

## Seed bank dynamics of two obligate seeders, *Cistus monspeliensis* and *Rosmarinus officinalis*, in relation to time since fire

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**Abstract** Many species in Mediterranean-type ecosystems regenerate after fire by seed germination from soil seed banks. Seed bank dynamics of two of those obligate seeders, *Cistus monspeliensis* and *Rosmarinus officinalis*, were investigated in relation to stand age since fire in southwestern Portugal. Soil seed density, annual seed input, annual seed losses through germination and seed persistence were compared between species at stands differing in age since fire (5, 10 and 35 years).

Soil seed density and seed input increased over the first decade after fire and were lowest at 35-year-old stands for *C. monspeliensis*. In *R. officinalis*, few seeds were produced and found in the soil at early stages, and maximum seed input and soil seed density were attained at 35-year-old stands. Soil seed density was mostly driven by seed production in both species, which is largely dependent on plant traits and population dynamics related to fire. Overall, stand age since fire had

a negligible effect on seed germination, seed persistence and viability. Ten to 39% of buried seeds were not recovered after 1 year, and viability of seeds recovered was 97–100% for *C. monspeliensis* and only 0–3% for *R. officinalis*.

Variation in plant traits within the seeder syndrome was evidenced by this study. *R. officinalis* evidenced lower seed persistence, lower proportion of viable seed produced and lower density of viable soil seed than *C. monspeliensis* at any stage after fire. *R. officinalis* is expected to depend largely on previous year seed production for population replacement after fire.

**Keywords** Mediterranean species · Post-fire succession · Seed burial experiment · Seed persistence · Seed viability

### Introduction

Seed banks are ecologically and evolutionarily important in the dynamics of plant populations. Acting as a reservoir of plant propagules, seed banks reduce the probability of population extinctions, buffer against local extinction of genotypes, facilitate the coexistence of competing species and are a major source for the recovery of plant communities after disturbances (Harper 1977; Pake and Venable 1996). The dynamics of soil seed banks are complex, and the size and the rate

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of turnover of the seed bank of a species depend on the balance between seed production, dispersal movements, predation, pathogenesis, viability, dormancy and germination, and also on the variability of these factors at spatial and temporal scales (Harper 1977; Keeley 1977; Lonsdale 1993; Pake and Venable 1996).

In Mediterranean-type ecosystems several plant species are killed by fire and regeneration of their populations depends on the germination of seeds stored in canopy or soil seed banks (Keeley 1986; Traubald 1981). In those obligate seeders accumulating soil seed banks, seeds are added to the soil in periods between fires and remain there until the next fire, when heat shock or other fire-related cues release dormancy or stimulate seed germination (Keeley 1991; Thanos et al. 1992; Brown and van Staden 1997). Plant composition after a fire will depend largely on the seed bank size of each species, as well as on the direct and indirect effects of fire on seed germination and seedling survival (Ne'eman et al. 1992; Bond and van Wilgen 1996; Lloret 1998; Lamont et al. 1999; Odion and Davis 2000).

A steady accumulation of seeds in the soil was predicted for species with persistent seed banks (Thompson and Grime 1979), and would be expected in species depending on recurrent fires for recruitment. However, many obligate seeders have shown fluctuations in seed production and large annual losses from the seed bank (Keeley 1977; Pierce and Cowling 1991; Kilian and Cowling 1992; Zammit and Zedler 1992; Troumbis 1996; Auld and Denham 1999), limiting a steady accumulation of seeds in the soil. Population processes may also affect the rate of seed bank build up. Some obligate seeders are short-lived and decline with stand age since fire (Keeley 1992; Zammit and Zedler 1992). If their populations die out prior to a fire, seed longevity will determine seed bank size (Parker and Kelly 1989), and become critical for population replacement after fire (Musil 1991; Pierce and Cowling 1991; Meney et al. 1994).

Despite the importance of seed bank dynamics in the persistence of populations of obligate seeders, most studies in fire-prone communities have focused on estimates of species composition and size of seed banks (e.g. Ne'eman and Izhaki 1999; Ferrandis et al. 1999b). Fewer studies have

attempted to characterise simultaneously the processes involved in seed bank dynamics (Musil 1991; Pierce and Cowling 1991; Kilian and Cowling 1992; Meney et al. 1994; Troumbis 1996), including estimates of seed survival (Auld 1986; Troumbis and Traubald 1987; Lunt 1995; Morgan 1995; Auld et al. 2000).

*Cistus monspeliensis* L. and *Rosmarinus officinalis* L. are co-occurring obligate seeders at Serra da Arrábida, a natural park dominated by Mediterranean maquis in southwest Portugal. Previous studies evidenced different demographic patterns for the two species in relation to fire. *C. monspeliensis* recruits a high number of seedlings in the first few years after fire, followed by a decline in shrub density at the end of the first decade, whereas *R. officinalis* recruits a lower number of seedlings but does not exhibit large differences in population numbers after the first 5 years following fire (Clemente et al. 1996; Clemente 2002). Those differences in population dynamics are expected to be related to seed bank dynamics, which could determine different patterns of regeneration under varying fire regimes.

In this study we addressed the patterns of seed bank dynamics in relation to stand age since fire for these two species. Specifically, we aimed to compare soil seed density, annual seed input into the soil, annual seed losses through germination and seed persistence between species at stands differing in age since fire.

