different pattern across years in their initial acorn crop size (sum of aborted, depredated, and sound acorns). Nevertheless, interannual differences in summer water stress modified the likelihood of abortion during acorn ripening and enforced within- and, particularly, between-species synchrony and population variability in acorn production. The increase in CVp from initial to mature acorn crop (after summer) accounted for 33% in *Q. ilex*, 59% in *Q. humilis*, and 60% in the two species together. Mean yearly acorn predispersal predation by invertebrates was considerably higher in *Q. humilis* than in *Q. ilex*. Satiation and starvation of predators was recorded for the two oaks, and this effect was increased by the year-to-year variability in the size of the acorn crop of the two species combined. Moreover, at a longer time scale (over seven years), we observed a significant reduction in the mean proportion of acorns depredated for each oak and the variability in both species' acorn production combined. Therefore, our results demonstrate that similar patterns of seeding fluctuation over time in coexisting species mediated by an environmental cue (summer drought) may contribute to the reduction of the impact of seed predation at a within-species level. Future research should be aimed at addressing whether this process could be a factor assisting in the coexistence of *Q. ilex* and *Q. humilis*.

*Key words:* Curculio *spp.; fruit abortion; fruiting synchrony; Mediterranean mixed-oak forests; oaks; predator satiation;* Quercus humilis; Quercus ilex; *resource matching.*

## Introduction

Synchronous, highly variable production of large seed crops by plant populations (usually termed "masting") has been reported in many taxa. Several studies have stressed the important role of this phenomenon for seedling recruitment (Negi et al. 1996, De Steven and Wright 2002, Henkel et al. 2005), for abundance of seed consumers (Yasaka et al. 2003, Yu et al. 2003), and at higher trophic levels (Liebhold et al. 2000). However, the definition of masting and the causes of this phenomenon have long been controversial (see Herrera 1998, Kelly and Sork 2002). The hypotheses underlying the occurrence of masting were respectively categorized by Norton and Kelly (1988) and Kelly (1994) into two main groups: (1) "resource matching," in which reproductive effort in plants varies in response to fluctuating resources with no need of adaptive value, and (2) "economy of scale," in which an occasional large reproductive event is more efficient than regular smaller ones, with a clear adaptive value.

Among the processes that would benefit from this economy of scale in reproduction, "predator satiation," i.e., escaping seed predation by satiating and starving seed predators through variable seed production (Silvertown 1980), is the one that has received most support (Kelly and Sullivan 1997, Kelly et al. 2000, Kon et al. 2005). The causes and consequences of masting as a reproductive strategy become more tantalizing when the phenomenon is examined at a community level, in which various species differing in functional traits but subjected to the same seed predator may coexist. In particular, the existence of environmental cues synchronizing between-species fruiting and whether these species obtain mutual benefits from this pattern to escape seed predation remains relatively unexplored.

Manuscript received 9 February 2007; revised 19 June 2007; accepted 25 June 2007. Corresponding Editor: W. D. Koenig.

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In spite of the importance of investigating masting throughout community-level tests, there are very few studies conducted with more than one tree species in which processes from seed initiation to predation have been investigated (although, for temperate deciduous forests, see Shibata et al. [1998, 2002]). Studies carried out with North American oaks have shown between-species synchrony, although synchrony was relatively low, probably due to the different number of years (one or two) required by the coexisting species for acorn maturation (Koenig et al. 1999, Liebhold et al. 2004). Concerning masting in Japanese temperate deciduous forests, Shibata et al. (2002) observed in a study of seed production by 16 tree species that there was among-species synchrony in the annual fluctuation of reproduction, even for distant taxonomic groups, and that predator satiation occurred at the population and community levels. Therefore they concluded that predator satiation at the community level could stabilize synchronized annual fluctuation in seed production among species (Shibata et al. 2002). However, these studies failed to explain what environmental cue would trigger synchronous reproduction among the different species involved, nor did they prove that synchrony at the community level influenced predation at the within-species level.

Mixed-oak (*Quercus* spp.) forests offer an interesting opportunity to investigate the causes and the consequences of masting at within- and between-species levels because: (1) oak species show large interannual variability in acorn production, (2) oaks have contrasting functional attributes (e.g., deciduous and evergreens), potentially with a different response to environmental cues triggering seeding, and (3) acorns of all these species are subjected to predation by the same insects (e.g., the *Curculio* spp. beetles and the *Cydia* sp. moth) and vertebrates (e.g., *Garrulus glandarius*).

The main aim of our study is to find the environmental cue triggering within- and between-species temporal variability in fruit production and the consequences on within-species and between-species predispersal seed predation for two sympatric Mediterranean oaks: the evergreen *Q. ilex* and the winter-deciduous *Q. humilis*. Most studies have focused on the effects of temperature in triggering flower buds that may induce synchronized reproduction (see, among others, Norton and Kelly 1988, Yasuda et al. 1999, Schauber et al. 2002). In contrast, this study investigates the role of water stress, under a Mediterranean-type climate, in controlling the likelihood of abortion during acorn ripening that alters synchrony in reproduction. Therefore, our first hypothesis is that interannual differences in summer water stress will be the main cause determining within- and, particularly, between-species synchrony in acorn production, notwithstanding possible differences in the initial intensity of flowering in the two oaks. Moreover, as suggested by Kelly and Sork (2002) for less-productive sites, we predict that population variability in acorn production will be higher in the areas where supra-annual differences in summer drought may be expected to have a larger impact (e.g., sites with lower water availability). The second hypothesis addresses the extent to which variability in acorn production, considering the yearly acorn production of both oaks together, can influence predispersal seed predation at the within-species level. As acorns of *Q. ilex* and *Q. humilis* are depredated by the same insects, we hypothesize that predation at the within-species level will decrease when variability in acorn production of the two species combined increases. To test these two hypotheses we have monitored the patterns of individual tree acorn production and predispersal acorn predation in 15 mixed *Q. ilex* and *Q. humilis* forests (a total of 450 trees) in a protected natural area near Barcelona, Catalonia, northeastern Spain, over seven years (1998–2004).

## MATERIALS AND METHODS

### *Species and study site*

The evergreen *Q. ilex* and the winter-deciduous *Q. humilis* are two Mediterranean oaks that form extensive monospecific and mixed forests on the western rim of the Mediterranean Basin (de Bolós and Vigo 1990). The two species differ in their leaf habit but they share other similar life-history traits, such as maturation of acorns in a year, resprouting ability after disturbances (Bonfil et al. 2004), and the regeneration niche (Espelta et al. 2005). This study was conducted in Collserola Natural Park (Barcelona, Spain), a coastal massif with a rough relief conformed by narrow valleys with steep slopes facing contrasting aspects. Climate is typically Mediterranean, with 620 mm of mean annual precipitation and mean monthly temperatures with a maximum of 23.2°C in August and a minimum of 7.8°C in January. Summer is the warmest and driest season with high variability. Soils are predominantly developed above lithological strata of shales and granite. The park covers a total area of 85 $km^2$, of which *Quercus ilex* is present in 94.7% of the forested area and *Q. humilis* in 75.4%.

