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Factors affecting post-dispersal seed predation in two coexisting oak species: Microhabitat, burial and exclusion of large herbivores

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ABSTRACT

Post-dispersal seed predation can cause an important “bottleneck” in the natural regeneration of many oak populations. In this study, we experimentally quantified post-dispersal seed predation for two oak species – *Quercus canariensis* and *Quercus suber* – coexisting in a Mediterranean forest located in southern Spain. Acorn predation was monitored for 2 consecutive years in two different forest sites, with a total of 3360 acorns experimentally dispersed among different types of microhabitat. Most of the acorns were removed (probably by rodents) and assumed to be consumed. Patterns of post-dispersal acorn predation varied depending on various factors. There was a significant effect of oak species, *Q. suber* acorns being removed faster and in a higher proportion than those of *Q. canariensis*. There were also significant effects of burial and microhabitat: the highest predation rates occurred for acorns set on the ground surface (not buried), and especially in the most-densely vegetated microhabitats, where rodents usually show a higher activity. The lowest predation rates appeared in the years and forest sites where the estimated seed production – and consequently the natural resource availability – was higher, thus supporting the *predator satiation* hypothesis. The use of fences to exclude large herbivores did not significantly decrease the probability of acorn predation. Moreover, in microhabitats located under dense shrubs, losses of acorns were higher inside fenced plots than outside, probably as an indirect consequence of an increase in rodent populations. Based on the results obtained in this study, we discuss the consequences of seed predation on the natural regeneration of oaks and make some practical recommendations for assisted regeneration in oak restoration plans.

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1. Introduction

Oak trees produce big seeds with a high nutritional content, which are subjected to intensive predation pressure, both pre- and post-dispersal. In particular, post-dispersal seed predation has been considered one of the main factors limiting natural regeneration in many oak species (e.g., Shaw, 1968; Crow, 1992; Herrera, 1995; Santos and Tellería, 1997; Gómez et al., 2003). There is a compromise between two opposing selective pressures: on one hand, a greater size of cotyledons can favour germination, survival and growth of seedlings; on the other, a higher content of nutritional substances can increase the probability of seed predation (Gómez, 2004a). Acorns constitute an important part of the diet for many animals, which can consume a large proportion of the seed production and, consequently, could endanger seedling recruitment of tree populations.

The pattern of post-dispersal seed predation can vary both spatially and temporally. Firstly, seed production and dispersal vary in space and time. Although most oak seeds are dispersed by gravity, a small number can be dispersed by animals, mainly by birds (Darley-Hill and Johnson, 1981; Gómez, 2003), rodents (Jensen and Nielsen, 1986; Pulido and Díaz, 2005; Gómez et al., 2008) and even large insects (Pérez-Ramos et al., 2007). The small proportion of buried, surviving seeds discarded or forgotten by dispersers in caches is crucial for tree population dynamics and genetic diversity (e.g., Díaz, 1992; Gómez et al., 2003, 2008). Seasonal production of acorns by oaks means a temporary abundance of resources for many animals, with a strong inter-annual variability due to the well-known masting phenomenon (Silvertown, 1980). Seed removal can also vary spatially because predator and disperser foraging is not random, but usually responds to preferences for certain microhabitats and rejection of others (Clark et al., 1999; Jordano and Schupp, 2000). Thus, the spatial distribution of the “seed rain” across different microhabitats can alter the probability of seed survival and seedling establishment (Rey and Alcántara, 2000). Furthermore, the high temporal variation in resource (seed) availability at ground level can also modify seed removal rates. According to the *predator*

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satiation hypothesis (Janzen, 1971; Silvertown, 1980), a higher abundance of resources increases the probability of a seed's escaping from predators and establishing as a seedling (Kelly, 1994; Kelly and Sork, 2002). Supporting this hypothesis, density-dependent seed predation, with lower consumption rates in more productive years, has been documented in other forest types (Shaw, 1968; Kennedy, 2005; López Barrera et al., 2005; Xiao et al., 2005).

The probability of seed predation can also vary depending on the type of predator. In many Mediterranean oak forests, the highest losses of acorns are attributed to large herbivores, both wild and domestic ungulates (Gómez et al., 2003; Leiva and Fernández-Alés, 2003), which can also intensely browse seedlings and saplings. For this reason, a common silvicultural practice in grazed woodlands is to fence a portion temporarily to exclude large herbivores, and thereby promote the natural regeneration of oak species. In contrast, most seed losses in other oak forests are caused by rodents (Borchert et al., 1989; Gómez et al., 2003; Pons and Pausas, 2007; Acácio et al., 2007), which are not excluded by fencing.

The main objectives of this study were to investigate experimentally the role of post-dispersal acorn predation in the natural regeneration of two coexisting oak species – *Quercus canariensis* (Algerian oak) and *Quercus suber* (cork oak) – in a Mediterranean woodland located in southern Spain, and to analyse the main factors affecting spatio-temporal variation in seed predation at different scales. In particular, among possible factors related to the seed dispersal process, we explored (i) the importance of microhabitat type, (ii) the role of acorn burial, simulating the process of biotic dispersal, and (iii) the enclosure of large herbivores by fences. In a separate paper, we analysed the effects of seed size and dispersal timing (Pérez-Ramos et al., 2008, in review).

On the basis of the results obtained in this study, we present a set of practical recommendations for reforestation and restoration procedures aimed at increasing successful recruitment in both oak species and reducing economic costs. As far as we know, this is the first study on seed predation for the Algerian oak (*Q. canariensis*), which is compared with that for the more studied cork oak (*Q. suber*).