## Species and study sites

*Cistus monspeliensis* (Cistaceae) and *Rosmarinus officinalis* (Labiatae) are summer semi-deciduous shrubs of similar height (1–1.5 m). The normal flowering period in the study sites is March to June for *C. monspeliensis*, peaking normally in April. This species produces a capsule containing approximately 12 seeds, released from July to October. Mean seed length and width at the study site is 1.44 mm and 1.13 mm, respectively, and mean seed mass 1.07 mg. *Rosmarinus officinalis* flowers from November to June, but two flowering peaks can be observed: November–February and April–June. Seed maturation in this species occurs within a few weeks after anthesis, overlapping the

flowering period. Each flower produces four seeds, which become loose within the calyx and fall to the soil surface when ripen. Mean seed length and width is 2.23 mm and 1.16 mm, respectively, and mean seed mass 0.32 mg. Both species have unspecialised seed dispersal. A life-span of 15 and 25 years was reported for *C. monspeliensis* (Roy and Sonié 1992) and *R. officinalis* (Lloret et al. 2003), respectively.

The study was carried out on a Mediterranean shrubland at Serra da Arrábida, south of Lisbon, Portugal (38°27′–38°29′ N, 8°57′–9°01′ W). The area has a Mediterranean climate, with an average annual rainfall of 747 mm at the closest weather station (Setúbal, 15 km east). A pronounced summer drought occurs from June to August, with only 4% of total annual rainfall. Mean maximum temperature for the hottest month (August) is 29°C and mean minimum temperature of the coldest month (January) is 6°C; mean annual temperature is 16°C. Human activities (e.g. wood cutting, pastoralism) in the site decreased after the creation of the natural park (1977) but fire is still a common disturbance.

Two sites were selected, according to their well-known fire history: Creiro and El Carmen. Mature vegetation is dominated by evergreen sclerophylls and by the two obligate seeders (*C. monspeliensis* and *R. officinalis*). At El Carmen, *Quercus coccifera* L. accounted for 30% of total plant cover; *Arbutus unedo* L., *Myrtus communis* L., *Phillyrea angustifolia* L., *P. latifolia* L. and *Pistacia lentiscus* L. accounted altogether for 40%. At Creiro, 30% of total plant cover was more evenly distributed among sclerophylls (*Myrtus communis* L., *P. angustifolia*, *P. lentiscus*, *Olea europaea* var. *sylvestris* Brot. and *Rhamnus lycioides* subsp. *oleoides* (L.) Jahandiez & Maire). Creiro was burned by a small wildfire (<1 ha) in June 1986 and El Carmen by a large fire (180 ha) in September 1991. Elevation is 30 m and 210 m at Creiro and El Carmen, respectively. Both sites were located on south facing slopes and distance between them was approximately 5 km. At each site, we selected adjacent older stands with similar characteristics. Historical fire records and age estimates from ring count on stem sections were used to determine age since fire. The most recently burned stands were 5 and 10 years old

(El Carmen and Creiro, respectively) at the beginning of the study (1996), and older stands were 34 and 35 years old. For simplification, the latter will be considered 35 years old.

## Methods

### Soil seed density

Soil seed density was estimated after the two species had set seed, but prior to autumn germination (last week of October 1996). Thus, our estimates included the seed input from the current year, as well as the older components. Those estimates would represent seed available for germination after a typical summer fire. Seeds found at the most recently burned stand represented seeds accumulated only after the fire, because seed reserves of both species are depleted during the 2 years following fire (Ferrandis et al. 1999a, b).

Seed density was estimated by pooling subsamples taken from large units. This method is recommended due to the arrangement of seeds in clusters (Bigwood and Inouye 1988). Eight soil cores (5 cm diameter and 5 cm deep) were collected at random from each of thirty-five 3 m × 3 m plots (only 28 at El Carmen 35-year-old stand), which were previously established for estimates of plant density and cover (Clemente 2002). Each soil core was separated by depth (0–2.5 cm and 2.5–5 cm) and the sub-samples from each depth were pooled for each plot ( $n = 28\text{--}35$  samples for each soil depth).

Seed density in the soil was estimated by the physical separation method (seed counting), which has been advised for species with dormant seeds (Ferrandis et al. 1999a). Soil samples were allowed to dry at room temperature during approximately 1 week. Afterwards, soil aggregates were broken up, large stones were removed, the soil was mixed up, and each sample was halved by mass, assigning half for the seed counting method and half for assessments of seed germination (see below, *Seed losses through germination*). Soil samples were stored at room temperature during three months, after which they were washed successively through 2 mm,

0.6 mm and 0.2 mm wire mesh sieves to remove seeds. The portion retained was examined and apparently intact seeds were identified to the species level and counted under a dissecting microscope.

### Seed input into the soil

Annual seed input into the soil was estimated from seeds falling to the soil surface, which were trapped by seed traps distributed over the sampling area. Traps consisted of 16.7 cm diameter and 12 cm deep plastic containers (catchment area 219 cm<sup>2</sup>) with holes in the bottom for drainage (smaller than seeds of the studied species). A total of 50 containers (only 25 at the El Carmen 35-year-old stand) were placed on the ground at each stand, attached to a metal stake. Containers were regularly positioned (1.5–3 m apart) along transects parallel to those used for seedling recruitment surveys (see below, *Seed losses through germination*). This distribution assured minimal disturbance to the vegetation, by using the same path for seed input and seedling germination assessments, and guaranteed an easier and less time consuming location of the seed containers. Seed collections were made in 1996 and 1998, at approximately 1 month intervals during the seed dispersal period of the two species (January to November). Seeds fallen into each collector were taken to the laboratory, where apparently intact seeds from both species were counted. During the study, several seed containers were discarded as they were broken, turned over or had obstructed holes, with evident decomposition of seeds. These were replaced for sampling in the following year. Our estimates of seeds entering the soil do not account for predation on the soil surface, since we expect that seeds falling inside the collectors were protected from seed predators foraging on the soil surface, and few signs of predation were detected on seeds recovered.

