



Original article

Seedling establishment along post-fire succession in Mediterranean shrublands dominated by obligate seeders

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ARTICLE INFO

Article history:

Received 11 January 2011

Accepted 5 December 2011

Available online xxx

Keywords:

Fire severity

Germination

Open gaps

Population dynamics

Regeneration niche

ABSTRACT

Seedlings are expected to be particularly sensitive to the environmental conditions at the time of establishment. Within succession, environmental conditions vary over time and a species will have a better chance to regenerate on a particular place depending on the intrinsic traits that determine its regeneration niche. We examined the regeneration niche and the pattern of seedling establishment along succession of the main species present in a Mediterranean shrubland. The establishment of *Cistus albidus*, *Rosmarinus officinalis* and *Ulex parviflorus* was monitored for three years using seasonal cohorts in three different stages along a successional gradient (post-fire, building and mature). There was a flush of establishment immediately after fire in all species. After this event, there was a decline in establishment as succession progressed, until practically no seedling establishment was found at mature stages. The presence of a thick litter layer probably precluded seedling establishment at this stage. The establishment of *Cistus* was very closely tied to the post-fire environment, while recruitment of *Rosmarinus* and *Ulex* also occurred in the building stage. In contrast to what has been reported in other Mediterranean shrublands, recruitment in our study area was not restricted solely to post-fire stages, and shrubs also recruited opportunistically when open gaps in the canopy were available along succession. The differences in preferred micro-sites for the establishment suggest a differentiation in regeneration niches and a particular set of environmental conditions where the different species would be particularly competitive through succession. Thus, *Cistus* regenerates mostly in highly perturbed environments, whereas *Ulex* and *Rosmarinus* benefit from environments with longer inter-fire periods.

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1. Introduction

The succession of plant communities is basically governed by adult decline and seedling establishment (Harper, 1977). Seedlings are expected to be particularly sensitive to the environmental conditions at the time of establishment, when they are most vulnerable (Kitajima and Fenner, 2000), and their dynamics drive the potential replacement of adults in future stages (Kellman and Kading, 1992). Within successional gradients, environmental conditions vary over time and, consequently, a species will have a better chance to regenerate on a particular place depending on the intrinsic traits that determine its regeneration niche (Grubb, 1977; Bazzaz, 1979; Fowler, 1988). Therefore, approaches covering

a broad range of environmental conditions within successional gradients are basic for understanding both the requirements for establishment of a species and the role of seedling dynamics in driving population patterns.

The occurrence of fires is a key factor driving plant population patterns in Mediterranean shrublands (Pierce and Cowling, 1991; Roy and Sonié, 1992; DeSimone and Zedler, 1999; Keeley et al., 2006). In fact, the persistence of obligate seeders relies completely on seeds stored in the seed bank, as most individuals of these species die from the effects of fire (Pausas et al., 2004). In these shrublands, the regeneration of species with soil seed banks is almost completely tied to the flush of seedling emergence and establishment promoted by direct (e.g., heat, smoke, charred wood) and indirect fire effects, which change the environmental conditions and trigger the availability of resources (e.g., increases in nutrient levels, increases in light, decreases in competition, shifts in daily soil temperature regime) during the first stages after the disturbance (Keeley, 1991; Bell et al., 1993; Thanos and Rundel, 1995; DeBano et al., 1998;

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Moreira et al., 2010; Santana et al., 2010a). These fire effects break seed dormancy or stimulate germination and enhance seedling survival. As a result, the regenerated population is almost totally composed of even-aged individuals (Keeley, 1992). Later successional stages without fire provide opportunities to regenerate the populations of those species that do not depend exclusively on fire to become established; however, these regeneration processes are very rare and are mainly attributed to bird-dispersed resprouting species (Keeley, 1992, 1995; Siles et al., 2008). Probably for this reason, most studies on seedling dynamics in Mediterranean shrublands have been centred on early post-fire successional stages, neglecting later stages (Moreno and Oechel, 1992; Quintana et al., 2004; De Luis et al., 2008). Nevertheless, it has been suggested that the establishment of seeder species in the Mediterranean Basin may not be so closely tied to fire events and that, in some cases, new individuals could become established during inter-fire periods (Clemente et al., 1996; Lloret, 1998; Lloret et al., 2005). Therefore, accurate knowledge on the micro-habitats that are suitable for the recruitment of these species, and whether there is a particular set of environmental conditions in which the different species would be more competitive during succession, remains to be specifically assessed in Mediterranean shrublands.

