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Soil seed bank, fire season, and temporal patterns of germination in a seeder-dominated Mediterranean shrubland

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Abstract Soil seed banks play a major role in the post-fire regeneration of Mediterranean shrublands. They vary throughout the year in species composition, abundance, and readiness to germinate. After fire, germination occurs mainly during the following fall to spring. Time of germination can determine recruitment success. It is unclear what factors control post-fire germination and its timing. We tested the effects of season and fire on the readily germinable soil seed bank of a seeder-dominated shrubland. Plots were burned early and late in the summer season (ES, LS). Soil samples were collected before and after fire, and germinated in a chamber simulating successively autumn, winter, and spring conditions. Samples were kept moistened at all times. Fire intensity was similar between ES and LS. Several species of *Cistus* and herbs, mostly annuals, were dominant. Most germination occurred during the simulated-autumn period, with little subsequent germination during the following two periods. Germination speed (T_{50}) during simulated-autumn was similar for shrubs and herbs, and independent of season or fire. Germination was lower for two shrubs (*Rosmarinus officinalis*, *Cistus salvifolius*) and higher for herbaceous dicots in LS than in ES soils. Fire reduced monocots and enhanced *Cistus*. Germination period significantly interacted with fire and season in some groups or species, altering the simulated-autumn germination peak. We demonstrate that the seed bank can germinate swiftly under simulated-autumn conditions. Hence, water availability is the main controlling factor of germination. Fire season differentially affected some species or groups, and could affect the post-fire regeneration.

Keywords Cistus · Germination temperature · Global change · Rainfall patterns · Regeneration strategy · Rosmarinus

Introduction

Fire-prone shrublands cover large areas in the Mediterranean region, and many are dominated by seeders, that is, species that re-establish from seeds stored in the soil (Trabaud 1994). In the western part of the Mediterranean region, rainfall occurs from fall to spring. Germination of shrubs after fire usually proceeds after the onset of the first significant rainfall. However, not all seeds germinate at the same time. Often, germination occurs from early fall to the end of spring of the first post-fire year. In addition, some germination can occur during the second and third year (Quintana et al. 2004; De Luis et al. 2008). While rainfall patterns are assumed to cause these variations (Daskalakou and Thanos 2004; Quintana et al. 2004), seed dormancy can also play a role in controlling time

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of germination (Ooi 2010). Time of germination can be critical since early germination during the first year can increase survival success, while second or third year germinated seedlings have a much reduced chance of surviving (Quintana et al. 2004; De Luis et al. 2008). Therefore, knowledge of the temporal patterns of germination of shrubs once soils have appropriate moisture levels, and the factors that control them is needed to understand plant demographic changes in relation to fire.

Herbs, particularly annuals, are a common component of Mediterranean shrublands. After fire, they regenerate from seeds stored in the soil (Ortega et al. 1997; Valbuena and Trabaud 2001), forming a dense, species-rich layer of vegetation in the first few years after fire (Arianoutsou-Faraggitaki 1984; Pérez and Moreno 1998; Keeley et al. 2006). Although the temporal post-fire germination pattern of herbaceous species in shrublands is poorly understood, studies in grasslands indicate that germination proceeds as soon as soils have appropriate moisture, following the first autumn rains (Espigares and Peco 1993; Traba et al. 2006). Since herbs may interact with shrub establishment and growth (Moreno and Oechel 1992; Keeley et al. 2006; Seifan et al. 2010), an understanding of the factors that control their abundance and their temporal germination after fire can be equally important for determining the fate and composition of the post-fire plant community (Figueroa et al. 2004).

In the Mediterranean region, fires commonly occur during summer, but can span several months within a year, from spring to fall (Vázquez and Moreno 1998). The time of fire within the year, or fire season, can be important (Enright and Lamont 1989; Knox and Clarke 2006), since it can interact with the post-fire regeneration from the soil seed bank in various ways. Fuel characteristics and soil moisture content vary during the year, and could affect fire severity and impact seed mortality or release from dormancy (Auld and Bradstock 1996). In addition, the amount of seeds in the soil will vary depending on the time of fire. Seed dispersal is highest during the summer for both shrubs and herbs (Espigares and Peco 1993; Bastida and Talavera 2002; Traba et al. 2006). However, among shrubs, there is great disparity in temporal patterns of dispersal. Some species (e.g., *Cistus ladanifer)* disperse from summer to spring of the next year; others (e.g., *Rosmarinus officinalis*) start dispersing in spring and proceed until early summer (Moreno and Cruz 2000; Bastida and Talavera 2002; Clemente et al. 2007). Data on temporal patterns of seed dispersal of herbaceous species in shrublands are sparse (Buisson et al. 2006), but studies in Mediterranean grasslands indicate that dispersal occurs mainly in summer, with little variability among species (Espigares and Peco 1993; Ortega et al. 1997).