### Seed losses through germination

Seed losses through germination were estimated from field surveys, and from seedling emergence

from soil samples in a greenhouse trial. The two approaches were considered minimum and maximum estimates of seed losses through germination, respectively, since some germination episodes might have been missed in the field, while germination in greenhouse conditions is expected to exceed that occurring under natural conditions. We assumed that dormant seeds of *C. monspeliensis* would not germinate in the greenhouse, because a large fraction of seeds remain dormant in seedling emergence trials (Ferrandis et al. 1999a). Thus, only seeds germinating would represent potential seed losses from the seed bank.

Seed germination in the field was estimated on an annual basis, by direct counting of seedlings emerged on 32–75 permanent 1 m × 1 m plots (Clemente 2002). Seedlings were counted approximately at 1 month intervals, from October to June, in 1996/1997 and 1997/1998. Data were averaged over the 2 years. Assessments of seedling emergence in the greenhouse were conducted approximately during the same period of the field surveys, from January to August 1997. Soil samples were spread over a 2 cm layer of sterile sand in 10.0 cm × 14.5 cm × 4.5 cm (depth × length × height) trays. Thickness of the soil layer did not exceed 1 cm. Trays were watered regularly in order to maintain the soil constantly moist. There was no control over air temperature in the greenhouse; daily minimum and maximum temperatures ranged between 10–21°C (January) and 19–40°C (August). Observations of seedlings emerging were made every 2 days during 2 months, and weekly afterwards. Seedlings were identified and removed after counting. No seedlings emerged during the last month of the experiment.

### Seed persistence

Seed persistence in the soil was estimated at each stage after fire from a seed burial and recovery experiment. Seeds were placed inside 14 cm × 12 cm nylon mesh bags (860 μm), buried soon after seed release and recovered after 1–3 years for viability tests.

Seeds of *C. monspeliensis* were buried in early November 1995. Twenty five seeds were placed in

each of 48 bags. Three bags were buried under shrub canopies at approximately 1 cm depth, in each of four randomly selected points per stand. A coloured metal stake was used to locate each burial point and to fix the seed bags. One bag was recovered from each of the four points after 11, 23 and 35 months (October 1996, 1997 and 1998, respectively). Those periods will be referred to as 1, 2 and 3 years. Seeds used in this experiment were collected from several plants near the study sites, in late September 1995. Prior to burial, seeds were air-dried, placed in paper bags and stored in the dark at room temperature. Seed viability was assessed on a sample of 100 intact seeds using the tetrazolium method (14 h in the dark on a 0.1% tetrazolium chloride solution, Moore 1973).

Seeds of *R. officinalis* were buried in early July 1997. One bag containing 25 seeds was buried at each of five randomly selected points at each stand, using the same procedure as for *C. monspeliensis*. All bags of *R. officinalis* were recovered after 1 year. Seeds used in the experiment were collected near the study sites in late May 1997. As for *C. monspeliensis*, seed viability was assessed on a sample of 100 intact seeds using the tetrazolium method.

Recovered seeds were counted under a dissecting microscope and inspected for evidences of germination or predation. Since the fate of most non-intact seeds was difficult to determine, seeds were first classified as empty (only cracked seed coats remaining, those seeds could have either germinated or been predated) or intact (apparently filled seeds with intact seed coats). Intact seeds were tested for viability by the tetrazolium method.

### Statistical analyses

All comparisons between stages after fire were made within sites. Soil seed density, seed input and total number of seeds germinated per year were compared between stages and between species with Mann–Whitney *U* tests, because assumptions of normality and homogeneity of variance were not met by data transformations. A Wilcoxon matched pairs test was used for

comparisons of seed density between soil layers. The effect of time of burial and stage after fire on the fate of seeds in the soil was determined using a two-way ANOVA, with the factors stage and time of burial, for *C. monspeliensis*. A one-way ANOVA was used for *R. officinalis*, as seeds of this species were buried for 1 year only. Data were arcsin transformed when necessary. All analyses were carried out using the STATISTICA package (Stat Soft Inc.).

## Results

### Soil seed density

Soil seed density after dispersal ranged from 640 seeds/m<sup>2</sup> to 4388 seeds/m<sup>2</sup> in *C. monspeliensis* and from 102 seeds/m<sup>2</sup> to 3061 seeds/m<sup>2</sup> for *R. officinalis* (Table 1). Although the sample design used was expected to overcome the effect of seed clustering, the variance was still very high at all stages for both species. Five years after fire, soil seed density of *C. monspeliensis* did not differ from that of the 35-year-old stand (El Carmen), whereas 10 years after fire it was already two times larger (Creiro). This indicates that seed numbers of this species increase with time since fire during early stages, but decrease afterwards. *Rosmarinus officinalis* showed a different pattern of variation of seed density with stand age, with

**Table 1** Soil seed density ( $n/m^2$ ) of *Cistus monspeliensis* and *Rosmarinus officinalis* at different stages after fire at two sites, Creiro and El Carmen

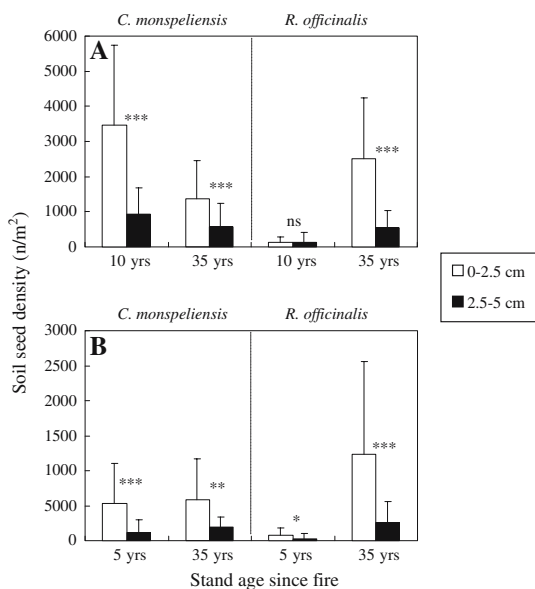
Site	Age since fire	<i>C. monspeliensis</i>	<i>R. officinalis</i>
Creiro	10 years	4388 ± 2682	196 ± 253
	35 years	1945 ± 1505	3061 ± 2089
	<i>U</i>	233***	101***
El Carmen	5 years	640 ± 619	102 ± 137
	35 years <sup>a</sup>	779 ± 664	1493 ± 1559
	<i>U</i>	4118 ns	121***