### *Sampling design of acorn production*

In 1998 we established 15 sampling sites in mixed *Q. ilex* and *Q. humilis* forests in Collserola Natural Park. The sampling sites were distributed to cover as much as possible different topographic conditions (i.e., altitude, slope, aspect) in which the two species were present. Distance between sampling sites was $4.7 \pm 2.4$ km (mean ± SE). Species composition and structural characteristics of each sampling site were determined in a 10 m radius plot, where we recorded diameter at breast height (dbh) of all *Q. ilex* and *Q. humilis* trees with dbh $> 5$ cm and density and basal area of all tree species per plot.

For each plot we also determined the annual water deficit (WD) as: $\text{WD} = \text{PCP} - \text{PET}$, where PCP is the precipitation value and PET is the potential evapotranspiration. Water deficit per plot was obtained by positioning the 15 plots in the $180 \times 180$ m resolution

Digital Climatic Atlas of Catalonia (Pons 1996, Ninyerola et al. 2000). Calculation of PET in this atlas is based on solar radiation and continentality (Ninyerola et al. 2000). Due to the location of our study plots in sites that varied in slope and faced contrasting aspects, WD values ranged from −302 to −7 mm (largest and smallest water deficit, respectively). Suitability of this index to estimate differences in water deficit locally has been satisfactorily confirmed by previous studies (Arnan et al. 2006). Species composition, main topographic and structural characteristics, and annual water deficit of the sampled plots are summarized in Appendix A. Density of *Q. ilex* and *Q. humilis* trees did not vary with the water deficit of the plot, whereas for the two species, mean dbh and basal area decreased with water deficit ($R^2 = 0.48$, $P < 0.01$ and $R^2 = 0.33$, $P = 0.03$ for *Q. ilex*; $R^2 = 0.31$, $P = 0.03$ and $R^2 = 0.41$, $P = 0.01$ for *Q. humilis*, for dbh and basal area, respectively; $N = 15$ in all cases).

To monitor acorn production we selected 15 trees per species at each sampling site (450 trees in total, 225 per species). Trees were randomly selected of those with most of their crowns exposed to full sun and with similar dbh. Trees were preferentially selected inside the plot where specific composition and forest structure had been determined, except when the low density made it necessary to select some individuals in the surrounding area. Mean dbh of the selected trees did not significantly differ between the two species (paired *t* test, $t = 0.46$, $P = 0.65$, $\text{df} = 14$; $\text{dbh} = 12.5 \pm 0.7$ and $12.4 \pm 1.0$ cm for *Q. ilex* and *Q. humilis*, respectively).

At the beginning of the study (i.e., 1998) trees were tagged and four branches of similar size (~2–3 cm diameter) were randomly chosen in different parts of the canopy of each selected tree and marked with a plastic tag. From 1998 to 2004 we counted acorn production on these branches at the peak of acorn crop in the area (usually in early to mid-September). If a branch was lost, we tagged and counted acorns on a neighboring branch in the next census. We selected this sampling protocol (i.e., counting acorns on branches) rather than the use of traps or the visual scan of the crown (see Koenig et al. 1994) because of the intermingling of branches of trees of the two species in the same plot and the similar shape and color of *Q. ilex* and *Q. humilis* acorns. Censuses were conducted when acorns were sufficiently developed to be classified into one of three categories (see also Sork et al. 1993, Shibata et al. 2002): (1) aborted (e.g., maldeveloped or some unidentifiable source of mortality), (2) insect depredated (e.g., having a gnaw mark or hole caused by insect predation), or (3) sound (e.g., attaining mature seed size). Most initially insect-depredated acorns are totally consumed, and predispersal predation by insects is well recognized as being a major source of acorn losses in oak woodlands (Bonal et al. 2007). However, not all of them are destroyed, and some can germinate if damage to the embryo is not total. Sampling was done before acorns were ripe enough to fall or to be harvested in appreciable number by birds (see Abrahamson and Layne 2002). Inspection was carried out after gently bending the selected branch with a pole or climbing on the focal tree or on the nearest neighbor.

Data from acorn censuses were used to calculate two variables: initial acorn production and mature acorn production per tree. Initial acorn production was the sum of the number of immature, insect-infested and sound acorns and could be considered a rough estimate of pollinated female flowers that potentially would produce acorns (flowering intensity sensu Yasaka et al. [2003]). Mature acorn production was the sum of the number of sound and insect-depredated acorns. Initial and mature acorn production per tree were estimated as the mean number of these acorns on the four sampled branches multiplied by the total number of branches per tree. The total number of branches was estimated indirectly from the crown projection of each tree. Thus, in 1998, we selected a sample of 33–38 individuals of each species within the range of tree sizes used in the study, and we counted the number of branches and measured the crown projection of each of them. Then we constructed regressions between these variables for each species (*Q. ilex*, $R^2 = 0.6$, $P < 0.001$, number of branches $= 24.1 + 6.4 \times$ crown projection; *Q. cerrioides*, $R^2 = 0.6$, $P < 0.001$, number of branches $= 10.8 + 3.9 \times$ crown projection). The mean values of initial and mature acorn crop and proportion of acorns depredated in *Q. ilex* and *Q. humilis* trees are summarized in Appendix B.

### *Data analysis*

For each experimental site and species we calculated the percentage of flowering trees as those that produced acorns at least one out of the seven sampling years, irrespective of whether those acorns attained maturity or not. Similarly, fruiting trees were those that produced mature acorns at least one out of the seven sampled years.

Annual variability in initial and mature acorn production was examined both within species and for the two species together using the mean temporal variation of individual trees (CVi, calculated by averaging across individuals the coefficient of variation of seed production across years for each individual) and the population-level coefficient of variation (CVp, calculated as the ratio of the standard deviation to the mean of yearly average acorn production among individuals for each sampling area). Synchrony in the pattern of initial and mature acorn production within and between species was determined by calculating the Pearson's coefficient of correlation (*r*) of non-log-transformed data of all possible pairs of trees in the stand and then calculating the mean of those correlation coefficients. The values of CVi, *r*, and CVp per plot are listed in Appendix C. For the calculation of CVi, Cvp, and *r* we excluded those trees that never flowered (for initial acorn crop) or that never fruited (for mature acorn crop) during the seven-year study (see Koenig et al. 2003). None of the abovementioned variables departed significantly from normality according to the Shapiro-Wilk normality test, except the percentage of flowering and fruiting trees.

*Within- and between-species annual variability in acorn production.*—To assess the importance of supra-annual differences in summer drought for acorn production and synchrony in acorn production we conducted three different analyses.

First, for each species, we evaluated to what extent the final mature acorn crop size was determined by summer drought by conducting a regression analysis using a yearly summer drought index as the independent variable and the mean yearly percentage of mature acorns of the initial acorns produced per tree in the whole study area as the dependent variable. The summer drought index was calculated similar to Sork et al. (1993) as: summer drought = (mean daily temperatures from June to August) – [0.33 × (mean daily rainfall from June to August)]. Temperature and precipitation records during summer from 1998 to 2004 were obtained from a meteorological observatory (Observatori Fabra) located in the Collserola Massif (see Appendix D).