In addition, the degree to which seeds will be exposed to heat in case of fire is also likely to change during the season. Recently dispersed seeds may be more vulnerable to the lethal effects of heat than older seeds, some of which may have escaped predators by occupying protected sites that may be less exposed to fire (Auld and Bradstock 1996; Traba et al. 2006). Therefore, the current seed rain might not be so important in determining the post-fire germination (Clemente et al. 1996; Bastida and Talavera 2002; Traba et al. 2006).

After fire, and once seeds are exposed to the appropriate moisture and temperature conditions, temporal germination patterns may differ among species due to their different sensitivity to environmental cues for germinating (Reyes and Trabaud 2009). Furthermore, even within a species, not all seeds may germinate simultaneously due, among other factors, to variation in dormancy status. For instance, in species with enforced dormancy, older seeds are more likely to have their dormancy broken than younger seeds (Baskin and Baskin 1998). In addition, seed sensitivity to dormancy-breaking cues also varies seasonally (Ooi 2010). Hence, fires occurring early in the season may affect a different proportion of non-dormant seeds than late season fires. As a result, the temporal pattern of germination may vary depending on when a fire occurs.

The objectives of this study were to determine the effect of season and fire on total germination and temporal patterns of emergence of the soil seed bank of a seeder-dominated Mediterranean shrubland. To investigate this, soils were collected from plots before and after burning in early and late summer, and were germinated in a chamber in which the course of autumn, winter, and spring conditions was consecutively simulated. The questions addressed were to what extent the readily germinable soil seed bank varies between early and late summer? How does fire affect this? Assuming that rainfall starts in fall and proceeds until spring, in which period of time (autumn, winter, or spring) will germination occur?

Does germination period vary between soils collected in early and late summer or with fire?

Materials and methods

Study area

The study site was located at Los Puntales, in the Sierra Morena mountain range, southwestern Spain (4°43′W, 38°03′N; 550 m elevation) (Fig. 1a). The climate is Mediterranean, with mean annual temperature of 17.3°C, and mean annual rainfall of 633 mm (Guadalmellato Reservoir meteorological station, located at 5 km from the site). Mean minimum temperatures occur in January, and freezing conditions are common during winter. Mean maximum temperatures occur in July (Fig. 1a). The dry season lasts from May to September, and mean rainfall in this period is 50 mm. The bedrock is granitic and the soils are regosols (FAO 1974). Fires in the region occur mainly between June and September (Fig. 1b).

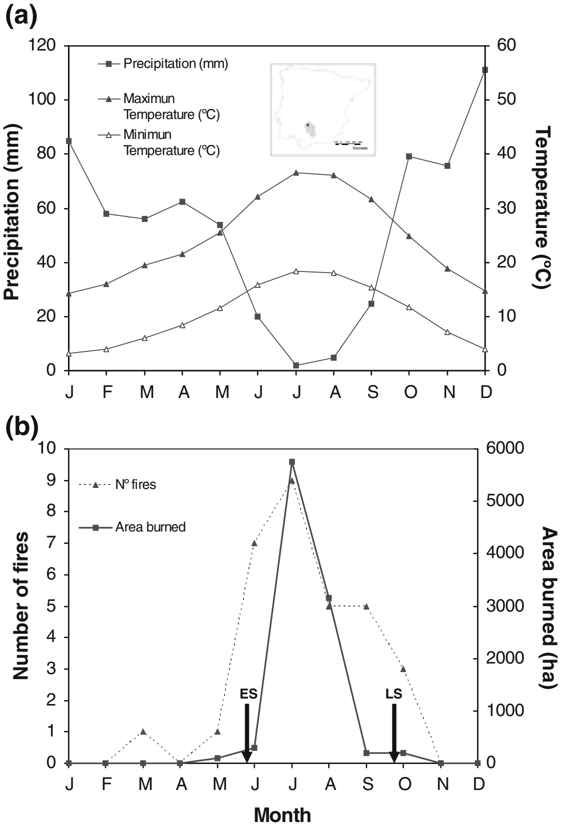

Fig. 1 **a** Monthly mean rainfall and temperature trends from 1970 to 2003 measured at the Guadalmellato Reservoir meteorological station (Córdoba), 4°40′W, 38°02′N, 217 m elevation. Location of the study site (Los Puntales, Córdoba province, Spain) is shown in the embedded figure. **b** Number of fires and total area burned during 1974–2008 within the 10 × 10 km UTM grid cell where the study area is located. *Arrows* indicate the time of experimental fires in early (ES) and late (LS) summer

The study area was covered by a 12-year-old shrubland. Pre-fire plant abundance was estimated in 20, 1 m × 1 m squares, regularly distributed along two, 20 m transects within each of eight plots (see below). The 1.5–2.5 m high, dense (75% cover) vegetation was dominated by obligate seeders, including *Cistus ladanifer* L. (23% cover), *C. albidus* L., *C. populifolius* L. and *C. salvifolius* L. (approx. 5% cover each), and *Rosmarinus officinalis* L. (7% cover). Other abundant facultative seeders (i.e., resprout but also regenerate from seeds) were *Adenocarpus telonensis* (Loisel.) DC. (17%), and *Teucrium fruticans* L. (5%). Herbaceous cover was 14%.