In the Mediterranean Basin, ecosystems dominated by obligate seeders are mainly linked to landscapes with long histories of disturbances caused by human exploitation (agriculture and livestock) and/or fire recurrence (Baeza et al., 2007). These ecosystems typically stay in early successional stages, and are dominated by pioneering species with persistent soil seed banks (Verdú, 2000; Pausas et al., 2004). In addition, these species accumulate large amounts of standing dead fine fuels, making them one of the most problematic vegetation types in terms of fire-risk (Saura-Mas et al., 2010). Species composition in these ecosystems is highly influenced by the fire regime; the fire-return interval can, in fact, drive shifts in species dominance (Eugenio and Lloret, 2006; Baeza et al., 2007). This issue has a special relevance in the light of climate change, where shifts in fire regimes are predicted (Pausas, 2004), and the presence of these species could be enhanced (Verdú and Pausas, 2007).

The aim of this paper was to determine the patterns of seedling emergence and establishment in Mediterranean Basin shrublands dominated by obligate seeders at different successional stages after fire. In addition, we aimed to identify a series of biotic and abiotic factors that could potentially drive the availability of suitable micro-habitats for seedling emergence. Our initial hypothesis was that fire would trigger the availability of micro-habitats needed for seedling establishment. As a consequence, seedling establishment would occur mainly at the immediate post-fire stage; at later successional stages, micro-habitat availability would decrease and seedling establishment would be restricted. To test this hypothesis, we used a chronosequence of shrublands with three successional stages: an immediate post-fire stage, a building stage where the community was composed of individuals in a growth phase (10–12 years after fire), and a mature stage where the community was composed of individuals at a mature or senescent phase (22–27 years after fire). Then we monitored seedling emergence and survival of the three dominant obligate seeders (*Cistus albidus* L., *Rosmarinus officinalis* L. and *Ulex parviflorus* Pourr.) using seasonal cohorts (Autumn and Spring) during a three-year period.

2. Methods

2.1. Study area and site selection

The study was carried out at three sites from the interior of the Valencia region (south-east Spain): Onil (38°39'N–0°39'W), Pardines (38°40'N–0°39'W) and Ayora (39°07'N–0°57'W). The study

sites were in all cases old-field terraces abandoned ca. 50–60 years ago, and have a well-documented history of exploitation and fire occurrence (Santana et al., 2010b). Their altitude ranges between 900 and 1050 m.a.s.l. and their climate is typically Mediterranean. Mean annual rainfall ranges between 466 mm (Onil) and 537 mm (Ayora). There is a pronounced summer drought from June to August, with no more than 65 mm of rain. The mean annual temperature is approximately 14 °C, and the mean maximum temperature for the hottest month (July) is 30 °C. To minimise environmental variability between sites, all sites were oriented north and located on marls; their soils are Regosols (FAO, 1988). At the onset of the study, the vegetation consisted of shrublands (ca. 1–1.5 m in height) dominated by nanophanerophytes at different successional stages. The obligate seeders *Cistus*, *Rosmarinus* and *Ulex* dominated the vegetation, whereas resprouting shrubs such as *Quercus coccifera* L. and *Juniperus oxycedrus* L. were scarce. The grass *Brachypodium retusum* (Pers.) Beauv. was the main herbaceous species.