Values (mean ± s.d.) were estimated from seed counts on 35 (<sup>a</sup>28) soil samples collected after seed dispersal and before the germination season. *U*: Mann–Whitney *U* tests for comparisons between stages within sites. Significance levels: ns = non significant, \*\*\**P* < 0.001

substantially lower seed numbers at early stages after fire than at 35-year-old stands.

The largest difference in soil seed density between the two species was recorded 10 years after fire (Creiro)—*C. monspeliensis* had 22 times more seeds than *R. officinalis*. At 35-year-old stands, seed numbers were similar, or larger for *R. officinalis*.

Soil seed density of the two species was 2–5 times higher in the top soil layer (0–2.5 cm) as compared to the deeper layer (2.5–5 cm), except for *R. officinalis* 10 years after fire (Fig. 1A, B). Differences between layers were larger at 5-year-old and 10-year-old than at 35-year-old stand for *C. monspeliensis* while *R. officinalis* showed the opposite trend. Differences between species in seed densities at each soil layer followed the pattern of total seed numbers at 5-year-old and 10-year-old stands. At 35-year-old stands, the top layers had two times more seeds of *R. officinalis* than *C. monspeliensis*, while similar values were found at the deeper layers.



**Fig. 1** Soil seed density of *Cistus monspeliensis* and *Rosmarinus officinalis* at two soil depths (0–2.5 cm and 2.5–5 cm) at different stages after fire at two sites, Creiro (A) and El Carmen (B). Values are mean  $\pm$  s.d. of intact seeds on 28–35 soil samples collected after seed dispersal and before germination season. Differences between the two soil layers within stages are indicated by ns = non significant, \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$  (Wilcoxon test)

## Seed input into the soil

Seed input into the soil was highly variable on an annual basis for both species (Table 2). Size of the seed input differed significantly between stages, showing a trend of variation with stand age similar to that of the soil seed numbers (Table 1). *Cistus monspeliensis* recorded highest seed input at early stages. Only 5 years after fire, the seed input of *C. monspeliensis* was already threefold to fivefold higher than at 35-year-old stands (El Carmen); this difference was still observed 10 years after fire at Creiro. At early stages, annual seed input was approximately two times larger than our estimates of soil seed after dispersal, whereas at 35-year-old stands density of the seed input was similar or lower than that of the soil.

The seed input of *R. officinalis* showed a pattern of variation with stand age opposite to that of *C. monspeliensis*, with lowest seed input 5 and 10 years after fire (Table 2). This species recorded the largest differences in seed input between stands—at El Carmen the seed input was 30–50 times smaller at 5-year-old than at 35-year-old stand. The density of the seed input was lower than that of the soil at all but one stand.

Seed input of *C. monspeliensis* was larger than that of *R. officinalis* at 5-year-old and 10-year-old stands. At 35-year-old stands the differences between the two species were smaller.

## Seed losses through germination

Mean number of seedlings emerged was higher in the greenhouse than in the field for the two species (Table 3). The highest differences were recorded for *R. officinalis*, especially at El Carmen, where very few seedlings of this species emerged in the field. Overall, seedling emergence was lower at this site as compared to Creiro.

Seedling emergence of *R. officinalis* was 7–10 times greater at 35-year-old stands than at early stages after fire, while for *C. monspeliensis* differences were dependent on the type of estimate. Mean seedling density of *C. monspeliensis* was approximately 60 times higher than that of *R. officinalis* at early stages in the field surveys, but only 8 times higher in the greenhouse. At 35-year-

**Table 2** Number of seeds per m<sup>2</sup> of *Cistus monspeliensis* and *Rosmarinus officinalis* (mean  $\pm$  s.d.) added annually to the soil at different stages after fire at two sites, Creiro and El Carmen

Site	Age since fire	<i>Cistus monspeliensis</i>			<i>Rosmarinus officinalis</i>			<i>n</i>
		1996	1998	Mean (%s.s.)	1996	1998	Mean (%s.s.)	
Creiro	10 years	6506 $\pm$ 5689	9019 $\pm$ 6153	7839 (179)	366 $\pm$ 855	267 $\pm$ 497	341 (174)	41
	35 years	1713 $\pm$ 2716	2621 $\pm$ 3279	2134 (110)	947 $\pm$ 1190	552 $\pm$ 702	738 (24)	43–49
	<i>U</i>	1234***	1339***		567***	655**		
El Carmen	5 years	1006 $\pm$ 1222	2183 $\pm$ 2275	1504 (235)	19 $\pm$ 59	10 $\pm$ 56	15 (15)	44
	35 years	356 $\pm$ 682	394 $\pm$ 595	391 (50)	962 $\pm$ 1896	311 $\pm$ 363	827 (55)	27–29
	<i>U</i>	330***	603***		193***	220***		

Mean values and mean values expressed as a percentage of soil seed density (%s.s.) are given. Seeds were trapped on 219 cm<sup>2</sup> containers and regularly recovered over the seed dispersal period. Number of seed traps is indicated by *n*. *U*: Mann–Whitney *U* tests for comparisons between stages within sites. Significance levels: \*\**P* < 0.01, \*\*\**P* < 0.001

old stands, the differences between species were smaller.