Second, for each species and also for the two species combined, we also examined whether acorn development during summer influenced variability and synchrony in acorn production by comparing the CVi, *r*, and CVp of the initial acorn crop with the CVi, *r*, and CVp of the mature acorn crop by means of Student's paired *t* tests. If the CVp and *r* of the mature acorn production were larger than those of the initial acorn production, this would indicate that abortion during acorn-ripening in summer was an important factor in the increase of variability and synchrony in acorn production both at the within- and between-species levels. Contribution of *r* and CVi to the variation in CVp of initial and mature acorn crops within species and for both species together was assessed by means of a stepwise multiple regression (Herrera 1998, Koenig et al. 2003).

Third, to examine the impact of local environmental conditions of water availability and forest structure on the size and temporal variability of acorn crop size, we conducted a forward stepwise regression for each species and the two species combined. In these analyses, mean yearly initial and mature acorn production, CVi, Cvp, and *r* were the dependent variables, and WD and the specific basal area of the plot were the independent variables. We included basal area in the analysis to control for the effects of forest structure in acorn production.

*Effects of within- and between-species variability for acorn production in predispersal acorn predation.*—First, we tested for differences between *Q. ilex* and *Q. humilis* in mean yearly acorn predation per plot and on a year-to-year basis by means of Student's paired *t* tests.

In the two species, potential effects of masting in the reduction of seed predation by satiation and starvation of seed predators were analyzed by the standard methods used in masting studies (see Kelly and Sullivan 1997, Shibata et al. 1998, Satake et al. 2004). To examine whether predation satiation occurred in years with high acorn production, we analyzed the yearly proportion of seeds suffering insect predation as a function of mature acorn crop size produced annually per plot. To assess a possible starvation of predators by annual fluctuation of seed production, we analyzed the yearly percentage of seeds suffering insect predation as a function of the ratio of mature acorn crop size in year $t$ to that in year $t-1$ per plot. When acorn crop size of year $t-1$ was zero, we added a small constant value (one) to avoid undefined ratios (see Kelly and Sullivan 1997). These analyses were conducted considering mature acorn crop both within species and with the two species combined, to test for the effects of the simultaneous presence of crops of two species subjected to common predators (see Shibata et al. 2002). In all the abovementioned analyses, plot values were calculated as the sum of the acorn crop of the sampled trees. Finally, as proposed by Satake et al. (2004), we also tested the ultimate influence of variability in fruiting on overall fruit survival by examining the relationship between the mean proportion of acorns of *Q. ilex* and *Q. humilis* depredated per tree throughout the seven-year study as a function of the temporal variability in mature acorn production (CVp) within species and for the two species combined per plot.

All the abovementioned analyses were conducted by means of generalized linear models (GLM) with a binomial error and a logit link function (Crawley 2002). Instead of using the percentage of acorns depredated, which lacks information on the sample size from which the proportion is estimated, this procedure uses the number of acorns depredated as the response variable and the number of non-depredated ones as the binomial denominator. In all our GLM we detected signs of overdispersion, which could affect the estimates of the standard errors of the parameters. Following Crawley (2002) we tackled this problem in two ways. First, we used a quasi-binomial approach, thereby directly estimating the dispersion parameters from the data set. Second, in the satiation and starvation analyses we used generalized linear mixed models in which "plot" was incorporated as a random factor so as to check for variation in responses between plots. Both approaches yielded similar results in terms of the significance of the predictor and here we present only the results obtained with the simpler quasi-binomial approach. The significance of the predictors was assessed by means of log-likelihood ratio tests. Percentage of variance explained by significant models was calculated as the ratio (null deviance – residual deviance)/null deviance. All analyses were conducted with the R statistical package (R Development Core Team 2006).

## RESULTS

Both *Q. ilex* and *Q. humilis* showed strong among-year variation in initial and mature acorn production (Fig. 1). The two species experienced a failed crop in

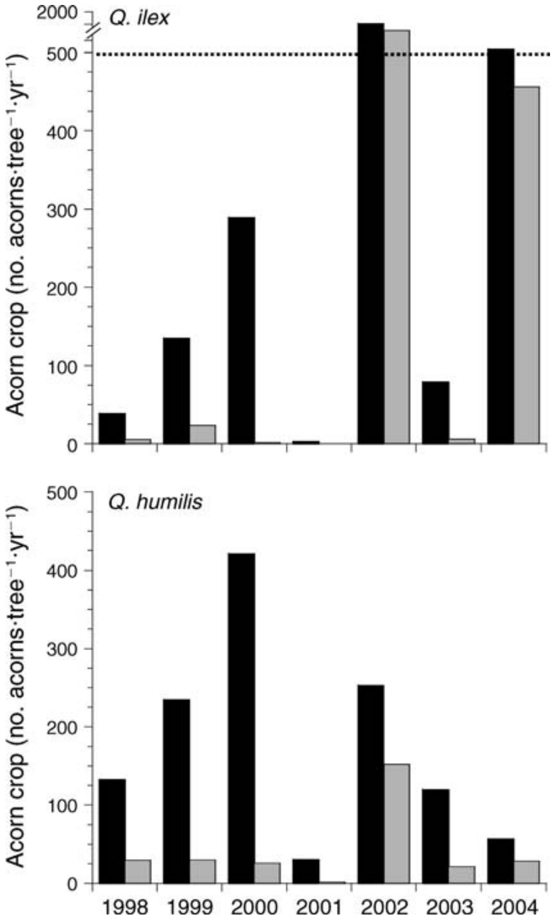

FIG. 1. Mean yearly initial acorn crop size (solid black bars) and mature acorn crop size (gray bars) of *Quercus ilex* and *Q. humilis* trees in the whole study area from 1998 to 2004. The study was conducted in Collserola Natural Park, Barcelona, Spain. Note the broken *y*-axis scale for *Q. ilex*.

2001 and a high production of acorns in 2002, but while *Q. humilis* had experienced a previous large crop year in 2000, the other maximum crop size for *Q. ilex* was attained in 2004.

Considering the general mean yearly values of acorn production of the two species in the whole study area, *Q. ilex* and *Q. humilis* exhibited different patterns in the year-to-year variation in initial acorn crop size ($r$, $N = 7$, $z = 0.48$, $P = 0.63$). Mature acorn crop was correlated between species ($r$, $N = 7$, $z = 3.58$, $P < 0.001$), although this can be considered an artifact caused by the exceptional reproductive event in 2002. Removing this 2002 odd scatterplot from the analysis, there was no significant correlation between the two species in mature acorn crop ($r$, $N = 6$, $z = 0.48$, $P = 0.63$).

### *Within- and between-species annual variability in acorn production*

In the two oaks, among-years variation in mature acorn crop size paralleled that of initial acorn production, mostly in years when initial acorn production was high but less so in years of medium or low production (Fig. 1). For the two species the extent of summer drought appeared as a major factor in the determination of acorn ripening success: the yearly percentage of initial acorns that matured decreased with increasing summer drought (Fig. 2).