Each site consisted of three sub-areas that had been burned in different years and that we assumed to be at different successional stages after fire. Two different wildfires burned the Onil and Pardines sites in 1984; then an experimental fire was performed in 1994 at each site over part of the area burned before (see Baeza et al., 2002 for details). The Ayora site was affected by a wildfire in 1979, and part of this site was burned again by another wildfire in 1996. Finally, an experimental fire was applied in June of 2006 to burn again part of the areas that had already been burned twice on the three sites (see Santana et al., 2011 for details). This fire history allowed us to define a chronosequence with three different stages along succession at each site: first, an immediate post-fire stage resulting from the experimental burnings in 2006 (post-fire, hereafter); second, a 10–12 year-old building stage resulting from the 1994 to 1996 fires, in which the vegetation consisted of individuals in the growth phase (building, hereafter); and third, a 22–27 year-old mature stage resulting from the first fires in 1979 and 1984, where the vegetation was mainly composed of individuals in the mature or senescent phase (mature, hereafter). At each site, the three different successional stages were located no farther than 500 m away from each other, and thus shared the same soil and climatic characteristics.

2.2. Characterisation of the successional stages

We studied the seedling dynamics of the three dominant species (*Cistus*, *Rosmarinus*, and *Ulex*). Together, these species had a relative cover greater than 75% in the shrub layer at every successional stage. To assess the factors influencing seedling emergence at each successional stage, we considered a series of biotic and abiotic factors that characterise suitable micro-habitats. To do this, a 10 m × 10 m plot was laid out within each successional stage, and 20 points within this plot were randomly chosen from a 1 × 1 m grid. At each point, we set twenty 0.5 m × 0.5 m quadrats for monitoring seedling dynamics. In June 2006, we visually estimated at each quadrat the percentage cover for shrubs, herbs, stones (>2 cm in diameter) and litter (>2 cm deep). Stones larger than 2 cm in diameter and litter accumulations with depth greater than 2 cm were considered unsuitable micro-habitats for seedling emergence because the mean height of seedlings of our study species was less than 2 cm (Lloret, 1998). Proximity to the nearest adult plant of *Cistus*, *Rosmarinus* and *Ulex* was also measured for each quadrat as a proxy of seed availability. The distances for the post-fire stage had already been measured previous to the experimental fires. An additional index of fire severity was estimated in the post-fire stage according to Ryan and Noste (1985). This index was intended to infer soil temperatures reached during the passage

of fire, and it ranged from 0 (low) to 5 (high). Levels of severity were estimated as follows: 0) unburned (plant parts green and unaltered, no direct effect of heat); 1) very low (more than 50% of plants and litter remained unburned); 2) low (between 10 and 50% of plants and litter remained unburned); 3) moderate (less than 10% remained unburned); 4) high (only stems >5 mm in diameter remained, black ash deposition); and 5) very high (all plants and litter practically consumed, white ash deposition).

The composition of the shrub community at each stage was evaluated with three parallel 20 m long transects spaced 7 m apart across the maximum slope. A metal rod was used to record contacts with individual species, and measurements were taken every 20 cm along the transects (100 points per transect). Cover values were estimated for both alive and dead individuals.

2.3. Seedling monitoring

Seedling monitoring started in October 2006. Seedling emergence and survival was monitored in the quadrats previously described every two months until June 2009. To facilitate their identification during subsequent samplings, seedlings were tagged with colour-coded rings indicating the time of germination, and their coordinates within the quadrat were recorded. The fate of each seedling was tracked over the whole study period. Germination of Mediterranean Basin shrubs occurs preferentially in the wet seasons of autumn and spring, whereas it is negligible in summer (Lloret, 1998; Quintana et al., 2004; De Luis et al., 2008). Therefore, and to simplify the analyses of our data, we pooled the emergent seedlings into 2 annual cohorts according to their time of emergence. Seedlings emerging in the October and December samplings were considered autumn cohorts, whereas those emerging in February, April and June were pooled in the spring cohort of the respective years. The last monitoring for the survival of previously emerged seedlings was performed in September 2009 (after the last summer drought period).