2. Methods

2.1. Study area and species

The study area is located in the mixed oak forests of the Aljibe Mountains, near the Strait of Gibraltar, in southern Spain. The dominant bedrock is Oligo-Miocenic sandstone, with a rough relief and a highest peak of 1092 m a.s.l. The climate is subhumid Mediterranean-type, with mild, wet winters, alternating with warm, dry summers. The mean temperature is 17 °C, and annual rainfall varies from 700 to 1200 mm, depending on the effects of the orographic relief.

The vegetation is dominated by evergreen cork oak (*Q. suber*) forests, mixed with semi-deciduous oaks (*Q. canariensis*), which are more abundant near streams (Urbieta et al., 2008a). The shrubby understorey is diverse and rich in endemic taxa (see general vegetation description in Ojeda et al., 2000). Most of the forested area has been protected within *Los Alcornocales* (meaning cork oak forests) Natural Park, covering about 1680 km². Large herbivores, such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and free-range cattle are abundant in this forested landscape.

Two mixed oak forest sites were selected for the experiments: San Carlos del Tiradero (TIR) (36°9'46"N, 5°35'39"W), and Panera (PAN) (36°31'54"N, 5°34'29"W), which are about 40 km apart. The forest sites differed in structure and understorey composition (Quilchano et al., 2008; Pérez-Ramos et al., 2008a) and in cattle grazing, which was very sporadic at TIR but regular through all

seasons at PAN. At each site, in 1999, a plot of about 1 ha was fenced to exclude large herbivores, with the purpose of monitoring woody species regeneration in the absence of large herbivores (Pérez-Ramos, 2007).

Q. suber L. (cork oak) is an evergreen tree dominating forests in sub-humid Mediterranean-type climate, on acidic soils. The fruit (acorn) of *Q. suber* is one of the largest of Mediterranean tree species (mean fresh weight of 5.9 ± 2.2 g S.D. and range of 2.3–17.3 g, $n = 576$). The seed production is restricted to the autumn/early winter season (between October and February), and there is a strong inter-year variability, due to the well-known masting behaviour. Estimates of acorn production at the TIR forest site varied (in dry weight) from 6.6 g/m² (2003/2004 cycle) to 168 g/m² (2004/2005 cycle). At the PAN forest site, mean values of acorn production were low during both years (about 2.3 g/m² yr) (Pérez-Ramos, 2007).

Q. canariensis Willd. is a semi-deciduous oak, locally abundant in the moister locations and usually mixed with *Q. suber*. Its acorns are somewhat smaller than those of *Q. suber* (mean fresh weight of 2.6 ± 1.03 g S.D. and range of 0.9–8.3 g, $n = 576$). The seed dispersal occurs earlier (September–December) and there is a strong inter-year variability in seed production. Estimates of acorn production at the PAN forest site varied between 344.2 g/m² (2003/2004 cycle) and 54.1 g/m² (2004/2005 cycle), while at the TIR forest site acorn production was low during both years (below 14 g/m² yr) (Pérez-Ramos, 2007).

2.2. Experimental design and data collection

Acorns were collected under several trees of each oak species during the period of peak production and dispersal: October–November for *Q. canariensis*, and December–January for *Q. suber*. A selection of healthy, normal-sized acorns was made, using a flotation method to discard those infected by moth or beetle larvae (Gribko and Jones, 1995). Selected acorns were then stored on a moist vermiculite bed, in plastic trays, and kept at 2–4 °C until their use in the experiment.

Acorns were individually marked with a small spot of paint and were randomly distributed into a total of 96 experimental units for each oak species and forest site, evenly distributed in three types of microhabitat (see below). In each experimental unit, four acorns (without cupule) were placed on the ground, in the corners of a 0.5 m² square. The experimental units were marked with small flags (one placed 0.5 m from each border, in order to avoid attraction effect). The approximate minimum distance between different units was 10 m.

Periodic monitoring of all the acorns was carried out until there was no longer any evidence of predation (after approximately 3 months), noting the number of acorns consumed *in situ*, the number removed and (when possible) the identity of the predators. Acorns predated by rodents or birds were identified by signs of gnawing or pecking, respectively. Acorns manipulated by the dung beetle, *T. lusitanicus*, showed a circular (beetle-sized) hole and were usually buried together with the beetle a few centimetres into the soil (Pérez-Ramos et al., 2007).

The experimental dispersal and subsequent monitoring were repeated during two reproductive cycles (2003–2004 and 2004–2005) at both forest sites (TIR and PAN), making a grand total of 3360 acorns of the two oak species. During the first cycle, censuses were carried out at 24 h, 7 days, 15 days and then monthly (up to 3 months). For the second cycle, three censuses were made: at 7 days, 1 month, and 3 months. This approach enabled us to calculate the time elapsing until each experimental acorn was predated or removed. Those acorns remaining unaffected at the end of the experiment were considered right-censored data. In early spring, a last census was made, and the number of established seedlings was recorded. One year later, seedlings that had emerged during the first cycle were revisited to record the surviving proportion.