The estimates of seed losses through germination represented a small proportion of total seed in the soil: generally below 1% for field estimates and reaching a maximum of 6% in greenhouse estimates (Table 3). Overall, differences between stands were very small compared to the differences observed in the seed input.

#### Seed persistence

The proportion of viable seeds in the seed lot of *C. monspeliensis* was higher than that of *R. officinalis*: 89% and 55%, respectively. Most non-viable seeds of the latter species were aborted, containing only remains of embryo

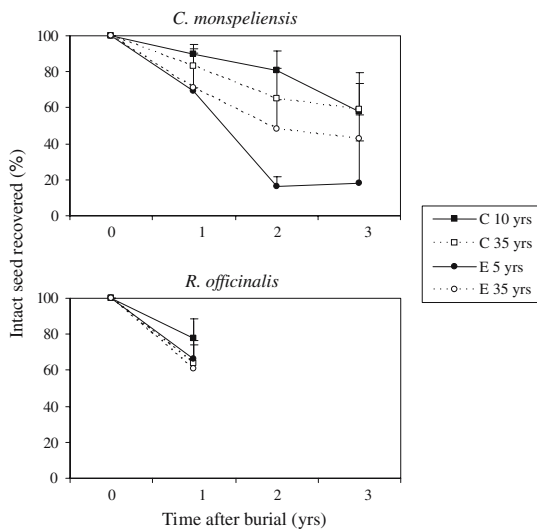
tissues inside the seed coat, but did not differ from filled seeds in external characteristics, due to the presence of an intact seed coat.

After 1 year, 61–90% of seeds buried were intact, the proportion of seeds recovered being slightly higher for *C. monspeliensis* than for *R. officinalis* (Fig. 2). The remaining proportions were missing and empty seed coats. Whether those germinated or decayed was impossible to determine. Very few seed remains had traces of dead seedlings, but *C. monspeliensis* seedlings were occasionally observed emerging from a seed bag, which indicates that many seeds missing could have germinated, and due to the restrictions imposed by the nylon mesh, seedlings were unable to reach the soil surface and decayed. Seeds could also be predated or infected by fungi, since some seeds were surrounded by mycelium.

**Table 3** Total number of seedlings (*n*/m<sup>2</sup>) of *Cistus monspeliensis* and *Rosmarinus officinalis* emerged annually (from October to June) at different stages after fire at two sites, Creiro and El Carmen

Site	Age since fire	<i>Cistus monspeliensis</i>			<i>Rosmarinus officinalis</i>		
		Field	Greenhouse	Mean (%s.s.)	Field	Greenhouse	Mean (%s.s.)
Creiro	10 years	18.61 $\pm$ 19.20 (0.4)	47.40 $\pm$ 79.73 (1)	33 (1)	0.33 $\pm$ 0.59 (0.2)	7.06 $\pm$ 25.82 (4)	4 (2)
	35 years	17.57 $\pm$ 19.74 (1)	99.63 $\pm$ 117.34 (5)	59 (3)	2.67 $\pm$ 3.70(0.1)	74.63 $\pm$ 125.10 (2)	39 (1)
	<i>U</i>	2024 ns	514*		705***	463***	
El Carmen	5 years				2.78 $\pm$ 4.09 (0.4)	32.74 $\pm$ 71.38 (5)	18 (3)
	35 years	1.06 $\pm$ 2.04 (0.1)	48.07 $\pm$ 88.89 (6)	25 (3)	0.11 $\pm$ 0.28(0.01)	32.63 $\pm$ 55.73 (2)	16 (1)
	<i>U</i>	820*	546 ns		1026 ns	925**	

Estimates of seedling emergence are displayed for field surveys and a greenhouse trial. Mean values and values expressed as a percentage of soil seed density (%s.s.) are given. Values are mean  $\pm$  s.d. *U*: Mann–Whitney *U* tests for comparison of emergence between stages within sites. Significance levels: ns = non significant, \**P* < 0.05, \*\**P* < 0.01, \*\*\**P* < 0.001. *n* = 31–75 1 m<sup>2</sup> plots (field), *n* = 28–35 soil samples (greenhouse trial)



**Fig. 2** Percentage of intact seed recovered at various intervals during the 3 years of a burial experiment for *Cistus monspeliensis* and *Rosmarinus officinalis*. Values are mean  $\pm$  1 s.d. The experiment was carried out at different stages after fire (5, 10 and 35 years) at two sites (C-Creiro and E-El Carmen).  $n = 4$  for *C. monspeliensis*;  $n = 5$  for *R. officinalis*

The effect of time of burial, which was tested only on *C. monspeliensis*, had a significant effect on the proportion of intact seed recovered at the two sites, with decreasing proportions over time (Table 4, Fig. 2). Overall, the rate of seed losses decreased from the second to the third year, when intact seeds persisting represented between 18% and 59% of the seed lot buried.

The pattern of seed decay over time at 35-year-old stands was similar at the two sites; 5-year-old

and 10-year-old stands showed quite different decay curves in the two sites, deviating as well from those of 35-year-old stands (Fig. 2). However, stand age did not affect significantly the proportion of intact seed recovered for *R. officinalis* and, for *C. monspeliensis*, the effect of stand age was significant only at El Carmen, with a lower proportion of seeds recovered at 5-year-old than at the 35-year-old stand (Table 4).