The two species did not differ in the percentage of flowering trees (those producing initial acorns) per plot (Table 1), indicating that, in spite of the higher density of *Q. ilex* compared to *Q. humilis* (Appendix A), a similar percentage of trees of each species flowered in each plot (Table 2). However, *Q. humilis* showed a lower percentage of fruiting trees (those producing mature acorns) than *Q. ilex* (Table 1; see mean values in Table 2), indicating that abortion of the whole acorn crop per tree was much higher in the former species. Mean initial and mature acorn production per tree and per year differed between *Q. ilex* and *Q. humilis* (Table 1), with higher values in *Q. ilex* (Table 2). However, this result

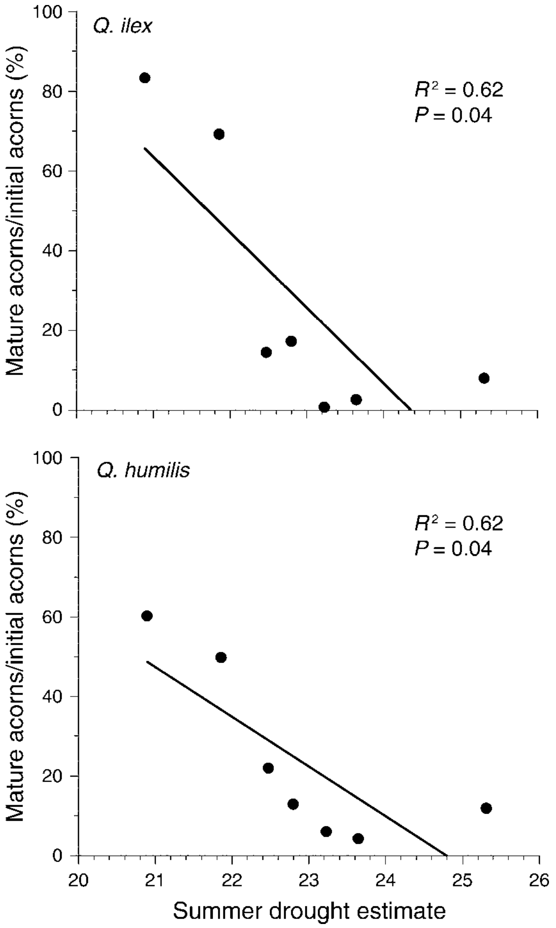

FIG. 2. Relationship between summer drought (estimated as: summer drought = (mean daily temperatures from June to August) − [0.33 × (mean daily rainfall from June to August)] and the mean yearly percentage of mature acorns out of the initial acorns produced per tree in the whole study area.

TABLE 1. Comparison between *Quercus ilex* and *Q. humilis* for several reproductive characteristics studied in Collserola Natural Park, Barcelona, Spain.

| Comparison between species | Initial acorns: Test statistic | Initial acorns: $P$ | Mature acorns: Test statistic | Mature acorns: $P$ |
|---|---|---|---|---|
| Percentage of trees | 0.71 | 0.48 | 3.18 | 0.002 |
| No. acorns·tree$^{-1}$·yr$^{-1}$ | 4.13 | <0.001 | 4.23 | 0.008 |
| No. acorns·tree$^{-1}$·yr$^{-1}$ – (2002, 2004) | 2.03 | 0.06 | 2.27 | 0.04 |
| CVi | 4.35 | <0.001 | 1.04 | 0.32 |
| CVp | 4.59 | <0.001 | 4.10 | 0.002 |
| Synchrony, $r$ | 7.99 | <0.001 | 3.69 | 0.002 |

*Notes:* The percentage of flowering trees (trees producing an initial acorn crop) and fruiting trees (trees producing a mature acorn crop) was compared using the Wilcoxon signed-ranks test. No. acorns·tree$^{-1}$·yr$^{-1}$ – (2002, 2004) represents the mean yearly acorn crop size with data from 2002 and 2004 removed. CVi and CVp are the coefficient of variation of seed production across years for each individual and at the population level, respectively; $r$ is the Pearson's coefficient of correlation between initial and mature acorn production. $N = 15$ plots.

TABLE 3. Comparison between initial and mature acorn production within *Quercus ilex* and *Q. humilis* and for the two oaks combined, based on the coefficient of variation of seed production across years for each individual (CVi) and at the population level (CVp) and on the Pearson's coefficient of correlation ($r$).

| Species and comparison | $t$ | $P$ |
|---|---|---|
| *Q. ilex* | | |
| CVi | 5.85 | <0.001 |
| CVp | 6.63 | <0.001 |
| Synchrony, $r$ | 5.64 | <0.001 |
| *Q. humilis* | | <0.001 |
| CVi | 7.07 | <0.001 |
| CVp | 6.28 | <0.001 |
| Synchrony, $r$ | 4.56 | <0.001 |
| *Q. ilex* + *Q. humilis* | | <0.001 |
| CVi | 9.74 | <0.001 |
| CVp | 9.83 | <0.001 |
| Synchrony, $r$ | 10.87 | <0.001 |

*Note:* The comparison was carried out by means of paired Student's $t$ tests.

was extremely conditioned by the outstanding acorn crops in this species in 2002 and to a lesser extent in 2004 (Fig. 1). If these two years were removed from the analysis, mean initial crop was similar between the two oaks and mature acorn crop size was higher in *Q. humilis* than in *Q. ilex* (Table 1; see mean values in Table 2).

The comparison of mean individual variability (CVi), synchrony ($r$), and population variability (CVp) in initial and mature acorn production between species revealed that *Q. ilex* showed higher $r$ and CVp than *Q. humilis* both in initial and mature acorn crop size (Table 1; see mean values in Table 2). Mean individual variability was larger in *Q. ilex* than *Q. humilis* for initial but not for mature acorn crop (Table 1). For the two species, CVp in initial and mature acorn crop size depended on $r$ (stepwise multiple regression; *Q. ilex*, $R^2 = 0.55$, $P < 0.01$ and $R^2 = 0.74$, $P < 0.01$; *Q. humilis*, $R^2 = 0.42$, $P < 0.01$ and $R^2 = 0.50$, $P < 0.01$).

Variability in acorn production increased significantly from initial to mature acorn crops both within species and when the two species were considered together (Table 3; see mean values in Table 2). The increase in CVp from initial to mature acorn crop accounted for 33% in *Q. ilex*, 59% for *Q. humilis*, and 60% for the two species together. In the light of the changes of CVi and $r$ from the initial to the mature acorn crop (Table 4) and the potential influence of both CVi and $r$ on CVp, the increase in the population variability of mature crop seemed to be closely fitted to an increase in mean individual variability (*Q. ilex*, 17%; *Q. humilis*, 33%; both species together, 12%), as well as to an increase in synchrony among individuals within species (*Q. ilex*, 23%; *Q. humilis*, 93%) and more strikingly between species (342%).