Three dispersal experiments were carried out to evaluate the effects of different factors on the probability of acorn predation:

- (1) *Type of microhabitat.* Acorns were distributed among 48 experimental units in three types of microhabitat, which spanned a wide gradient of plant cover and light availability: (i) inside dense shrub and tree overstorey (5–15% full sun); (ii) under trees without shrub understorey (16–30% full sun); and (iii) open grassland (30–90% full sun). The shrubby vegetation comprised mainly *Pistacia lentiscus*, *Phillyrea latifolia*, *Viburnum tinus*, *Erica arborea*, and *Erica scoparia*.
- (2) *Exclusion of large herbivores.* In a second and parallel experiment, a similar design with 24 experimental units (of four acorns) for each species was used, but outside the fenced plots, with the purpose of estimating the total acorn predation rate, adding the impact of large animals such as deer and cattle. Acorns were distributed among the three types of microhabitat, near the fenced plot (with a maximum distance of 15 m from the fence) but outside the enclosure.
- (3) *Burial of acorns.* The effect of burial on acorn predation rate was analysed using other 24 experimental units (each of four acorns) for each species, distributed among the three types of microhabitat, by burying seeds horizontally 1–3 cm deep in the mineral soil. The purpose was to simulate natural acorn dispersal and burial by European jays (Kollmann and Schill, 1996; Gómez et al., 2003), rodents (Jensen and Nielsen, 1986; Pulido and Díaz, 2005), or dung beetles (Pérez-Ramos et al., 2007). This experiment was carried out during the 2003/2004 cycle, both inside and outside the fenced plot, including a total of 336 experimentally buried acorns of each species. In this case, only one census was made (after 3 months) in order to avoid interference by unearthing and checking acorns.

The experiments started at different time, according to the typical seed dispersal phenology of each species: *Q. canariensis* acorns were experimentally dispersed in mid October (2003) or early November (2004), while *Q. suber* acorns were set in the forest floor later—December (2003 and 2004). Acorns of the two species were located in different but neighbouring units (with an average distance of 1–3 m between them) to avoid interference between the two species.

2.3. Statistical analyses

The effect of the three explored factors – type of microhabitat, exclusion of large herbivores and burial – as well as of forest site, oak species and their interactions on seed predation and seedling establishment, were tested using Generalised Linear Models (McCullagh and Nelder, 1989), assuming a logit relationship (link function) between the dependent and explanatory variables. The same type of analysis was repeated separately for each oak species. In all cases, both seed predation and seedling establishment were treated as binomial variables.

Because the time elapsing from seed dispersal until a seed is consumed or removed by predators can affect its capacity to establish as a seedling (Kennedy et al., 2004; Pérez-Ramos et al., 2008b), the same data sets were subjected to complementary failure time analyses (Pyke and Thompson, 1986). According to exploratory analyses, seed survival times were not normally distributed, and therefore differences between species and forest sites were analysed using a non-parametric test for multiple samples, which is a generalisation of Gehan's Wilcoxon test (Gehan, 1965). Survival functions for each oak species and forest site were estimated using the Kaplan–Meier method (1958). All analyses were carried out using Statistica (v. 6, StatSoft Inc., 2001).

3. Results

3.1. Seed predators

A high proportion of acorns was removed during the two sampled periods, whereas a low proportion was consumed *in situ* by different predators (Table 1). These differences between removed vs. consumed acorns were more pronounced for *Q. suber*, especially during the cycle when seed production was lower, and percentages of removal exceeded 90%. Most acorns consumed *in situ* showed signs of manipulation by rodents (probably *Apodemus sylvaticus*). In general, the highest percentages of acorn consumption by rodents were found inside fenced plots. The proportion of acorns with signs of post-dispersal predation by other small vertebrates was very low (the losses by birds were insignificant) and a small number of acorns were consumed by the dung beetle *T. lusitanicus* (see details in Pérez-Ramos et al., 2007).

3.2. Factors affecting seed predation rates

Post-dispersal seed predation varied depending on many factors. Oak species was a significant factor. The probability of seed predation was significantly higher for *Q. suber* than for *Q. canariensis* during the 2 sampled years ($\chi^2 = 19.69$; d.f. = 1; $p < 0.001$ in 2003/2004 cycle; and $\chi^2 = 50.24$; d.f. = 1; $p < 0.001$ in 2004/2005 cycle). Within each oak species, the seed predation rate was significantly affected by microhabitat type, burial, and forest site (Table 2). However, with the exception of certain microhabitats located under dense shrub, the use of fences to exclude large herbivores did not have a significant effect (Table 2).

3.2.1. Effect of the type of microhabitat

Seed predation rates of both oak species were significantly higher in more closed microhabitats (under dense shrub) than in those located under trees and open microhabitats (Fig. 1). This pattern was consistent for both buried and unburied acorns (Fig. 1). Differences between the three types of microhabitat were more marked inside fenced plots (see below).

3.2.2. Effect of excluding large herbivores

The use of fences had little effect on acorn predation probabilities in the two studied species. Contrary to our expectation, the probability of seed predation was often higher inside fenced plots, although this effect was significant only for microhabitats located under dense shrubs ($\chi^2 = 6.19$; d.f. = 1; $p = 0.01$ for *Q. suber* in 2003/2004, and $\chi^2 = 4.18$; d.f. = 1; $p = 0.04$ for *Q. canariensis* in 2004/2005) (Fig. 2).

3.2.3. Effect of burial

Burial of acorns significantly decreased predation rates for both oak species and in the three types of microhabitat (Fig. 1). The probability of a *Q. canariensis* acorn's being consumed varied from 0.90 (on ground surface, S) to 0.37 (buried, B) in microhabitats located under dense shrub ($\chi^2 = 95.46$; d.f. = 1; $p < 0.001$), from 0.72 (S) to 0.23 (B) in those located under trees ($\chi^2 = 71.59$; d.f. = 1; $p < 0.001$), and from 0.75 (S) to 0.27 (B) in open microhabitats ($\chi^2 = 68.27$; d.f. = 1; $p < 0.001$). In the case of *Q. suber*, the probability of acorn predation varied from 0.98 (S) to 0.47 (B) in denser microhabitats ($\chi^2 = 119.95$; d.f. = 1; $p < 0.001$), from 0.88 (S) to 0.23 (B) under trees ($\chi^2 = 128.98$; d.f. = 1; $p < 0.001$), and from 0.82 to 0.22 in open microhabitats ($\chi^2 = 104.13$; d.f. = 1; $p < 0.001$).