2.4. Statistical analyses

To evaluate whether environmental conditions (cover of shrubs, herbs, litter and stones, and proximity to adult individuals) differed globally between successional stages (post-fire, building and mature), the semi-parametric multivariate analysis of variance (PERMANOVA) developed by Anderson (2001) was performed. For this analysis, we used site as a random variable and successional stage as a nested variable within site. In addition, we conducted a principal-coordinates analysis (PCO) to identify the particular environmental variables responsible for the multivariate patterns observed. The first two axes were correlated with the environmental conditions measured using the Spearman's correlation coefficient. PERMANOVA and PCO were performed using the programs PERMANOVA 1.6 (Anderson, 2005) and CAP (Anderson, 2004), respectively (both can be freely downloaded from <http://www.stat.auckland.ac.nz/~mja/Programs.htm>). For these analyses, we used Bray–Curtis distance (appropriate for the dataset containing a miscellaneous mixture of variables and numerous zeros; Quinn and Keough, 2002) and 4999 permutations (permutation of raw data; Anderson and Ter Braak, 2003).

Differences in the number of emerged seedlings between cohorts of the same successional stage, and between successional stages in the same cohort, were checked with one-way ANOVA. Because in some cohorts the number of emerged seedlings was low (particularly in spring cohorts), seedlings for the three sites in the same census were pooled. Post hoc HSD Tukey tests were performed when differences were observed. The data were log-transformed when necessary to achieve a normal distribution of

the residuals and ensure homoscedasticity. We acknowledge that comparisons of seedling emergence between successional stages may be masked by the different history of recurrent fires at short intervals experienced at the building and post-fire stages. These recurrent fires could generate additional alterations in seed bank composition and species abundance besides those occurring as a consequence of successional processes. Species requiring a longer time to reach maturity and replenish their seed bank can reduce their presence as a result of recurrent fires (Santana et al., 2010b). This must be taken into account when interpreting the results of the analyses, which are however important to determine the patterns of seedling emergence along succession.

Redundancy Analysis (RDA) was used to explore the relationships between emerged seedlings and micro-site characteristics for each successional stage. We performed this analysis with the autumn 2006 cohort, which was the most representative of the flush of emergence in the post-fire stage, and the closest in time to the sampling of micro-site characteristics. Redundancy Analysis was performed using the Vegan 1.9 package (Oksanen et al., 2007) in the R software environment (version 2.6.1; R Development Core Team, Vienna, Austria, <http://www.r-project.org/>). The number of emerging seedlings in each quadrat for each species was used as dependent variables in the ordination. These data were $\log_e(x + 1)$ transformed. The forward selection procedure in the Vegan package using the AIC statistic (Oksanen et al., 2007) was used to select the model with the most significant explanatory variables determining seedling emergence. The explanatory variables used were: shrub, herb, litter and stone cover, proximity to adult individuals and fire severity (in the case of the post-fire stage only). The significance of both the model selected and the explanatory variables axes was tested using a permutation test ($n = 1000$). We used site as a conditional variable (covariable) in these analyses.

Seedling survival at the different successional stages for each species was analysed with the Survival package (Crawley, 2007) in the R software environment. We estimated the survival curves of each cohort with the non-parametric Kaplan–Meier analysis. We regarded as censored data the seedlings alive at the end of the study and those checked as alive at intermediate samplings but not detected in later samplings. Then, the shape differences in survival curves between successional stages were tested by log-rank tests (Pyke and Thompson, 1986). Since cohorts were not equally abundant, the statistical analyses were carried out only when the density of the respective cohort was at least 1 individual m^{-2} (Quintana et al., 2004). Therefore, for this analysis, seedlings for the three sites in the same census were pooled. The analysis could only be performed in autumn cohorts, which were the most abundant. However, even in some autumn cohorts of *Rosmarinus* and *Ulex*, the analysis could not be carried out due to their low individual densities at some successional stages.