Overall, these results suggest that environmental factors controlling the process from fertilized flowers to mature acorns have a preeminent role in increasing

TABLE 2. Variables used to describe the variability in initial and mature acorn production for *Quercus ilex*, *Q. humilis*, and for the two oaks together (*Q. ilex* + *Q. humilis*).

| Species | Percentage of trees | No. acorns·tree$^{-1}$·yr$^{-1}$ | No. acorns·tree$^{-1}$·yr$^{-1}$ – (2002, 2004) | CVi | CVp | Synchrony, $r$ |
|---|---|---|---|---|---|---|
| Initial acorn crop | | | | | | |
| *Q. ilex* | 91 ± 3 | 407 ± 76 | 110 ± 25 | 1.90 ± 0.06 | 1.51 ± 0.11 | 0.64 ± 0.04 |
| *Q. humilis* | 88 ± 4 | 174 ± 32 | 182 ± 35 | 1.61 ± 0.04 | 0.97 ± 0.07 | 0.29 ± 0.04 |
| *Q. ilex* + *Q. humilis* | | | | 1.75 ± 0.04 | 1.19 ± 0.09 | 0.14 ± 0.02 |
| Mature acorn crop | | | | | | |
| *Q. ilex* | 86 ± 3 | 266 ± 59 | 8 ± 3 | 2.22 ± 0.05 | 2.01 ± 0.08 | 0.79 ± 0.04 |
| *Q. humilis* | 68 ± 4 | 41 ± 8 | 22 ± 8 | 2.14 ± 0.06 | 1.54 ± 0.10 | 0.56 ± 0.06 |
| *Q. ilex* + *Q. humilis* | | | | 2.18 ±0.03 | 1.90 ± 0.07 | 0.62 ± 0.05 |

*Notes:* "Percentage of trees" refers to the percentage of trees that produced initial acorns and the percentage of trees that produced mature acorns. No. acorns·tree$^{-1}$·yr$^{-1}$ – (2002, 2004) is the mean yearly acorn crop size with data from 2002 and 2004 removed. CVi and CVp are the coefficient of variation of seed production across years for each individual and at the population level, respectively; $r$ is the Pearson coefficient of correlation between initial and mature acorn production. $N = 15$ plots. Data are means ± SE.

TABLE 4. Effect of current-year mature acorn crop per plot on the percentage of acorns depredated in *Quercus ilex* and *Q. humilis*.

| Model components, by species | Estimate | SE | *t* | df | *P* | Variance explained (%) | Estimated acorns depredated for different *x* values (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | $x = 10$ | $x = 100$ | $x = 1000$ |
| *Q. ilex* | | | | | | | | | |
| Model 1 | | | | | 0.003 | 14.2 | 42 | 35 | 29 |
| Intercept | 1.00 | 0.96 | 1.04 | 52 | 0.301 | | | | |
| log(*Q. ilex*) | −0.31 | 0.10 | −3.07 | 51 | 0.003 | | | | |
| Model 2 | | | | | 0.001 | 16.7 | 41 | 33 | 26 |
| Intercept | 1.44 | 1.01 | 1.43 | 52 | 0.157 | | | | |
| log(*Q. ilex* + *Q. humilis*) | −0.35 | 0.10 | −3.37 | 51 | 0.001 | | | | |
| *Q. humilis* | | | | | | | | | |
| Model 1 | | | | | 0.003 | 9.4 | 80 | 75 | 70 |
| Intercept | 1.66 | 0.67 | 2.47 | 80 | 0.016 | | | | |
| log(*Q. humilis*) | −0.27 | 0.09 | −2.94 | 79 | 0.004 | | | | |
| Model 2 | | | | | 0.003 | 9.2 | 71 | 68 | 65 |
| Intercept | 1.06 | 0.47 | 2.25 | 80 | 0.028 | | | | |
| log(*Q. ilex* + *Q. humilis*) | −0.16 | 0.05 | −2.93 | 79 | 0.005 | | | | |

*Notes:* The analyses were conducted by means of generalized linear models with a logit link function and a quasi-binomial approach. See *Materials and methods* for the calculation of the model significance (*P* value for model) and percentage of variance explained. Model 1 is the within-species current acorn crop; model 2 is the two species' current acorn crops combined. To better illustrate the values predicted by the models, the estimated percentage of acorns depredated for different current acorn crop values (*x*, the number of acorns per plot) is presented.

synchrony and mean individual variability and thus population variability in acorn production within species and for the two oaks together. From a within-species perspective this means that some *Q. ilex* or *Q. humilis* trees can produce initial acorns (flowers fertilized) in poor or even nonproductive years for the rest of conspecific trees, but abortion of acorns in summer will increase mean individual variability (CVi) and synchrony (*r*): namely, it will lead to more individuals that have a similar pattern concerning high and low years of acorn production. From a between-species perspective, we can conclude that *Q. ilex* and *Q. humilis* flowering may be related to somewhat different environmental cues, as may be expected from their different leaf habit (evergreen vs. deciduous), but that acorn abortion during summer increases between-species synchrony in the final mature acorn crop size.

Differences in acorn production among sites were determined mainly by different local environmental conditions in the two species. Initial and mature acorn production in *Q. ilex* increased with the basal area of this species in the stand (stepwise multiple regression; $R^2 = 0.30$, $P = 0.04$ and $R^2 = 0.28$, $P = 0.04$, respectively), while for *Q. humilis* mean acorn crop sizes were much more dependent upon water availability, decreasing with water deficit (stepwise multiple regression; $R^2 = 0.35$, $P = 0.02$ and $R^2 = 0.28$, $P = 0.04$, respectively). Concerning variability in acorn production, no effects of local conditions were detected for *Q. ilex* in CVi, *r*, or Cvp, while for *Q. humilis* synchrony in mature acorn production was higher in the areas with higher water deficit (Fig. 3B), and this resulted in a marginally significantly higher CVp in these sites ($R^2 = 0.24$, $P = 0.06$).

Therefore, for *Q. humilis* different situations can be identified along the water deficit gradient, i.e., more xeric areas have lower acorn production but higher synchrony among individuals, whereas in more mesic areas acorn production is higher but synchrony is lower than in xeric sites. When variability in acorn production was analyzed for the two species together, between-species synchrony in initial acorn production was low and similar throughout the whole water deficit gradient, while between-species synchrony in mature acorn production decreased from the xeric to the mesic end of the water availability gradient (Fig. 3C).

### *Effects of within- and between-species variability in acorn production on predispersal acorn predation*

Mean yearly acorn predation per plot was considerably higher in *Q. humilis* than in *Q. ilex* (paired *t* test, $N = 15$, $t = 7.73$, $P < 0.001$; *Q. humilis*, 49% ± 12%; *Q. ilex*, 19% ± 15% [mean ± SE). On a yearly basis, acorn predation was higher in *Q. humilis* than in *Q. ilex* in the four years (1999, 2000, 2002, and 2004) in which acorn production of the two species in a sufficient number of plots allowed this comparison (Fig. 4). For both species, the percentage of seeds suffering insect predation in the mature acorn crop produced annually showed a significant negative trend, either when related to within-species acorn crop size or when considering the two species acorn crop sizes together. This indicated the existence of a satiation effect of predators by large crop sizes (Table 4). For the two oaks, the inclusion in the model of acorn crop size of the two species combined reduced within-species percentage of acorns depredated, suggesting that predator satiation at a within-species level benefited from the simultaneous presence of *Q. humilis* and *Q. ilex* acorns.