3.2.4. Effect of forest site

There were differences in seed survival between the two forest sites depending on the annual cycle. During 2003/2004, final seed survival of *Q. suber* was higher at PAN site (0.19) than at TIR site (0.01) ($T = 6.817$; g.l. = 1; $p < 0.01$), while *Q. canariensis* had similar

Table 1
Number of predated acorns and resulting seedlings as function of the type of predator

	Removed acorns	Acorns consumed <i>in situ</i>				Intact acorns	Emergenced seedlings	Surviving seedlings
		Rodents	Birds	Beetles	No identified			
Surface acorns								
03/04 cycle								
<i>Quercus canariensis</i>								
Panera								
Inside	48 (25)	39 (20.3)	0 (0)	21 (10.9)	11 (5.7)	73 (38)	28 (14.6)	8 (4.2)
Outside	47 (48.9)	5 (5.2)	1 (1.04)	7 (7.3)	6 (6.3)	30 (31.3)	7 (7.3)	2 (2.1)
Tiradero								
Inside	57 (29.7)	59 (30.7)	1 (0.5)	2 (1.04)	20 (10.4)	53 (27.6)	33 (17.2)	1 (0.5)
Outside	34 (35.4)	19 (19.8)	0 (0)	1 (1.04)	3 (3.1)	39 (40.6)	17 (17.7)	2 (2.1)
<i>Quercus suber</i>								
Panera								
Inside	115 (59.9)	12 (6.3)	0 (0)	7 (3.6)	20 (10.4)	38 (19.8)	13 (6.8)	2 (1.04)
Outside	73 (76)	1 (1.04)	0 (0)	5 (5.2)	0 (0)	17 (17.7)	3 (3.1)	0 (0)
Tiradero								
Inside	167 (87)	6 (3.1)	0 (0)	9 (4.7)	8 (4.2)	2 (1.04)	0 (0)	0 (0)
Outside	76 (79.2)	7 (7.3)	0 (0)	3 (3.1)	8 (8.3)	2 (2.1)	1 (1.04)	0 (0)
04/05 cycle								
<i>Quercus canariensis</i>								
Panera								
Inside	128 (66.7)	32 (16.7)	0 (0)	6 (3.1)	19 (9.9)	7 (3.6)	9 (4.7)	–
Outside	61 (63.5)	3 (3.1)	0 (0)	15 (15.6)	4 (4.2)	13 (13.5)	11 (11.4)	–
Tiradero								
Inside	56 (29.2)	10 (5.2)	0 (0)	0 (0)	15 (7.8)	111 (57.8)	72 (37.5)	–
Outside	20 (20.8)	9 (9.4)	0 (0)	2 (2.1)	6 (6.3)	59 (61.5)	40 (41.7)	–
<i>Quercus suber</i>								
Panera								
Inside	181 (94.3)	1 (0.5)	0 (0)	1 (0.5)	5 (2.6)	4 (2.1)	4 (2.1)	–
Outside	79 (82.3)	0 (0)	0 (0)	3 (3.1)	1 (1.04)	13 (13.5)	15 (15.6)	–
Tiradero								
Inside	124 (64.6)	8 (4.2)	0 (0)	2 (1.04)	4 (2.1)	54 (28.1)	49 (25.5)	–
Outside	77 (80.2)	2 (2.1)	0 (0)	0 (0)	0 (0)	17 (17.7)	14 (14.6)	–
Buried acorns								
03/04 cycle								
<i>Quercus canariensis</i>								
Panera								
Inside	17 (17.7)	1 (1.04)	0 (0)	3 (3.1)	4 (4.2)	71 (74)	25 (26)	5 (5.2)
Outside	15 (20.8)	1 (1.4)	0 (0)	2 (2.8)	3 (4.2)	51 (70.8)	14 (19.4)	3 (4.2)
Tiradero								
Inside	22 (22.9)	5 (5.2)	0 (0)	3 (3.1)	5 (5.2)	61 (63.5)	21 (21.9)	2 (2.1)
Outside	10 (14.7)	4 (5.9)	0 (0)	0 (0)	2 (2.9)	52 (76.5)	19 (27.9)	3 (4.4)
<i>Quercus suber</i>								
Panera								
Inside	25 (26)	1 (1.04)	0 (0)	1 (1.04)	2 (2.1)	67 (69.8)	24 (25)	4 (4.2)
Outside	12 (21.1)	0 (0)	0 (0)	0 (0)	0 (0)	45 (78.9)	18 (31.6)	4 (7)
Tiradero								
Inside	29 (30.2)	1 (1.04)	0 (0)	0 (0)	5 (5.2)	61 (63.5)	32 (33.3)	4 (4.2)
Outside	19 (28.4)	1 (1.5)	0 (0)	0 (0)	7 (10.4)	40 (59.7)	23 (34.3)	4 (6)

Data have been separated according to burial (surface vs. buried acorns), oak species (*Q. canariensis* vs. *Q. suber*) and exclusion treatment of large herbivores (inside vs. outside fenced plots). Percentages respect to the total of experimentally dispersed acorns are shown in parentheses.

survival (about 0.3) at the two forest sites ($T = -1.327$; g.l. = 1; $p = 0.184$) (Fig. 3). During 2004/2005, there were significant differences in seed survival between forest sites for the two oak species. *Q. canariensis* had seed survival values of 0.59 at TIR site vs. 0.07 at PAN site ($T = -12.645$; g.l. = 1; $p < 0.001$), while for *Q. suber* the values were 0.25 at TIR site and 0.06 at PAN site ($T = -8.899$; g.l. = 1; $p < 0.001$). In both annual cycles and at both forest sites, the highest seed survival probabilities were for *Q. canariensis*.