Because our data did not meet the assumption of homogeneity of variances, Kruskal–Wallis tests were used to test the differences in the number of established seedlings between cohorts of the same successional stage, and between successional stages in the same cohort. Post hoc HSD Tukey tests were performed when significant differences were observed.

3. Results

3.1. Successional gradient after fire

Environmental conditions differed between successional stages (PERMANOVA, d.f. = 6, $F = 21.49$, $P < 0.001$). Moreover, there were significant differences among sites (PERMANOVA, d.f. = 2, $F = 5.59$, $P < 0.001$). The first two PCO axes explained approximately 68% of the variation observed in the data, and clearly separated the three

Table 1
Micro-plot characteristics and correlation matrix with the first two axes of the principal-coordinate analysis (PCO) conducted. Data represent means \pm SE ($n = 60$). The highest correlation coefficients ($|\rho| \geq 0.6$) and their P values are shown in bold.

Micro-plot characteristics	Successional stage			Axis 1		Axis 2	
	Post-fire	Building	Mature	Spearman's ρ	P	Spearman's ρ	P
Litter cover (%)	37.8 \pm 3.2	46.3 \pm 4.4	90.1 \pm 2	-0.756	<0.001	-0.166	0.026
Stones cover (%)	12.7 \pm 1.7	11.3 \pm 1.5	3.7 \pm 1.7	0.507	<0.001	0.178	0.017
Herbs cover (%)	1.3 \pm 0.2	31.3 \pm 3.1	13.2 \pm 2.7	-0.237	0.001	0.328	<0.001
Shrubs cover (%)	10.4 \pm 1.4	59.5 \pm 4.1	76 \pm 3.8	-0.772	<0.001	0.202	0.007
<i>Cistus albidus</i> proximity (cm)	32.8 \pm 4.9	30.5 \pm 2.9	144 \pm 15.4	-0.406	<0.001	-0.622	<0.001
<i>Rosmarinus officinalis</i> proximity (cm)	177 \pm 13.1	125.8 \pm 12.2	36.5 \pm 5.6	0.898	<0.001	-0.17	0.023
<i>Ulex parviflorus</i> proximity (cm)	54.3 \pm 6.27	32.7 \pm 3.5	104.3 \pm 9.7	-0.319	<0.001	-0.665	<0.001
Fire severity (1–5)	2.5 \pm 0.2	–	–	–	–	–	–

successional stages along axis 1. Time since fire was negatively correlated with axis 1 (see Appendix A). All the environmental conditions measured were significantly correlated with the first two axes, but we emphasize only those variables with correlation coefficients (ρ) $\pm \geq 0.6$. Litter and shrub cover were the most important variables changing environmental conditions along the successional gradient and they were negatively correlated with the first ordination axis (Table 1). The proximity of *Rosmarinus* to the seedling monitoring quadrats was positively correlated with the first axis of the PCO, indicating a greater proximity in mature stages (Table 1). Those of *Cistus* and *Ulex* were negatively correlated with axis 2, and had a slighter proximity in building stages (Table 1). The post-fire stage experienced intermediate values of fire severity according to our index (Table 1).

The shrub stratum was clearly dominated by the three study species in all successional stages, although their abundance varied through succession. At the post-fire stage, vegetation cover was low (ca. 16%) and it was dominated mainly by dead individuals of *Ulex* and *Cistus*. At the building stage, *Cistus* and *Ulex* were co-dominant and, reached 30 and 21% of cover respectively. *Rosmarinus* was scarce and only reached a 2% cover. However, this species became dominant at mature stages (55% of cover), while *Cistus* and *Ulex* experienced a senescent phase, since most of their cover were from dead individuals (42% approximately). See Appendix B for more details of shrub cover.

3.2. Suitable micro-habitats for seedling emergence

During the three years of the study, a total of 3664 seedlings were recorded. The most abundant species was *Cistus* (3003), followed by *Ulex* (471) and *Rosmarinus* (190). Seedling emergence for the three species was generally higher in autumn than in spring cohorts (Table 2).