Viability of seeds persisting after 1 year differed greatly between the two species: 97–100% for *C. monspeliensis* and only 0–3% for *R. officinalis* (Table 5). Nonviable seeds of *R. officinalis* were mostly seeds with an aborted embryo. Thus, the unbalanced proportion of viable and nonviable seeds of *R. officinalis* in the burial experiment seems to result from a net disappearance of filled seeds. Viability of recovered seeds of *C. monspeliensis* was still high in third year of the experiment, with a minimum value of 70%. Stand age since fire had a significant effect on seed viability of *C. monspeliensis* only at Creiro, with lower seed viability at the 10-year-old stand (Tables 4 and 5). At the end of the experiment, the proportion of initial *C. monspeliensis* viable seed persisting reached 50% at all but one stand (the 5-year-old stand, where a great proportion of seeds were missing) (corresponding values were  $49.44 \pm 28.42\%$  and  $57.30 \pm 13.42\%$  at 10-year-old and 35-year-old stands, respectively, at Creiro and  $20.22 \pm 26.59\%$  and  $46.07 \pm 12.91\%$  at 5-year-old and 35-year-old stands, respectively, at El Carmen).

**Table 4** *F*-values of the analysis of variance testing for the effects of stage after fire and time of burial on the proportions of intact seed recovered and viable seed of *Cistus monspeliensis* and *Rosmarinus officinalis* at two sites, Creiro and El Carmen

	<i>Cistus monspeliensis</i>			<i>Rosmarinus officinalis</i>		
	Intact seed	Viable seed	d.f.	Intact seed	Viable seed	d.f.
<i>Creiro</i>						
Stage	1.60 ns	5.00*	1	3.52 ns	0.27 ns	1
Time of burial	7.77**	6.70**	2			
Stage $\times$ time	0.72 ns	1.41 ns	2			
<i>El Carmen</i>						
Stage	9.92**	0.43 ns	1	0.23 ns	1.00 ns	1
Time of burial	17.13***	1.15 ns	2			
Stage $\times$ time	2.10 ns	0.34 ns	2			

Significance levels: ns = non significant, \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .  $n = 4$  and  $n = 5$  replicates of 25 seeds, for *C. monspeliensis* and *R. officinalis*, respectively. Seeds were buried at 1 cm depth inside mesh bags during 1, 2 and 3 years for *C. monspeliensis* and 1 year for *R. officinalis*



**Table 5** Percentage viability of seeds of *Cistus monspeliensis* and *Rosmarinus officinalis* recovered from a burial experiment after 1, 2 and 3 years at different stages after fire (5, 10 and 35 years) at two sites, Creiro and El Carmen

Time (years)	<i>Cistus monspeliensis</i>			<i>Rosmarinus officinalis</i>
	1	2	3	1
<i>Creiro</i>				
10 years	98.91 ± 2.17	73.64 ± 18.30	69.99 ± 21.03	1.32 ± 2.63
35 years	98.61 ± 2.78	95.95 ± 4.82	87.37 ± 12.25	2.36 ± 3.24
<i>El Carmen</i>				
5 years	97.14 ± 3.30	83.33 ± 19.25	75.00 ± 50.00	2.86 ± 6.39
35 years	100.00 ± 0.00	81.84 ± 19.04	96.06 ± 4.66	0.00

Initial seed % viability was  $89.00 \pm 6.83$  and  $55.20 \pm 9.12$  for *C. monspeliensis* and *R. officinalis*, respectively. Values are mean  $\pm$  s.d.,  $n = 4$  for *C. monspeliensis* and  $n = 5$  for *R. officinalis*

## Discussion

### Seed bank size in relation to time since fire

Variation of soil seed density with stand age since fire closely followed variation in seed input for both species. Since losses due to germination or decay did not show large variations with stand age, these results suggest that seed bank size is mostly driven by the seed input at any stage after fire. This is also supported by the positive correlation between seed bank size and crown cover on a plot basis (Clemente 2002), also reported in other species from Mediterranean-type ecosystems (Keeley 1977; Pierce and Cowlings 1991; Zammit and Zedler 1992, 1994; Troumbis 1996).

Soil seed numbers and seed input of *R. officinalis* increased with stand age since fire, while those of *C. monspeliensis*, although increasing during the early stages after fire, were consistently lowest at 35-year-old stands. The patterns of variation of soil seed numbers and seed input also indicated a lower rate of seed bank build-up in *R. officinalis* than in *C. monspeliensis*. Studying *Cistus* species in Israel, Ne'eman and Izhaki (1999) found a pattern of seed bank accumulation with stand age since fire similar to the one observed in *C. monspeliensis*. Similar studies were not found for *R. officinalis*.

Seed production at any stage after fire may be determined by age, size and/or plant density and differences in soil seed numbers between *C. monspeliensis* and *R. officinalis* can be explained

with reference to their life-history traits and population dynamics related to fire. *Cistus monspeliensis* is a medium-lived species and has a short juvenile period whereas *R. officinalis* seems to have a longer life-span and lower growth rates (Clemente 2002; Lloret et al. 2003). At early stages after fire, the high plant density of *C. monspeliensis* and early maturation, with massive seed production in the third year (Clemente et al. 1996), contributed to the rapid re-build of the seed bank 5 years after fire. Conversely, *R. officinalis* has low plant density and plants are smaller than those of *C. monspeliensis* (Clemente 2002). Thus, due to high seed input, *C. monspeliensis* replenishes the seed bank shortly after fire while soil seed density increases at a slow rate in *R. officinalis*.