3.3. Establishment of seedlings

Effects of different factors on seed predation rates had consequences on the pattern of emergenced and surviving seedlings

established from the experimentally dispersed acorns (Tables 1 and 3). There were marked differences between oak species: the highest percentages of emergenced seedlings were recorded for *Q. canariensis*, especially in the year when more acorns were produced ($\chi^2 = 6.09$; d.f. = 1; $p < 0.001$ in 2003/2004, and $\chi^2 = 14.77$; d.f. = 1; $p < 0.001$ in 2004/2005). Within each oak species, the number of established seedlings was affected by microhabitat type, burial and forest site (Table 3). First, with regard to the type of microhabitat, fewer seedlings proceeding from unburied *Q. suber* acorns were established in those microhabitats located under dense shrubs (Fig. 4). Surprisingly, the probability of seedling establishment for acorns set in open grasslands was low, despite the low acorn predation rates detected in this type of

Table 2
Results of generalized linear models evaluating the effects of all factors and their interactions on the probability of seed predation

	d.f.	2003/2004 cycle		2003/2004 cycle		2004/2005 cycle		2004/2005 cycle	
		<i>Q. canariensis</i>		<i>Q. suber</i>		<i>Q. canariensis</i>		<i>Q. suber</i>	
		χ^2	P	χ^2	P	χ^2	P	χ^2	P
Microhabitat	2	27.91	<0.001	21.82	<0.001	10.64	0.005	33.74	<0.001
Exclusion	1	3.11	0.078	0.00	1.000	9.93	0.002	0.03	0.865
Burial	1	236.14	<0.001	367.80	<0.001	–	–	–	–
Forest site	1	0.41	0.524	24.05	<0.001	184.68	<0.001	41.60	<0.001
Microhabitat × Exclusion	2	0.28	0.871	1.38	0.502	11.19	0.004	2.83	0.243
Microhabitat × Burial	2	2.15	0.341	2.94	0.229	–	–	–	–
Microhabitat × Forest site	2	3.93	0.140	3.20	0.202	1.19	0.551	14.27	<0.001
Exclusion × Burial	1	0.00	0.968	0.00	1.000	–	–	–	–
Exclusion × Forest site	1	0.16	0.686	0.00	1.000	7.73	0.005	18.87	<0.001
Burial × Forest site	1	0.12	0.730	12.00	0.001	–	–	–	–
Microhabitat × Exclusion × Burial	2	11.25	0.004	0.44	0.803	–	–	–	–
Microhabitat × Exclusion × Forest site	2	13.96	0.001	1.11	0.573	6.93	0.031	0.14	0.869
Microhabitat × Burial × Forest site	2	0.10	0.952	0.98	0.322	–	–	–	–
Exclusion × Burial × Forest site	1	3.53	0.060	0.00	1.000	–	–	–	–
Microhabitat × Exclusion × Burial × Forest site	2	4.64	0.098	0.29	0.587	–	–	–	–

Data have been separated for each oak species (*Q. canariensis* and *Q. suber*) and each reproductive cycle (2003/2004 and 2004/2005).

microhabitat (Fig. 4). Second, there was a significant effect of burial: a higher proportion of buried acorns survived predation; hence the number of established seedlings was higher than in acorns placed on the ground surface. The effect of burial was highly significant for the three types of microhabitat in the case of *Q. suber*. Differences between buried and unburied acorns were consistent for those of *Q. canariensis*, though the effect was significant only for open grassland microsites (Fig. 4). Finally, there were marked differences between the two forest sites, especially during the 2004/2005 cycle (Table 3). In that year, the number of seedlings was higher at TIR site, where a higher seed production of

Q. suber was found (Table 1). The low number of 1-year-old surviving seedlings in the experiment carried out during the 2003/2004 cycle is also remarkable. At best, less than 7% of the experimentally dispersed acorns escaped from predators and got established as seedlings (Table 1).

4. Discussion

Post-dispersal seed predation of the two oak species – *Q. canariensis* and *Q. suber* – was generally very high under all the