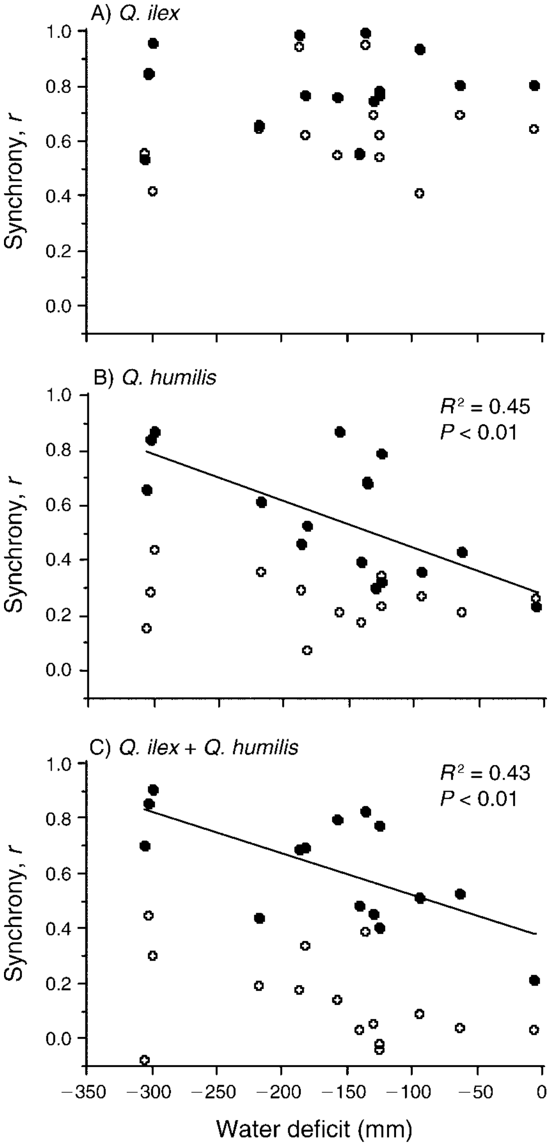

FIG. 3. Relationship between water deficit at the plot level and the synchrony ($r$) in initial acorn production (solid symbols) and mature acorn production (open symbols) within species (*Quercus ilex* and *Q. humilis*) and between species. Synchrony is calculated as the Pearson's coefficient of correlation ($r$). Each point represents a different plot; $N = 15$ plots.

A similar effect was observed when testing for the potential starvation effect of fluctuating acorn production among years (Table 5). Starvation was observed for both *Q. humilis* and *Q. ilex* when considering within-species acorn crop size, but inclusion in the model of the sum of acorn production by the two oaks in the previous year increased the within-species starvation effect. Although the simultaneous presence of *Q. humilis* and *Q. ilex* acorns increased both satiation and starvation effects for the two oaks, the estimated percentage of acorns depredated in *Q. humilis* was always higher than that in *Q. ilex*, a result that agrees with the higher levels of predation of *Q. humilis* acorns observed for most years (Fig. 4).

Mean percentage of acorns depredated during the total seven-year period decreased with increasing within-species CVp in *Q. ilex* but not in *Q. humilis* (model 1 in Table 6). Nevertheless, for the two species, a larger decrease in acorn predation was observed with increasing CVp of the two species considered together (model 2 in Table 6). This indicates that the greater the interannual variation in acorn production at the two-species level (*Q. ilex* + *Q. humilis* CVp), the lower the overall percentage of total seeds depredated for each species during the period analyzed (seven years).

## DISCUSSION

Overall, *Q. ilex* and *Q. humilis* trees produced very poor mean yearly acorn crops per tree, in comparison to more seed-productive oak forests ("dehesas") in the southwestern Iberian Peninsula (Pulido and Díaz 2004) and to Californian oak woodlands (Koenig et al. 1994). Although sampled trees were mature enough to produce acorns, reproduction may be constrained, due to the consequences of the higher density of oaks and other tree species (e.g., *Pinus halepensis*) in the stands. This high density could be responsible for a lower tree size, competition for resources, shadowing, and interference among tree canopies. However, this is the common structure of most oak woodlands in the northern rim of the Mediterranean Basin (Terradas 1999). Natural

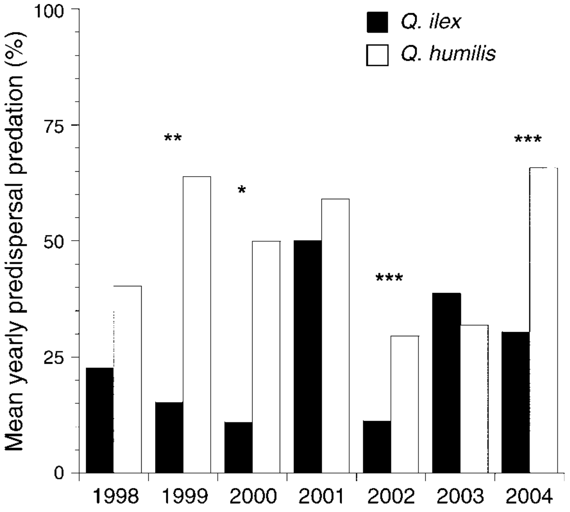

FIG. 4. Mean yearly percentage of predispersal seed predation (the percentage of total seeds produced preyed upon before dispersal) in *Quercus ilex* (solid bars) and *Q. humilis* (open bars) trees in the entire study area from 1998 to 2004. Significant differences in mean yearly acorn predation between *Q. ilex* and *Q. humilis* for a given year were tested by means of paired $t$ tests considering the 15 sampled plots. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Tests could not be applied in 1998, 2001, and 2003 due to the low number of plots in which *Q. ilex* produced mature acorns.

TABLE 5. Effect of the ratio of mature acorn crop in year $t$ to that in year $t - 1$ per plot on the percentage of acorns depredated in *Quercus ilex* and *Q. humilis*.

| Model components, by species | Estimate | SE | $t$ | df | $P$ | Variance explained (%) | Estimated acorns depredated for different $x$ values (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | $x = 10$ | $x = 100$ | $x = 1000$ |
| *Q. ilex* | | | | | | | | | |
| Model 1 | | | | | <0.001 | 19.7 | 46 | 43 | 39 |
| Intercept | −0.62 | 0.35 | −1.75 | 56 | 0.09 | | | | |
| log(*Q. ilex*) | −0.15 | 0.04 | −3.65 | 55 | 0.001 | | | | |
| Model 2 | | | | | <0.001 | 24.0 | 26 | 23 | 21 |
| Intercept | −0.890 | 0.256 | −3.48 | 56 | 0.001 | | | | |
| log(*Q. ilex* + *Q. humilis*) | −0.150 | 0.037 | −4.03 | 55 | <0.001 | | | | |
| *Q. humilis* | | | | | | | | | |
| Model 1 | | | | | <0.001 | 24.2 | 55 | 51 | 47 |
| Intercept | 0.37 | 0.14 | 2.61 | 80 | 0.01 | | | | |
| log(*Q. humilis*) | −0.16 | 0.03 | −5.01 | 79 | <0.001 | | | | |
| Model 2 | | | | | <0.001 | 20.7 | 47 | 43 | 40 |
| Intercept | 0.24 | 0.13 | 1.84 | 80 | 0.07 | | | | |
| log(*Q. ilex* + *Q. humilis*) | −0.13 | 0.03 | −4.54 | 79 | <0.001 | | | | |

*Notes:* The analyses were conducted by means of generalized linear models with a logit link function and a quasi-binomial approach. See *Materials and methods* for the calculation of the model significance ($P$ value for model) and percentage of variance explained. Model 1 is the within-species acorn crop in year $t - 1$; model 2 is the two species' acorn crops in year $t - 1$ combined. To better illustrate the values predicted by the models, the estimated percentage of acorns depredated for different acorn crops in year $t - 1$ ($x$, the number of acorns per plot) is presented.

recruitment of oak seedlings in these forests has been thoroughly reported (Espelta et al. 1995, Gracia et al. 2001).