Population dynamics of the two species also differs in periods between fire: reductions in plant density and cover at 35-year-old stands were observed for *C. monspeliensis*, while no changes in density and an increase in cover were recorded for *R. officinalis* (Clemente 2002). Thus, at 35-year-old stands, the highest soil seed density of *R. officinalis* seems to result from an increase in seed production, due to increases in individual shrub sizes, whereas a decline in shrub density and cover would account for the reduction in the seed bank of *C. monspeliensis*. Age and density also affect the reproductive output of individual plants (Bond and van Wilgen 1996; but see Roy and Sonié 1992; Zammit and Zedler 1992), but such effects probably would not over or under-compensate for the effect of decreasing numbers of *C. monspeliensis* plants per unit area.

Contrary to *C. monspeliensis*, the seed crops of *R. officinalis* comprised a very small proportion of viable seeds. This result, and the high proportion of nonviable seeds recovered in the burial experiment indicate that the seed banks of *R. officinalis* should also comprise a large fraction of nonviable seeds. As a consequence, the seed counting-method, recommended for species with a hard-coated seed fraction (Ferrandis et al. 1999a), like *C. monspeliensis*, may not give a reliable estimate of the seed bank in this species. Since the estimates of seed persistence and viability based on the burial experiment may be biased, because only one seed lot was used, we estimated the viability of the seed banks of *C. monspeliensis* and *R. officinalis* on seeds directly isolated from soil samples from the 35-year-old stand at Creiro. Those estimates were comparable with the values obtained in the burial experiment for *C. monspeliensis*, but slightly higher for *R. officinalis*—86% and 5%, respectively (data not shown). Using such estimates, the viable seed density of *R. officinalis* at 10-year-old and 35-year-old stands at Creiro would be 10 seeds/m<sup>2</sup> and 153 seeds/m<sup>2</sup>, respectively and corresponding values for El Carmen 5-year-old and 35-year-old stands would be 5 seeds/m<sup>2</sup> and 75 seeds/m<sup>2</sup>, respectively. Thus, viable seed densities in *R. officinalis* would still be 10 times smaller than those of *C. monspeliensis* at 35-year-old stands, despite similar or higher seed density estimated by seed counting. Considering the estimates of viable soil seed given above, seedling emergence in the greenhouse trial represented 44–72% of the total soil seed estimated for *R. officinalis*. Although seedling emergence was monitored over a short period and we did not intend to use it as an estimate of seed bank size, this indicates that the seedling emergence method would be the most appropriate for *R. officinalis*.

#### Patterns of seed persistence

This study evidences distinct patterns of seed persistence in the soil in the studied species. Three years after burial, approximately 50% of buried seeds of *C. monspeliensis* were still recovered and maintained high seed viability ( $\geq 70\%$ ). Since the great majority of the seed banks of

*Cistus* species comprise dormant hard-coated seeds (Troumbis and Trabaud 1987; Thanos et al. 1992; Ferrandis et al. 1999a), highest seed losses over the first 2 years after burial are likely to represent the germination or rotting of the soft-coated fraction. The persisting fraction had high seed viability and was probably more hard-seeded. This pattern of seed persistence resembles that of species with long-term persistent seed banks from other Mediterranean-type ecosystems (Lunt 1995; Auld et al. 2000; Holmes and Newton 2004).

In contrast, only 0–3% seeds were still viable 1 year after burial in *R. officinalis*, providing evidence of lower seed persistence than in *C. monspeliensis*. To our knowledge, this is the first report of very low seed persistence in an obligate seeder from the Mediterranean basin, although this syndrome is common among South-African and Australian species (Musil 1991; Pierce and Cowling 1991; Meney et al. 1994; Holmes and Newton 2004).

Low dormancy level is the likely cause of rapid seed bank attrition in *R. officinalis*. Higher seed germination in the greenhouse than in the field as compared to *C. monspeliensis* and the large fraction of seeds with aborted embryo among recovered seeds provide some evidence for this hypothesis. Germination experiments of Salvador and Lloret (1995) also indicated low seed dormancy in *R. officinalis*. It is likely that a large proportion of seeds recently added to the soil, present at the top soil layers, germinate as soon as the conditions required are met.

If seed longevity does not exceed 1 year, seed banks of *R. officinalis* could be classified as transient (Thompson et al. 1993). A longer seed burial experiment, with different aged seed crops, would provide a more reliable estimate of seed longevity for this species (Zammit and Zedler 1992; Pierce and Moll 1994). Moreover, in order to accurately estimate the size of persistent and transient fractions of the seed bank, it would require sampling soil seeds not only after seed dispersal, as in our approach, but also before dispersal. Although results from the burial experiment evidenced short seed persistence in *R. officinalis*, we cannot infer that there is no persistent seed fraction in the seed bank. At 35-year-old stands, the soil

had 2–4 times more seeds than the seed input, suggesting that soil seeds include both the recently dispersed fraction and a fraction that was already present. Provided that a small number of recently produced seeds does not germinate and is incorporated into the soil, those seeds could form a persistent seed bank. It should also be taken into account that, despite the low proportion of viable seeds persisting after 1 year, those represent only one component of the seed bank of *R. officinalis*. Since seed production occurs over a large period, new seeds are added almost continuously to the soil. Thus, low seed persistence may be compensated over a large period of seed production (Picó and Retana 2000).

There was no effect of stand age since fire in both the proportion of soil seeds that germinated and the fate of buried seeds. Only at one site a higher proportion of seeds germinated or decayed at early stages after fire as compared to 35-year-old stand. This could be related to post-fire vegetation dynamics, since more gaps are available at early stages (Clemente et al. 1996) and those, together with soil characteristics (e.g. low litter accumulation and large diurnal changes in soil temperature) are expected to affect seed survival (Lunt 1995).

Independence between seed fates and stand age was also reported for other species from Mediterranean-type communities (Parker and Kelly 1989), and was attributed to the effects of microsite characteristics on seed survival and germination. Those vary greatly within stands (Lunt 1995; Morgan 1995) and over time (Auld 1986; Auld et al. 2000), and this variability might have overridden any possible effects of stand age in this study.