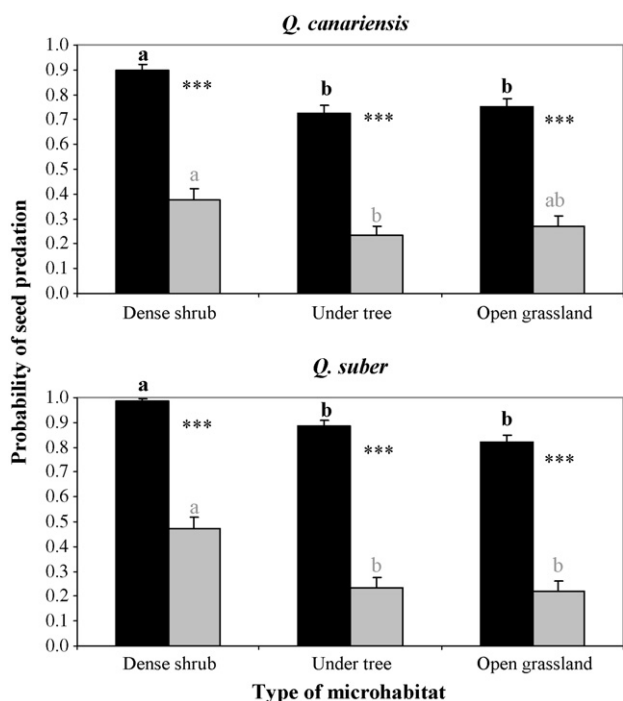


Fig. 1. Differences between burial treatments (on surface as black bars and buried as grey bars) on the probability of seed predation for the two oak species (*Q. canariensis* and *Q. suber*) and the three types of microhabitat (dense shrub, under tree, and open grassland). The significance level for effect of burial is expressed as: ns, not significant; **p* < 0.05, ***p* < 0.01, ****p* < 0.001. Statistically significant differences (at α < 0.05 level) between types of microhabitats, after pairwise comparisons, are represented across bars with different letters.

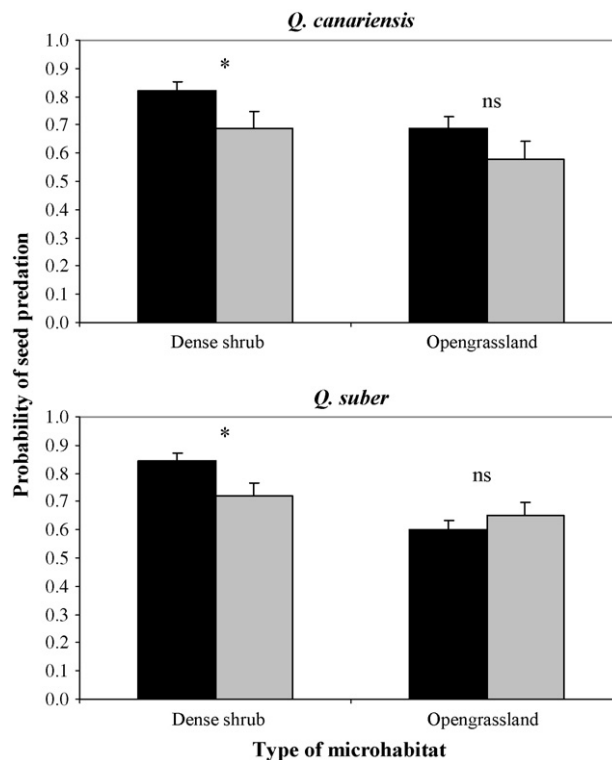


Fig. 2. Differences between exclusion treatments of large herbivores (fenced as black bars and unfenced plots as grey bars) on the probability of seed predation, for the two oak species (*Q. canariensis* and *Q. suber*) and two microhabitat types (open and dense understorey). Only significant results are shown: 2004/2005 cycle for *Q. canariensis* and 2003/2004 for *Q. suber*. The significance level for the effect of exclusion is expressed as: ns, not significant; **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

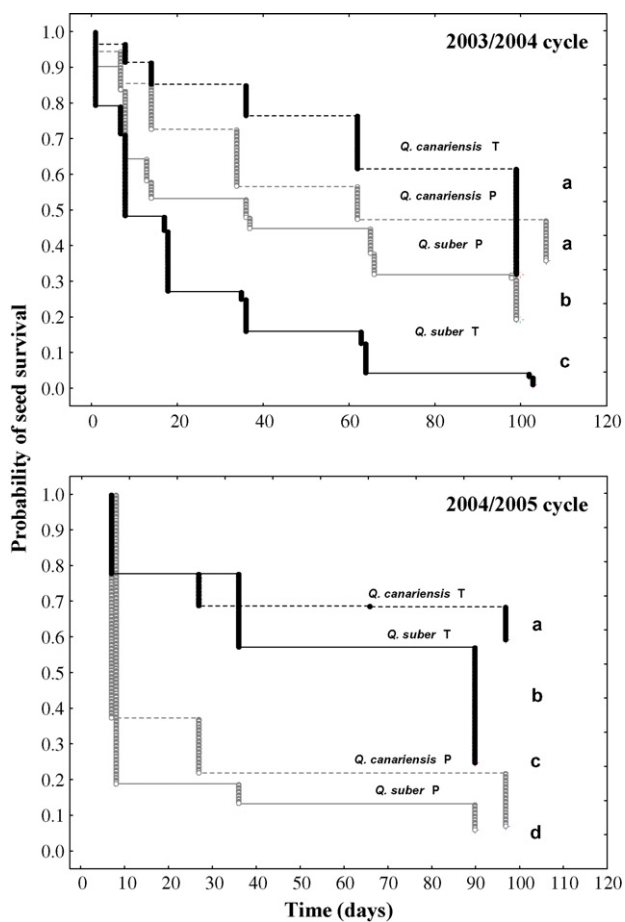


Fig. 3. Differences among species (*Q. canariensis* with dashed lines and *Q. suber* with solid lines) and forest sites (Tiradero with black symbols and Panera with white symbols) in seed survival rates during the two reproductive cycles. Different letters are used to show statistically different survival curves using non-parametric analyses for multiple samples.

conditions studied, and during the 2 years of study. In only 3 months, a large proportion of experimentally dispersed acorns were manipulated (removed or consumed *in situ*) by different animals; thus, seed–seedling transition could be considered an important bottleneck in the regeneration of the studied oaks, as