In the post-fire stage, the three species showed a flush of germination comprising the first 2–3 cohorts after fire (Table 2). This flush was especially pronounced in the first cohort after fire (autumn 2006), with an emergence of approximately 112 individuals \cdot m⁻², 2 individuals \cdot m⁻² and 7 individuals \cdot m⁻² for *Cistus*, *Rosmarinus* and *Ulex*, respectively (Table 2). After this event, germination decreased through time until it became very low three years after fire. Seedling emergence was slightly correlated with high-severity micro-habitats for *Cistus* and *Ulex*, although the effect of this variable was not significant within the model selected (Fig. 1A). In contrast, *Rosmarinus* was negatively affected by fire severity, and was positively correlated with the proximity of adult individuals of the same species (Fig. 1A).

In the building stage, seedling emergence of *Cistus* for the most numerous cohorts (autumn) was significantly lower than for the post-fire flush (11–19 individuals \cdot m⁻²; Table 2). Emergences of *Rosmarinus* ranged between 0 and 2 individuals \cdot m⁻² along all cohorts studied (Table 2). *Ulex* experienced a maximum of

Table 2
Seedling cohorts emerged throughout the three years of study in the different successional stages studied. Data represent mean \pm SE (ind m⁻²; $n = 3$). Values in the same row with different lowercase letters indicate that cohorts differ significantly within the same successional stage. Values in the same column with different capital letters indicate differences between successional stages in the same cohort (one-way ANOVA, $P < 0.05$, HSD Tukey test). P values below 0.05 are shown in bold.

Species and successional stage	Cohort						F	P
	Autumn 06	Spring 07	Autumn 07	Spring 08	Autumn 08	Spring 09		
<i>Cistus albidus</i>								
Post-fire	112.2 \pm 26.8 aA	4.8 \pm 3.5 bc	16.8 \pm 3 ab	1.6 \pm 0.4 cd	12.4 \pm 3.1 b	0.3 \pm 0.2 d	23.32	<0.001
Building	19.3 \pm 10.2 aB	1.6 \pm 0.7 abc	10.7 \pm 3.9 a	0.8 \pm 0.4 bc	11.1 \pm 4.9 ab	0.4 \pm 0.1 c	7.49	0.002
Mature	2.1 \pm 1.1 B	0.4 \pm 0.2	2.8 \pm 1.8	0.4 \pm 0.3	2.1 \pm 1.1	0.1 \pm 0.1	2.36	0.147
F	17.13	2.25	4.63	2.48	2.66	1.8		
P	0.003	0.186	0.61	0.164	0.149	0.244		
<i>Rosmarinus officinalis</i>								
Post-fire	1.9 \pm 0.5 a	1.3 \pm 0.3 ab	0.1 \pm 0.1 b	0.2 \pm 0.2 b	0.2 \pm 0.2 b	0.1 \pm 0.1 b	6.57	0.004
Building	1 \pm 0.4	0.2	1.5 \pm 0.9	0.5 \pm 0.3	0.7 \pm 0.6	0.2 \pm 0.1	1.08	0.417
Mature	1.3 \pm 0.3	0.3 \pm 0.2	2.5 \pm 2.1	0.3 \pm 0.2	0.4 \pm 0.2	0.3 \pm 0.2	0.63	0.681
F	1.05	5.14	1.42	1.49	0.59	1.37		
P	0.405	0.51	0.313	0.297	0.586	0.323		
<i>Ulex parviflorus</i>								
Post-fire	6.6 \pm 4 a	0.8 \pm 0.2 ab	1.1 \pm 0.1 ab	0.3 \pm 0.2 b	0.5 \pm 0.2 b	0.1 \pm 0.1 b	7.03	0.005
Building	3.5 \pm 2.2	0.5 \pm 0.3	3.5 \pm 2.2	0.4 \pm 0.3	10.6 \pm 5	0.6 \pm 0.3	2.68	0.075
Mature	1.6 \pm 0.3 a	0.13 \pm 0.1 b	0.8 \pm 0.3 ab	0.1 \pm 0.1 b	0.5 \pm 0.1 b	0.2 \pm 0.1 b	7.56	0.002
F	0.94	2.00	1.59	0.68	3.78	4.55		
P	0.441	0.216	0.278	0.54	0.086	0.63		