Experimental design

Four blocks were established, running parallel to a north-facing slope. The area was fenced to exclude large herbivores. Within each block, two 25 m × 25 m plots were established following a completely randomized blocks design to assign treatments. Burning treatments were conducted in early summer (end of June, referred to as "early season" or ES) and in late summer (end of September, "late season" or LS), coinciding with the beginning and end of the fire season. All plots were burned on the same day at each time (ES, LS) by igniting them at the bottom and letting the fire propagate upslope and downwind. Surface temperatures were monitored with 20 k-thermocouples (HOBO Type K Thermocouple; Onset Computer Corporation, Bourne, MA, USA) distributed throughout each plot. From these measurements, we calculated two indices of fire intensity: mean maximum soil surface temperature during fire, and time of residence of temperatures equal or greater than 100°C ($T_{r\geq 100^{\circ}\mathrm{C}}$).

Seed bank sampling and germination

Soil samples were collected shortly before fire (unburned soils) and immediately after it (burned soils), at five different locations within each plot. Each sample consisted of 15 cylindrical cores (diameter of 6 cm; depth of 4 cm). Samples were taken to the laboratory, air dried, and passed through a sieve (2 mm mesh). From each sample, 100 g of soil was evenly spread onto plastic trays (18 cm × 27 cm × 4.5 cm) that contained a 2 cm layer of sterilized sand. We used the seedling emergence method to estimate the size of the soil seed bank (Fenner and Thompson 2005). The layer of soil in the trays did not exceed 1 cm depth. Eighty-four trays were used, with 40 trays per season (ES and LS), 20 of which were burned (+), and 20 unburned (−) soil samples. Four trays, filled with sterilized sand, were used to detect any seed contamination, although none was detected.

The experiment lasted 21 weeks, comprising three simulated seasonal periods, each corresponding to three different germination conditions that mimicked light/dark photoperiod and temperature in autumn (12 h/12 h, 17.5°C/10°C), winter (10 h/14 h, 12.5°C/5°C), and spring (12 h/12 h, 20°C/12.5°C). These temperature patterns were based on records from the Guadalmellato Reservoir meteorological station. Each period lasted 6 weeks, plus 1 week of transition from one period to the next. All trays were positioned randomly in a walk-in growth chamber. Trays were irrigated every 2 days to keep them permanently moist. Emerging seedlings were monitored weekly and identified to the species level. When the identification was not possible, seedlings were transplanted to pots and grown until this was possible. A number of *Poaceae* species could not be identified; therefore, they were combined into a single group as monocotyledons. Germination (seedling density; No m^{-2}) was recorded by periods (simulated-autumn, simulated-winter, and simulated-spring) and analyzed for all species together or the various groups (woody or herbs), and, within these, by the main species of woody seeders, or by monocots and dicots within the herbs (monocots and dicots from now on), respectively. Species richness was analyzed only for the dicots.

Germination rates, that is, the time (weeks) required for 50% of all germinations (T_{50}) during the first period (simulated-autumn), were calculated for various species or group of species. Germination during the other two periods was very low (see "Results" section), and further testing within them became meaningless. Plant nomenclature followed Flora Europaea (Tutin et al. 1964–1980).

Statistical analysis

Differences between fires in early (ES) and late (LS) summer for mean maximum surface temperatures and $T_{r \geq 100^\circ\mathrm{C}}$ were analyzed by one-way ANOVA. Species richness and seedling density of all species combined, or of the various groups or main woody species were tested for the effects of season (S) [two levels, early season (ES), and late season (LS)], fire (F) [two levels, unburned (−) or burned (+)], and germination period (P) [three levels, simulated-autumn, simulated-winter, and simulated-spring]. This was done by employing a repeated measures, three-factor ANOVA, using general linear models (GLM) in which season and fire were between-subjects factors and germination period the within-subject factor (repeated measures). Differences in T_{50} (weeks) were analyzed by two-way (fire, season) ANOVA. Prior to all statistical analyses, the data were tested for normality and homoscedasticity, and transformed as appropriate. Species richness and seedling densities were square root-transformed and T_{50} was log-transformed. All statistical analyses were completed using the SPSS Statistic 17.0 package for Windows (SPSS, Chicago, IL, USA).