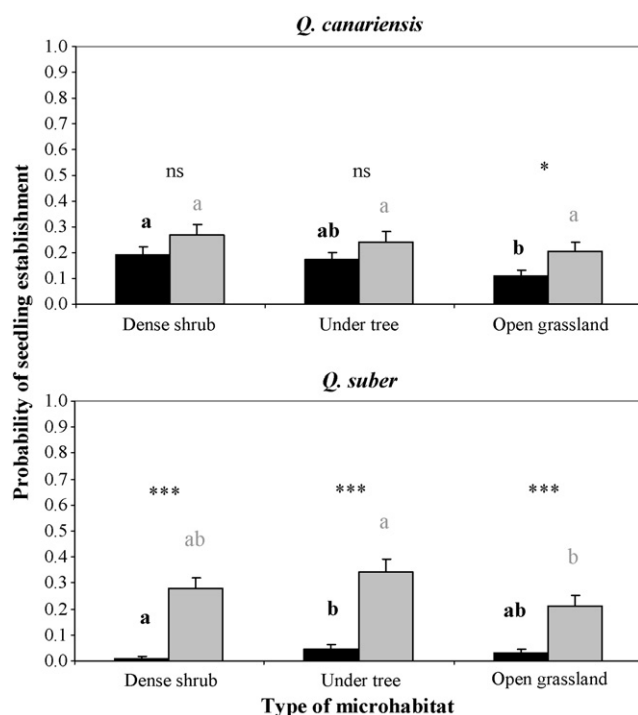


Fig. 4. Differences between burial treatments (unburied as black bars and buried as grey bars) on the probability of establishment of seedling for the two oak species (*Q. canariensis* and *Q. suber*) and the three types of microhabitat (dense shrub, under tree, and open grassland). The significance level for the effect of burial is expressed as: ns, not significant; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Statistically significant differences ($\alpha < 0.05$ level) between types of microhabitats, after pairwise comparisons, are represented across bars with different letters.

has been documented for other oak species (Crow, 1992; Herrera, 1995; Santos and Tellería, 1997; Gómez et al., 2003). Most acorns were completely removed by animals to be relocated, hoarded and (we assume) consumed later, as shown by other studies (Bossemma, 1979; Kikuzawa, 1988; Iida, 1996; Kollmann and Schill, 1996). However, it is likely that a small fraction escapes consumption, in which case these animals (especially birds, rodents or beetles) act as secondary dispersers (Jensen and Nielsen, 1986; Gómez, 2003; Pulido and Díaz, 2005; Acácio et al., 2007; Pérez-Ramos et al., 2007; Gómez et al., 2008). Therefore, it would be interesting to carry out

Table 3

Results of generalized linear models evaluating the effects of all factors and their interactions on the probability of establishment of seedling

	d.f.	2003/2004 cycle		2003/2004 cycle		2004/2005 cycle		2004/2005 cycle	
		<i>Q. canariensis</i>	<i>Q. suber</i>	<i>Q. canariensis</i>	<i>Q. suber</i>				
		χ^2	P	χ^2	P	χ^2	P	χ^2	P
Forest site	1	4.38	0.036	2.00	0.158	83.84	<0.001	47.14	<0.001
Exclusion	1	3.73	0.054	0.43	0.511	0.88	0.348	0.27	0.601
Burial	1	9.34	0.002	117.60	<0.001	–	–	–	–
Microhabitat	2	10.92	0.004	5.74	0.057	4.50	0.105	18.18	<0.001
Forest site × Exclusion	1	7.45	0.006	0.11	0.742	0.10	0.755	13.80	<0.001
Forest site × Burial	1	1.41	0.234	13.91	<0.001	–	–	–	–
Exclusion × Burial	1	1.63	0.202	1.16	0.282	–	–	–	–
Forest site × Microhabitat	2	7.44	0.024	4.21	0.122	0.95	0.621	14.05	<0.001
Exclusion × Microhabitat	2	9.44	0.009	2.74	0.254	9.64	0.008	4.83	0.090
Burial × Microhabitat	2	2.09	0.352	6.12	0.047	–	–	–	–
Forest site × Exclusion × Burial	1	0.57	0.449	3.55	0.060	–	–	–	–
Forest site × Exclusion × Microhabitat	2	6.91	0.032	1.42	0.492	4.06	0.131	2.46	0.117
Forest site × Burial × Microhabitat	2	5.31	0.070	5.77	–	–	–	–	–
Exclusion × Burial × Microhabitat	2	2.33	0.312	5.36	0.021	–	–	–	–
Forest site × Exclusion × Burial × Microhabitat	2	1.85	0.397	0.00	–	–	–	–	–

Data have been separated for each oak species (*Q. canariensis* and *Q. suber*) and each reproductive cycle (2003/2004 and 2004/2005).

future studies to quantify the proportion of acorns predated vs. dispersed in these forests. Since most of the experimental acorns that were consumed *in situ* showed evidences of being gnawed or partially eaten by rodents (probably *A. sylvaticus*), these small animals could be considered the main acorn predators in the study area, as reported for other Mediterranean landscapes (e.g., Borchert et al., 1989; Gómez et al., 2003; Pons and Pausas, 2007; Acácio et al., 2007).

In general, seed predators showed a higher preference for *Q. suber* acorns than for those of *Q. canariensis*. This inter-specific difference in seed predation seems to depend strongly on the seed size (*Q. suber* acorns are usually bigger than those of *Q. canariensis*), although other features, such as defensive compounds (e.g., tannins), may be involved (Pérez-Ramos et al., 2008b). Within each oak species, the probability of acorn predation depended on many factors, as is discussed next.