We estimated that a maximum of 6% of the total number of seeds present in the soil after dispersal would germinate over 1 year, while estimates of seed losses from the burial experiment ranged between 10% and 39%. Those figures suggest that for both species many seeds present in the soil after dispersal are lost over 1 year and do not incorporate the seed bank. Given the differences between the above estimates, factors other than germination are expected to be operating. High losses from the seed bank were recorded for several

Mediterranean species (Keeley 1977; Troumbis and Trabaud 1987; Parker and Kelly 1989; Pierce and Cowling 1991; Kilian and Cowling 1992; Meney et al. 1994); seed predation has been reported as the major cause of those losses (e.g. Lonsdale 1993; Garner and Witkowski 1997; Auld and Denham 1999), and is expected to be higher under natural conditions than in the burial experiment, where it could be prevented by the nylon mesh. The high proportion of seeds present in the top soil layer is expected to represent the fraction most recently added to the soil, and is more likely to be predated than the buried seed fraction (Thompson and Grime 1979; Thompson et al. 1993). Further research is needed to investigate whether seed predation differs between the two species and between stages after fire.

#### Implications for species persistence under varying fire regimes

The persistence of obligate seeders after fire depends on: (i) the capacity to produce enough seeds to fill up seed banks during inter fire periods, (ii) enhancement of recruitment by fire and/or recruitment responses associated with the fire event and (iii) seed longevity and dormancy (Kilian and Cowling 1992; Lamont et al. 1999; Auld et al. 2000; Pausas and Lavorel 2003). The combination of these traits will be important in shaping the abundance of species with similar regeneration strategies (Kilian and Cowling 1992; Lamont et al. 1999). It is already known that germination and recruitment enhancement by fire are higher in *C. monspeliensis* than in *R. officinalis* (Thanos et al. 1992; Salvador and Lloret 1995). In this study we provided evidence of further traits differing between the two species: seed bank recovery is faster and seed longevity is higher in *C. monspeliensis* than in *R. officinalis*. Such differences are expected to affect the species ability to survive under varying fire regimes.

Species with long-term persistent seed banks are unlikely to become locally extinct under long fire intervals, whereas species with transient or short-term persistent seed banks would be at risk of local extinction if the fire interval exceeds the life-span (Bond and van Wilgen 1996; Auld et al. 2000). Lloret et al. (2003) predicted higher abun-

dance of *R. officinalis* and *Cistus* species at intermediate fire recurrences, but *R. officinalis* would attain maximum abundance at longer fire intervals (100, 40 and 20 years) than *Cistus* (20 and 10 years). These predictions are in accordance with our data, since seed production and soil seed density of *R. officinalis* would be largest at the time of fire for such fire intervals. However, if the fire interval largely exceeds the life-span, we would expect *C. monspeliensis* to survive longer fire intervals than *R. officinalis*, because a large fraction of seeds would persist beyond the death of plants in the former while the latter would be dependent on the presence and longevity of a small fraction of persistent seeds. On the other hand, occasional recruitment between fires occurs in both species and could ensure seed production if fire intervals exceed the life-span. Recruitment in the absence of fire is higher in *C. monspeliensis* than in *R. officinalis*, but provided that the life-span is higher in *R. officinalis*, it could compensate for low recruitment (Clemente 2002).

Seed accumulation rate is particularly important for survival under a regime of short fire intervals (Bradstock et al. 1997; Keeley et al. 1999). *Cistus monspeliensis* had already re-build the seed bank 5 years after fire, which accounts for the expected survival of *Cistus* under a fire interval of 5 years (Pausas 1999). The lower seed production and soil seed density during the first decade after fire observed in *R. officinalis* indicate that this species might be more vulnerable to a short fire interval than *C. monspeliensis*. At the El Carmen site, viable seed density of *R. officinalis* 5 years after fire exceeds the density of seedlings established only by one order of magnitude, whereas those differ by two orders of magnitude in *C. monspeliensis* (Clemente 2002). Thus, low soil seed density of *R. officinalis* may hamper replacement of pre-fire populations if fires occur at short intervals.

Some obligate seeders from fynbos have short-term persistent seed banks and seem to rely on annual seed inputs to maintain a soil seed bank (Musil 1991; Pierce and Cowling 1991; Meney et al. 1994). Such species may be dependent on the previous seed crop for replacement of populations after a fire and are at risk of local extinction following a fire event when soil-stored seed reserves are low (Auld et al. 2000).

Considering the low seed persistence and viability of soil seeds, a decrease in size and viability of the seed crop immediately after a fire is also expected to affect the post-fire recruitment.

Plant functional classifications have been used to estimate plant responses to disturbances (Rusch et al. 2003). However, the testing of those plant functional classifications is still limited by a lack of knowledge on plant traits, especially on seed persistence (Pausas and Lavorel 2003). As demonstrated in this study and in several studies from other Mediterranean-type ecosystems (Pierce and Cowling 1991; Auld et al. 2000; Holmes and Newton 2004), there is substantial variation in seed persistence among obligate seeders, and generalizing predictions of plant responses to fire regime on the basis of the seeder syndrome may have limited power. Powerful predictive models of plant trait responses to change in disturbance regimes require more refined plant functional classifications (Pausas and Lavorel 2003), which already include traits like seed persistence. Such approach was used by Lloret et al. (2003), and although lacking quantitative data on seed persistence, their predictions of population persistence under varying fire regimes also differed between *Cistus* species and *R. officinalis*. In this study we provided quantitative evidences for differences in seed bank dynamics between *C. monspeliensis* and *R. officinalis* which confirm the necessity of more refined plant functional classifications.

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