Results

The mean (±SE) maximum surface temperature during fire was 550 ± 28°C for ES fires and 699 ± 45°C for LS fires. Mean (±SE) $T_{r \geq 100^\circ\mathrm{C}}$ was 5.8 ± 0.8 min for ES burns and 8.3 ± 1.1 min for LS burns (Fig. 2). The values of both parameters were higher, although more variable, for the LS than ES fires. There were, however, no significant statistical differences between fires ($F_{1,6} = 4.7$, $P = 0.073$ and $F_{1,6} = 0.27$, $P = 0.62$, for maximum temperatures and $T_{r \geq 100^\circ\mathrm{C}}$, respectively). Therefore, we accepted the null hypothesis that ES and LS fires were of similar fire intensity.

Forty-two species were identified in unburned soils, 34 in ES− and 35 in LS− (Table 1). The number of species in burned soils was 32 in ES+ and 34 in LS+. The majority of the species were herbs, which were common to the two treatments (season, fire); only three annuals appeared exclusively in ES soils and four in LS ones. Of all dicot species present in the prefire aboveground vegetation, 62% of them germinated from the soil seed bank, including all woody obligate seeders.

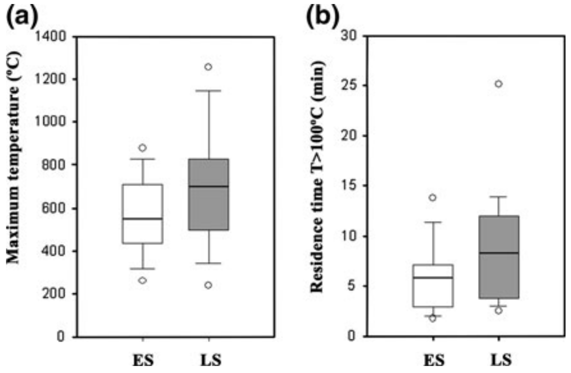

Fig. 2 Box plots of: **a** maximum soil surface temperatures reached during fire; **b** time of residence (min) at or above 100°C during the experimental fires carried out in early (ES) and late (LS) summer in a seeder-dominated Mediterranean shrubland at Los Puntales. The *boxes* show the mean (*solid line*), quartiles, 5 and 95% ranges (*error bars*) and extreme values (*outliers-open circles*)

Total seedling density was higher in LS than in ES soils, and lower in burned (+) than in unburned (−) soils (Table 1); however, differences due to season or fire were non-significant (Table 2). Woody species accounted for 11% of the seedling population; *Cistus* was the most abundant group, representing nearly 90% of the woody seedlings in all treatments, except in ES−, where *R. officinalis* was dominant, albeit very variable among treatments (Table 1). Herbs dominated the soil seed bank (89% of all seedlings), and were more abundant than woody seedlings under all treatment combinations. Among the herbs, about 33% of them were monocots (*Poaceae*), and the rest dicots; these had higher densities in all treatments (Table 1).

Germination began shortly after watering the soils, and progressed swiftly. By the end of the simulated-autumn period, 86% of the woody seedlings and 89% of the herbaceous seedlings had emerged (Fig. 3a, b). Germination during the simulated-winter period was very low (11 and 9% for woody plants and herbs, respectively), and even lower under the simulated-spring period (3 and 2% for woody plants and herbs, respectively) (Table 1). Almost all species recorded in the experiment had germinated before the end of the simulated-autumn period. Only two species appeared during the simulated-winter period and exclusively in burned soils. No new species were recorded during the simulated-spring period (Fig. 3c).

Herb seedling density was significantly affected by season of collection (Table 2), being greater in LS than in ES soils, owing mainly to the dicots (Fig. 4a). However, season neither significantly affected species richness (dicots, woody), nor woody species density, but did have a significant effect on the density of some species. This altered the relative dominance of the various species in the population of seedlings (Fig. 4b). For example, *R. officinalis* and *C. salvifolius* produced a significantly greater number of seedlings in ES than in LS soils. In contrast, the other woody species had greater absolute germination in LS than in ES, although the effect of season on these species was not statistically significant (Table 2; Fig. 4b).

Burned soils yielded a lower number of seedlings than unburned soils, particularly of herbs (Table 1), but differences among them were not always significant. Monocot seedling density was significantly lower in burned than in unburned soils in both seasons (Tables 1, 2). By contrary, differences were not statistically significant for woody species, despite having a larger number of seedlings in burned than in unburned soils. This resulted from the different species-specific response to fire. Germination of *Cistus* species was promoted by fire, most notably in the case of *C. ladanifer* and *C. albidus,* although only the last one showed statistically significant differences. There was no significant season–fire interaction for either woody or herbaceous species (Table 2).