4.1. Effects of the type of microhabitat

Seed predation was strongly affected by the type of microhabitat where the acorn was dispersed. The highest probability of predation for both oak species (over 90%) occurred in those microhabitats located under dense shrubs. This pattern can be attributed to the foraging behaviour of small rodents, which show a higher activity in more closed microhabitats (e.g., Kikuzawa, 1988; Wada, 1993; Herrera, 1995; Hulme and Hunt, 1999; Gómez et al., 2003; Xiao et al., 2005), where they find more protection against large predators (Díaz, 1992; Wada, 1993; Herrera, 1995; Kollmann and Schill, 1996; Alcántara et al., 2000; Gómez et al., 2003). In contrast, the probability of a seed's escaping from animal predation was higher in open grasslands for both oak species, but the conditions for seedling establishment were less suited in this type of microhabitat, partly due to a problem of water-saturation during the wet season (Urbietta et al., 2008b) and partly to more severe desiccation risk during the dry season (Gómez, 2004b). Thus, there seems to be a conflict between demographic stages (*sensu* Schupp, 1995): microhabitats with a low predation risk for seeds may exhibit less favourable conditions for subsequent sapling recruitment, and *vice versa*. These results support the importance of studying not only the intensity of plant–animal interactions, but also their dependence on the environment in spatially heterogeneous landscapes (Kolb et al., 2007).

4.2. Effects of excluding large herbivores

The drastic reduction of oak species recruitment over recent decades in the study area has been attributed to the increasing density of large herbivores (wild and domestic), which feed on acorns and browse seedlings (Anon., 2005). The use of temporary fences to exclude large herbivores is a common practice to favour oak regeneration. However, our results showed that the probability of seed predation was similar in open microhabitats of both treatments (outside and inside the fenced plot), and – contrary to expectations – it was higher inside the enclosure in the most-densely vegetated microhabitats. The use of fences in our study may have increased rodent density by indirectly excluding their own predators and reducing the resource competition with large herbivores. Therefore, in spite of the well-known importance of large ungulates as acorn predators in many oak species (Gómez et al., 2003; Leiva and Fernández-Alés, 2003), the highest losses of acorns in our study area can be assumed to be caused by small rodents.

4.3. Effects of seed burial

The process of acorn burial simulating the biotic dispersal by European jays, mice or beetles had a positive effect on regenera-

tion of both oak species, by reducing the predation risk and by favouring the seedling establishment. These results are consistent with earlier studies (Seiwa et al., 2002; Gómez, 2004b). On one hand, the probability of acorn predation was lower for buried acorns than for those exposed on the ground surface, probably because burial of an acorn decreases its probability of being found and eaten by predators (Shaw, 1968; Hulme, 1994; Herrera, 1995; Hulme and Borelli, 1999). On the other hand, more emerged and 1-year-old surviving seedlings were established from buried acorns than from those dispersed on the forest floor surface. Other studies have demonstrated that seed burial favours the recruitment of seedlings, preventing desiccation and stimulating germination (Borchert et al., 1989; Sonesson, 1994; Gómez, 2004b).

4.4. Effect of acorn availability on the ground

The observed differences in seed predation rates between years and forest sites were probably associated with differences in acorn availability, which led to variable food resources for seed consumers on the forest floor. Thus, the probability of acorn predation was significantly higher in those years and forest sites where the estimated seed production was lower. Furthermore, in low-production years, the proportion of removed acorns was higher than that of those consumed *in situ*. This temporal pattern of higher seed predation in non-masting years has been also documented in other studies (Shaw, 1968; Hulme and Borelli, 1999; López Barrera et al., 2005; Xiao et al., 2005). Contrarily, with high seed abundance, greater food availability probably satiates seed predators (Janzen, 1971; Silvertown, 1980; Kelly and Sork, 2002), and the proportion of surviving seeds is therefore higher (Janzen, 1971; Crawley and Long, 1995; Wolf, 1996).

Moreover, population densities of seed predators may vary depending on resource availability in the preceding years (e.g., Curran and Leighton, 2000; Shnurr et al., 2002), which could also affect seed predation rates.

5. Conclusions

Post-dispersal seed predation plays an important role in the natural regeneration cycle of the two oak species coexisting at *Los Alcornoques* Natural Park. The probability of seed predation varied in space and time depending on many factors. On one hand, various factors related to the process of seed dispersal, such as burial or the type of microhabitat where the acorn is dispersed to, significantly affected seed predation probability. The highest acorn predation rates were found for acorns dispersed on the ground surface (not buried), and especially in more closed microhabitats (dense shrubby understorey), where small rodents usually have highest foraging activity. On the other hand, acorn availability on the forest floor – that was very variable due to the masting phenomenon – also had a marked effect. The lowest rate of acorn predation occurred in those years and forest sites with the highest acorn production. The exclusion of large herbivores by fences did not significantly decrease the probability of seed predation in the open microsites, but rather increased it in the most-densely vegetated microhabitats, probably as an indirect consequence of an unwanted increase of rodent populations.

According to the results obtained in this study, the following recommendations concerning restoration and reforestation practices can be made. First, burying seeds 1–3 cm deep in the soil can reduce losses by more than 40%, as well as favour the establishment of seedlings. Second, it is better to use microhabitats with a low or moderate vegetation cover and try

to avoid those microsites under dense shrubs, where rodents tend to concentrate and are more active. Third, in mixed oak forests, sowing seeds of a target species (for example, the less common *Q. canariensis*) during mast-years of other oak species will reduce the seed predation rate and increase recruitment probability. Finally, since rodents can be the main acorn predators in many forests (unlike in oak savannas), the use of fences to exclude large herbivores does not reduce seed predation, although fences may be crucial to protect the relatively few established seedlings from browsing.

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