### *Within- and between-species annual variability in acorn production*

Both initial acorn production and mature acorn production in the evergreen *Q. ilex* and the deciduous *Q. humilis* were highly variable among years, with relatively high CVp values (1.5–2.0) on a world scale (Kelly et al. 2000, Kelly and Sork 2002). Notwithstanding this masting behavior in the two species, *Q. ilex* and *Q. humilis* exhibited very different trends in their reproduction, resulting in no significant synchrony across years in their initial or mature acorn crop size. Remarkably, significant acorn crops of *Q. ilex* occurred almost exclusively in two years out of seven (2002 and 2004), while *Q. humilis* exhibited a more regular pattern of fruiting with more regular but smaller mature acorn crops.

Differences in the patterns of seed production among coexisting oaks have been previously documented and attributed to various causes, such as specific differences in the time required for acorn maturation (see Liebhold

TABLE 6. Effect of the population-level coefficient of variation (CVp) of mature acorn crop per plot on the mean percentage of acorns depredated on *Quercus ilex* and *Q. humilis* trees during the seven-year monitoring.

| Model components, by species | Estimate | SE | $t$ | df | $P$ | Variance explained (%) | Estimated acorns depredated for different CVp values (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | CVp = 1.0 | CVp = 2.0 | CVp = 2.5 |
| *Q. ilex* | | | | | | | | | |
| Model 1 | | | | | 0.020 | 70.2 | 13 | 7 | 4 |
| Intercept | 0.50 | 1.11 | 0.45 | 14 | 0.66 | | | | |
| *Q. ilex*, CVp | −1.26 | 0.58 | −2.18 | 13 | 0.05 | | | | |
| Model 2 | | | | | 0.003 | 58.9 | 10 | 5 | 2 |
| Intercept | 0.77 | 0.93 | 0.83 | 14 | 0.42 | | | | |
| *Q. ilex* + *Q. humilis*, CVp | −1.47 | 0.51 | −2.90 | 13 | 0.01 | | | | |
| *Q. humilis* | | | | | | | | | |
| Model 1 | | | | | | | | | |
| Intercept | −0.23 | 0.53 | −0.43 | 14 | 0.67 | | | | |
| *Q. ilex*, CVp | 0.01 | 0.38 | 0.03 | 13 | 0.98 | | | | |
| Model 2 | | | | | 0.013 | 68.0 | 53 | 40 | 29 |
| Intercept | 1.64 | 0.47 | 2.21 | 14 | 0.05 | | | | |
| *Q. ilex* + *Q. humilis*, CVp | −1.03 | 0.42 | −2.43 | 13 | 0.03 | | | | |

*Notes:* The analyses were conducted by means of generalized linear models with a logit link function and a quasi-binomial approach. See *Materials and methods* for the calculation of the model significance ($P$ value for model) and percentage of variance explained. Model 1 is the within-species CVp; model 2 is the CVp of the two species' acorn crops combined. To better illustrate the values predicted by the models, the estimated percentage of acorns depredated for different CVp is presented.

et al. 2004; but not applicable to our species), environmental cues influencing the fruiting process (Koenig et al. 1996), and differences in endogenous cycles (Sork et al. 1993, Koenig et al. 1996). At least for our two species, we think that such differences in environmental cues or endogenous cycles could partly arise from the different leaf habit in the two oaks. On the one hand, initiation of floral structures takes place earlier (~4–6 weeks) in *Q. humilis* than in *Q. ilex*, and thus the two species may be subjected to a short timescale, but relevant environmental differences during flower initiation for the same year (particularly under a highly unpredictable Mediterranean-type climate). On the other hand, *Q. humilis* and *Q. ilex* show contrasting functional traits and patterns of biomass allocation (Valentini et al. 1992, Damesin et al. 1998, Espelta et al. 2005), and this might result in a different duration of endogenous cycles (inter-mast intervals) to accumulate and mobilize resources to produce a large seed crop.

The analysis of the contribution of mean individual variability in acorn production (CVi) and synchrony (*r*) to population variability (CVp) of initial and mature acorn crops revealed a preeminent role of synchrony rather than mean individual variability in the increase of CVp. These results differ from previous studies that have shown population variability to be more strongly correlated with individual variability (Herrera 1998, Koenig et al. 2003). As demonstrated by Buonaccorsi et al. (2003), the relationship between CVi, *r*, and CVp is complex and can also be influenced by additional factors, mainly sampling size and mean productivity per plant. The low mean acorn productivity observed in the two species in our study area as well as a great number of trees with nonproductive years could be important factors in the increase of the influence of synchrony on population variability. Furthermore, a comparison of the CVi, *r*, and CVp of our two oaks with the values reported for a large group of woody species in Koenig et al. (2003) reveal a larger *r*, a lower difference between CVi and Cvp, and a higher overall CVp in *Q. ilex* and *Q. humilis* than in all the Californian oak species listed in that study, even for a similar monitoring scheme (seven years). Strikingly, a similarly small difference between CVi and CVp to the one found for our two oaks was obtained in *Phyllirea latifolia* (an *Oleaceae* species also present in our study area) in southern Spain by Herrera (1998). This highlights the possibility that potential differences in forest structure and fine-scale climatic patterns may be of paramount importance in masting behavior, even for similar climatic areas (mediterranean-type climate in both California and the Mediterranean Basin).

In *Q. ilex* and *Q. humilis*, initial acorn production showed remarkable temporal variability. However, variability and synchrony were enforced in mature acorn crop size by seed survival from pollination to maturation (i.e., acorn abortion), mediated by annual differences in summer drought. Under the harsh environmental conditions during acorn maturation (summer) in our study area, heavy acorn abortion occurs (see Fig. 2), except in unusually wet summers (Siscart et al. 1999). The fact that temporal fluctuations in acorn production in these two oaks were largely driven by seed survival confirms our first hypothesis and disagrees with a pollination efficiency basis for masting in these species (see also similar evidences for other temperate oaks; Sork 1993, Sork et al. 1993, Shibata et al. 2002). Thus, it appears that our system resembles some of the extreme and highly unpredictable ecological scenarios (e.g., semiarid zones) reported by Kelly and Sork (2002) in which annual fluctuation in seeding would be better explained by resource availability during fruiting rather than by the benefits for pollination of episodic large flowering efforts.