The time to reach 50% of total germination (T_{50}) during simulated-autumn was generally between 2 and 3 weeks (Table 3). Woody species had higher T_{50} values than herbs (i.e., they germinated at a slower pace). However, there were no significant effects ($P > 0.05$) due to season, fire or their interactions for any of the groups analyzed.

Germination period (simulated-autumn, simulated-winter, or simulated-spring) was a significant factor on seedling density for most of the groups and species analyzed, including species richness (Table 2). This reflects that most germination occurred under the simulated-autumn period. Furthermore, germination period significantly interacted with season, resulting in a smaller simulated-autumn germination peak in LS than in ES soils in the case of *R. officinalis* and in the opposite effect in the dicots. In addition, germination period significantly interacted with fire for all herbaceous species and each of the two herbaceous groups (dicots and monocots)—there was a smaller simulated-autumn germination peak in burned than unburned soils. Interactions were also found between

Table 1 Average seedling density (seedlings/m^2) for all species, dominant woody shrub species, herbaceous (monocots, dicots), and species richness (dicots) recorded in early (ES) and late (LS) summer, before and after fire during three periods of germination simulating autumn (Au), winter (Wi), and spring (Sp)

Seedlings/m^2	Early season								Late season							
	Before fire				After fire				Before fire				After fire			
	Au	Wi	Sp	Total	Au	Wi	Sp	Total	Au	Wi	Sp	Total	Au	Wi	Sp	Total
All species	7870	497	172	8539 ± 2728	4619	564	96	5279 ± 847	10366	947	182	11494 ± 1397	7038	612	258	7908 ± 1073
Woody	622	38	39	699 ± 266	1014	96	19	1128 ± 223	478	67	19	564 ± 157	669	77	10	755 ± 226
Cistus spp.	172	38	29	239 ± 58	861	96	10	966 ± 215	430	57	19	507 ± 185	602	67	10	679 ± 246
C. albidus	38	0	10	48 ± 42	210	19	0	230 ± 31	163	29	10	201 ± 116	182	10	0	191 ± 231
C. ladanifer	57	0	0	57 ± 29	392	57	0	449 ± 223	230	29	10	268 ± 124	373	57	0	430 ± 245
C. populifolius	0	0	0	0	19	10	10	38 ± 31	10	0	0	10 ± 11	0	0	0	0
C. salvifolius	77	38	19	134 ± 60	239	10	0	249 ± 101	29	0	0	29 ± 33	48	0	10	57 ± 33
Rosmarinus officinalis	411	0	10	421 ± 233	48	0	0	48 ± 24	10	0	0	10 ± 10	0	10	0	10 ± 10
Herbaceous	7248	459	134	7841 ± 2474	3605	469	77	4150 ± 731	9888	880	163	10930 ± 1551	6369	536	249	7153 ± 1094
Dicotyledons	5116	316	115	5546 ± 2134	2257	249	48	2553 ± 578	6904	478	134	7516 ± 995	5049	430	230	5709 ± 1039
Monocotyledons	2132	143	19	2295 ± 453	1348	220	29	1597 ± 262	2984	402	29	3414 ± 615	1320	105	19	1444 ± 217
Species richness																
All species	34	8	7	34 ± 5.1	31	9	3	32 ± 0.8	35	11	6	35 ± 1.2	33	11	4	34 ± 2.3
Herbaceous[a]	27	7	4	27 ± 4.3	23	5	1	24 ± 0.8	28	8	4	28 ± 1.6	28	8	3	28 ± 2.7
Woody	7	1	3	7 ± 1.1	8	4	2	8 ± 1.1	7	3	2	7 ± 0.7	5	3	1	6 ± 0.7

Total is the sum of germinations recorded in the three simulated periods (mean ± SE)

[a] Only herbaceous dicots are considered

Table 2 *P* values from three-way, repeated measures ANOVA for seedling density (seedlings/m^2) for all species, dominant woody shrub species, herbaceous (dicots, monocots), and species richness (dicots)

Factor effects							
	S	F	S × F	P	P × S	P × F	P × S × F
Seedlings/m^2							
All species	0.071	0.120	0.914	**<0.001**	0.146	**0.041**	0.631
Woody	0.394	0.196	0.556	**<0.001**	0.377	0.136	0.752
Cistus spp.	0.941	**0.034**	0.162	**<0.001**	0.889	**<0.001**	0.066
C. albidus	0.256	**0.049**	0.061	**<0.001**	0.690	**0.018**	0.416
C. ladanifer	0.387	0.112	0.435	**<0.001**	0.679	0.067	0.658
C. populifolius	0.337	0.337	0.121	0.157	1.000	1.000	0.157
C. salvifolius	**0.036**	0.393	0.887	**0.001**	0.140	0.129	0.276
Rosmarinus officinalis	**0.026**	0.110	0.110	**0.003**	**0.005**	0.061	0.173
Herbaceous	**0.048**	0.080	0.971	**<0.001**	0.071	**0.009**	0.621
Dicotyledons	**0.045**	0.194	0.591	**<0.001**	**0.032**	**0.019**	0.773
Monocotyledons	0.335	**0.011**	0.068	**<0.001**	0.590	**0.010**	0.459
Species richness							
All species	0.135	0.463	0.976	**<0.001**	0.364	0.190	0.152
Herbaceous[a]	0.073	0.306	0.662	**<0.001**	0.329	0.663	0.320
Woody	0.559	0.409	0.417	**<0.001**	0.163	0.092	0.206