Moreover, both within- and, more dramatically, between-species synchrony increased from initial to mature acorn crop. This result indicates that environmental factors controlling acorn ripening (abortion patterns due to variable summer stress) play a preeminent role in increasing synchrony and thus population variability in acorn production not only within species, but especially between species. Among the different environmental cues identified as triggering synchrony in mast seeding, change in temperature has been the factor most thoroughly reported (see Kelly et al. 2000, Schauber et al. 2002). However, Piovesan and Adams (2001) identified drought extent in the years preceding masting as the main factor triggering masting in beech (*Fagus* spp.) forests in Europe and eastern North America. Although our study did not address the causes triggering synchrony in the initial crop of acorns produced (a surrogate of flowering intensity), the results obtained indicate, apparently for the first time, to our knowledge, that summer drought can be the key factor driving within- and, especially, between-species synchrony in masting for Mediterranean oak species.

The importance of water availability at a local scale is also confirmed by the lowest crop production and highest synchrony shown by *Q. humilis* trees and the highest synchrony in the two oak species considered together, when they grow in areas with higher water deficit (Fig. 3). This is an interesting point, because very few studies have identified potential causes for local differences in fruiting synchrony (but, for the effects of altitude, see Webb and Kelly [1993]). However, although Kelly and Sork (2002) hypothesized that at less productive sites (e.g., those where water is more limiting) population variability in seed production would be higher than at more productive ones, the increase in synchrony in *Q. humilis* only resulted in a marginal increase in CVp. Availability of a longer time series of acorn production in these sites may help to confirm this tendency and also to assess whether local differences in variability of seed production are important in the determination of the spatial patterns of fruit predation (Koenig et al. 2003). Conversely to the results obtained for *Q. humilis*, mean acorn production or variability in *Q. ilex* did not vary across the water stress gradient. This is probably because the major reproductive events in this species (2002 and 2004) were restricted to some particularly good years with unusually wet and cold summers, where differences between sites are of lesser importance.

### *Effects of within- and between-species variability for acorn production in predispersal acorn predation*

*Quercus ilex* and *Q. humilis* trees suffered heavy predispersal acorn predation, with values much higher than those reported for other more seed-productive oak forests (Pulido and Díaz 2004). However, interannual fluctuation in acorn crop sizes led to a satiation and starvation effect on seed predation, as previously reported in other studies dealing with the benefits of masting for escaping predation (Kelly et al. 2001, Schnurr et al. 2002, Satake et al. 2004, Bonal et al. 2007). Our results indicate that the extent of satiation and starvation of seed predators at a within-species level increased because of the simultaneous presence of acorns of the two coexisting oaks. Despite the reported benefits, predation of *Q. humilis* acorns was always higher than that of *Q. ilex* acorns. We hypothesize that this may be due to the slightly earlier ripening of acorns of *Q. humilis*. Namely, the acorns of this species would attain a minimum size susceptible for the attack of the three *Curculio* spp. present in our study area (*C. venosus*, *C. elephas*, and *C. glandium*) prior to *Q. ilex* (R. Bonal, *unpublished data*).

When considering predation figures on longer terms than year to year, the overall within-species proportion of acorns depredated during the seven-year period decreased in both *Q. ilex* and *Q. humilis* when fluctuation in acorn crops of the two species is considered together (Table 6). Results reported for satiation and starvation, as well as this more general test, suggest that these two species (both maturing acorns in one year) could benefit mutually from a combined fluctuation in seed production, escaping predispersal predation (Satake et al. 2004). This is an effect extensively suggested in the scientific literature dealing with the results of between-species synchrony in reproduction (see Shibata et al. 1998), but seldom experimentally tested. In light of our results, we have two potential hypotheses explaining the effect of the acorn crop of the two species combined for within-species predator satiation: (1) predator satiation in *Q. ilex* would benefit from the more regular (and potentially more sensitive to predation) acorn crops of *Q. humilis*, especially in years with a low production of acorns in the former species and (2) predator satiation in *Q. humilis* would benefit from the more highly irregular but larger acorn crop sizes of *Q. ilex*.

It remains to be clarified whether this "predation satiation" effect observed in our two oaks has a true adaptive value, stabilizing annual fluctuation in seed production among species as suggested by Shibata et al. (2002), or is merely an indirect effect of the "resource matching" of the fruiting output of these two oaks, mediated by summer water stress. To determine whether masting in these two oaks could have a true adaptive basis, it would be necessary to examine whether "switching" exists (sensu Norton and Kelly 1988, see also Monks and Kelly 2006), i.e., the preferential allocation of resources towards reproduction in mast years vs. non-mast years. Preliminary results obtained for *Q. humilis* (B. Sánchez-Humanes, *unpublished data*) show that annual tree growth rates from 1998 to 2004 parallel those of seed production (i.e., years with large acorn crops correspond to years with higher tree growth and vice versa), disproving the existence of "switching" and proving the existence of "resource matching" (Kelly and Sork 2002).

Whether adaptive or not, this fluctuation in acorn crops of the two species combined could be a factor aiding the coexistence of these two oaks. Previous studies have shown that *Q. ilex* and *Q. humilis* show a similar regeneration "niche" in terms of water, nutrients, and light intensity for seedling establishment, thus competing for similar microsites for recruitment (Espelta et al. 2005). A within-species reduction in seed predation due to variability in the sum of the acorn crop of the two oaks could favor the availability of seeds of the two species to potentially recruit. However, as pointed out by Curran and Leighton (2000), benefits of between-species synchrony in fruiting can be biased toward one of the species. Therefore, it is also necessary to clarify whether this beneficial effect for lower acorn predation is symmetrical or biased toward one of the two oaks species and whether it persists when considering other potential acorn predators, such as vertebrates. Moreover, several studies have indicated for the Mediterranean Basin an increasing occurrence of summer drought episodes (Piñol et al. 1998) and some dramatic changes in the phenology of plant and animal species (Peñuelas et al. 2002). In this scenario, it will be crucial to assess how sensitive these within- and between-species patterns of fluctuating acorn production and their effects on seed predation may be to the predicted effects of climate change in the area.

## ACKNOWLEDGMENTS

We thank Helena Barril, Berta Obón, and Ivette Serral for assistance during field work and Daniel Sol for advice in the use of the R statistical package. Raúl Bonal, Xavier Picó, and two anonymous reviewers provided helpful comments on an early draft of this manuscript. This research has been funded by the project INIA (RTA2005-00100) and the Consorci del Parc de Collserola.

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## APPENDIX A

Main topographic and structural characteristics of the sampling plots (*Ecological Archives* XX-XXX-XXXX).

## APPENDIX B

Mean values of initial acorn crop, mature acorn crop, and proportion of acorns depredated per tree in the 15 sampled plots (*Ecological Archives* XX-XXX-XXXX).

## APPENDIX C

Components of population-level variation in acorn production (*Ecological Archives* XX-XXX-XXXX).

## APPENDIX D

Meteorological characteristics during summer (June to August) in the study area from 1998 to 2004 (*Ecological Archives* XX-XXX-XXXX).