Statistically significant *P* values are shown in bold

S season, *F* fire, *P* period of germination

[a] Only herbaceous dicots are considered

germination period and fire for *Cistus*, particularly for *C. albidus* (Table 2). In this case, however, the effect was the opposite, and the simulated-autumn germination peak was greater in burned than unburned soils.

Discussion

Prompt germination after soil watering under simulated-autumn was the norm for shrubs and herbs. Three weeks after watering the soils, half of the total germination had already occurred, and 6 weeks later germination was nearly complete. Few seedlings continued to germinate under simulated-winter or simulated-spring. Mean T_{50} during simulated-autumn was 2–3 weeks, which is consistent with laboratory experiments (Reyes and Trabaud 2009; Moreira et al. 2010). Swift germination during simulated-autumn was particularly evident in species richness. Since our experiment simulated only one wet season cycle, we cannot exclude that further germination could occur if additional cycles had been simulated. Nevertheless, experiments in another shrubland in which soils were monitored for germination for 15 months, after allowing them to undergo a drying cycle, indicated that germination in the second cycle was minimal (Torres et al. 2012).

Fire did not affect the germination speed (T_{50}) of woody or herbaceous species during simulated-autumn. In woody species with physical dormancy (*Cistus*), this appears to contradict findings that germination speed varies depending on exposure of seeds to heat or other fire-cues (Reyes and Trabaud 2009). Indeed, the number of *Cistus* germinating was greater in burned than in unburned soils. That is, in burned soils a portion of the germinated seeds must have been initially dormant (Troumbis and Trabaud 1987; Roy and Sonie 1992; Clemente et al.1996). How many seeds germinating in burned soils belonged to the non-dormant or dormant but fire-stimulated fractions is unknown. Anyhow, either both types of seeds germinated at the same speed or if they differed in this characteristic, its number was not sufficient to produce significant differences in the germination speed of the soil seed bank.

Simulated-autumn was the period in which most germination occurred. There were, however, minor

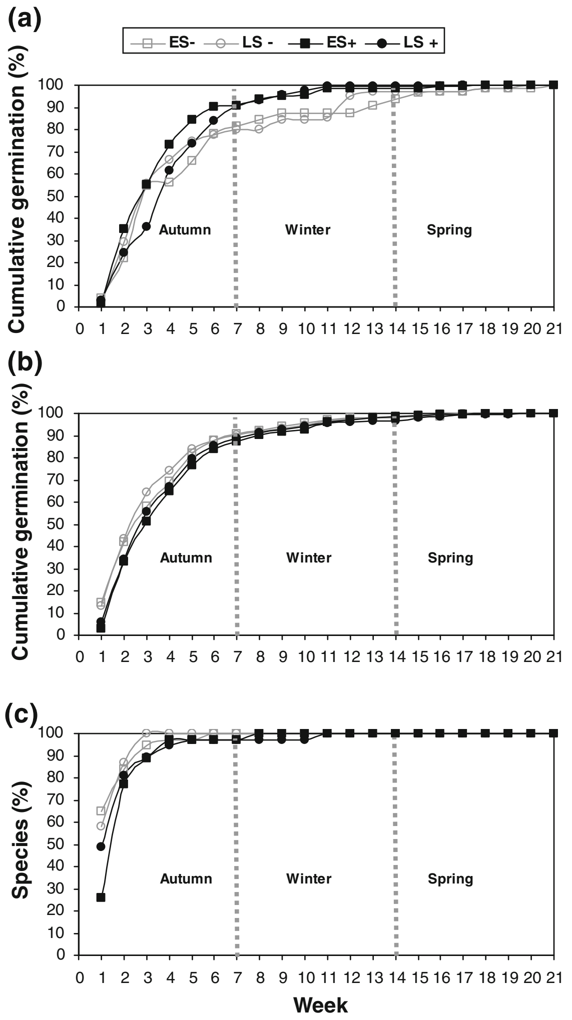

Fig. 3 Cumulative germination (%) through time under three periods of germination simulating autumn, winter, and spring, for soils collected in early (ES) and late (LS) summer, before (−) and after (+) fire, for **a** woody species; **b** herbaceous species; and **c** species richness

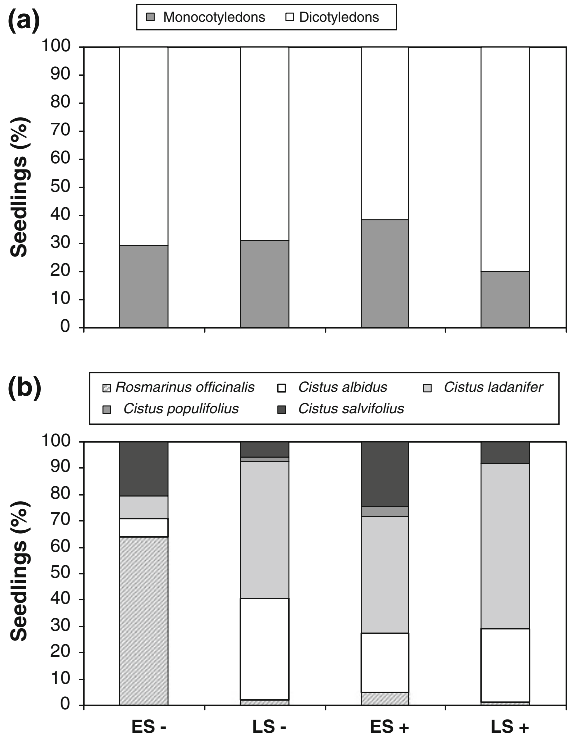

Fig. 4 Relative contribution (%) of the various plant groups to the total number of seedlings germinated for **a** herbaceous species (monocots, dicots); **b** dominant woody shrubs (*Cistus* spp. and *R. officinalis*), in early (ES) and late (LS) summer, before (−) and after (+) fire

changes to this pattern depending on the species, fire, and season. In *Cistus* and herbs, fire interacted with period of germination. Whereas in *Cistus,* fire tended to further increase germination in simulated-autumn, in the case of herbs it relatively reduced this peak. In absolute terms, however, the vast majority of germinations still occurred during simulated-autumn, which indicates that the impact of these changes, if they materialize in the field, are probably not important. A relative anticipation (*Cistus*) or delay (herbs) could be relevant if it affected the herbs–shrubs interactions (Moreno and Oechel 1992; Seifan et al. 2010), but this remains to be tested.

Season did not significantly affect germination speed (T_{50}); hence, seeds in ES soils germinated at a speed similar to those in LS soils. Assuming that the soil seed bank in LS soils was enriched with seeds dispersed during summer, it appears that they germinated at about the same speed as the older seeds of ES soils. Season significantly interacted with germination period for the dicots. In this case, the germination of this group during simulated-autumn was more pronounced in LS than in ES soils. No increased germination in simulated-winter or simulated-spring in LS soils in comparison with ES was observed, as would have been expected if cold requirements or other mechanisms of physiological dormancy had been present (Baskin and Baskin 1998). These data corroborate laboratory experiments that showed that cold exposure is not required for germination in several groups of Mediterranean species (Giménez-Benavides et al. 2005; Luna et al. 2008), although this

Table 3 Average (±SE) time (weeks) to reach 50% of the total germination (T_{50}) during the simulated-autumn period from soils collected in early (ES) and late (LS) summer, before and after fire, and for various groups of species

T_{50} (week)	Early season		Late season		Factor effects		
	Before fire	After fire	Before fire	After fire	Season	Fire	Season × fire
All species	2.44 ± 0.44	2.64 ± 0.43	2.08 ± 0.28	2.53 ± 0.25	0.515	0.280	0.664
Woody	3.08 ± 0.74	2.55 ± 0.34	2.42 ± 0.32	3.29 ± 0.32	0.836	0.565	0.096
Cistus spp.	3.79 ± 0.90	2.55 ± 0.39	2.54 ± 0.36	3.25 ± 0.38	0.716	0.722	0.070
Herbaceous	2.38 ± 0.42	2.41 ± 0.49	2.06 ± 0.27	2.44 ± 0.23	0.198	0.209	0.886
Dicotyledons	2.49 ± 0.31	2.85 ± 0.45	2.10 ± 0.28	2.45 ± 0.18	0.758	0.516	0.544
Monocotyledons	1.62 ± 0.29	2.32 ± 0.46	2.56 ± 0.42	2.43 ± 0.44	0.128	0.376	0.213

P values of the two-way ANOVA (fire, season) are shown

may not apply to all shrubby species (Trigueros Vera et al. 2010). As discussed above, the impact of these changes in the relative temporal patterns of germination on the shrub–herbs interactions is probably not very important since the simulated-autumn germination peak was dominant, although field studies need to verify this.

In unpredictable environments, species may increase their fitness by, among other, extending the time period during which germination occurs (Fenner and Thompson 2005). On the other hand, rapid germination has been suggested to be advantageous for plant fitness (Verdú and Traveset 2005). In this study, germination under both, simulated-winter or simulated-spring periods, was very low, since most seeds germinated under simulated-autumn. Thus, early germination was clearly favored.

Season and fire affected the germination of shrubs in different ways. For example, season significantly affected *R. officinalis* and *C. salvifolius* but not the other shrubs, by increasing germination in ES soils. This pattern could be supported by seed dispersal patterns in *R. officinalis* not in *C. salvifolius*. Indeed by the end of spring, *R. officinalis* has released most of its seeds (Moreno and Cruz 2000), which are non-dormant. Moreover, *R. officinalis* soil seed bank demonstrates substantial year to year fluctuations, is usually smaller than co-occurring *Cistus*, and the viability of its seeds is low (Salvador and Lloret 1995). Its seed bank, therefore, can be considered transitory (Clemente et al. 2007). Not being a fire-dependent species (Trabaud and Casal 1989; Salvador and Lloret 1995; Reyes and Trabaud 2009; but see Moreira et al. 2010), it seems a good candidate to be affected by fire season, whereby fire in late season would be more detrimental than in early season, as found here. The pattern found for *C. salvifolius* is difficult to explain since its phenology is similar to other *Cistus* species (Trabaud and Oustric 1989; Salvador and Lloret 1995), and points to the need to better understanding the interactions between phenology, seed production, and seed persistence in the soil seed bank for some dominant species in Mediterranean shrublands.

The lack of a significant season effect on the other shrub species is intriguing since a large number of seeds are produced every year, part of which must be incorporated into the soil bank (Bastida and Talavera 2002). On average, there were twice as many *Cistus* seedlings in the unburned plots in LS than in ES soils, a likely indication of the incorporation of new seeds to the soil bank. It is arguable that seed predation must be very high during summer, so that the abundance in the soil seed bank is lower than what would be expected based on seed production. Therefore, the long period of seed dispersal of *Cistus* might be advantageous to reduce the risk of seed predation, by releasing seeds throughout most of the year, including winter and spring, when the activity of ants is minimal (Bastida and Talavera 2002; Bastida et al. 2009). Fire significantly promoted the germination of *Cistus* as a group, but only in one species (*C. albidus)* reached the level of statistical significance, which emphasizes the importance of heat as a germination trigger in this genus. Nevertheless, the number of seedlings germinating without fire was still quite high, which corroborates that these species can benefit from fire but are not strict fire-dependent.

LS soils produced more herb seedlings than ES soils, mainly due to the dicots. Furthermore, on average, burned soils produced fewer seedlings than unburned soils, particularly for monocots. These results highlight the relevance of the fire season for functional group composition. Even though fire had a negative effect on herbs in both seasons, early season fires will produce fewer seedlings and will result in a community with similar proportion of monocots and dicots. By contrary, fires later in the season will produce more seedlings and these will be dominated by dicots.

We suggest that, provided moisture and appropriate temperature, germination proceeds rapidly in this shrubland. Thus, the extended period of germination observed in field studies (Quintana et al. 2004; Daskalakou and Thanos 2004; De Luis et al. 2008) is probably mostly due to lack of moisture. It is arguable that germination of this soil seed bank is primarily controlled by the availability of water (i.e., rainfall in the field). This implies that changes in rainfall patterns can affect overall germination. Because germination is highly sensitive to soil moisture (Thomas et al. 2010), one can argue that less frequent pulses of high precipitation might be less effective in triggering germination than more frequent pulses of less intense rainfall. Based on a range of emission scenarios, climate models project a decrease in precipitation for the Mediterranean region, rainfall being anticipated to occur as more intense, but less frequent events (Giorgi and Lionello 2008), which coincides with recent observations (Esteban-Parra et al. 1998). High-intensity less frequent rainfall can increase the growth of established plants (Heisler-White et al. 2008). It is therefore tenable that post-fire regeneration from seeds may be negatively affected by such a rainfall pattern, whereas regeneration by vegetative growth (i.e., resprouting) might be positively affected (Ojeda et al. 2005). Nevertheless, since in the current study most seeds germinated under simulated-autumn, it remains to be seen how germination would be affected if rainfall patterns were shifted toward colder, winter conditions. Further studies are needed to more clearly define the effects of precipitation changes due to climate change on the two mechanisms of regeneration.

In summary, this study shows that changes in the fire season can alter the relative proportion of shrub and herbs in the seedling community. ES fires produced a slightly more diverse community of shrub seedlings and a more balance abundance of the two main functional groups of herbs (monocots, dicots). In contrast, LS fires produced more herbaceous dicots, and favored *Cistus* dominance. The greater abundance of dicots and the low abundance of *R. officinalis* in LS fires suggest that a combination of ES and LS fires might be more beneficial for maintaining higher species diversity in this shrubland.

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