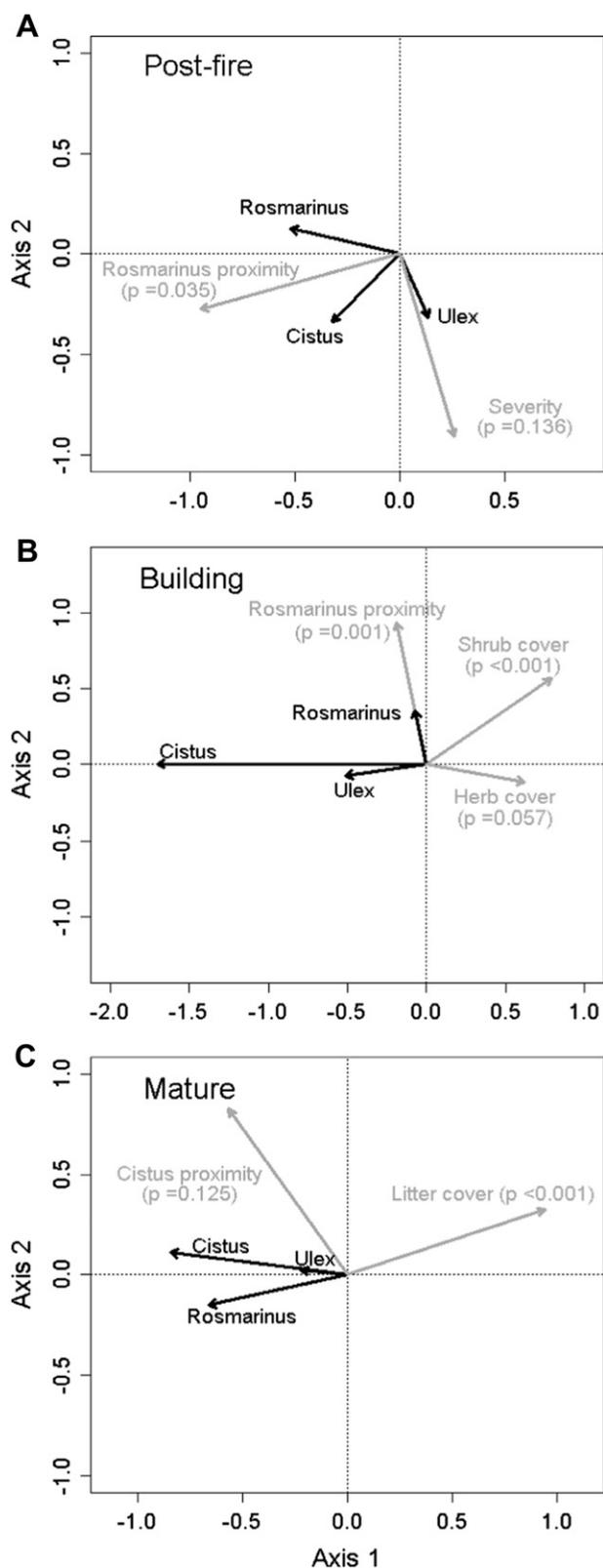


Fig. 1. Redundancy analysis (RDA) showing the relationships between emerging seedlings and micro-plot characteristics for the Autumn 2006 cohort. A) The model selected for the Post-fire stage ($F = 0.136$, $P = 0.032$) explained 29% of the total variance (axes 1 and 2 explained 5% and 2% and the conditional variable explained 22% of the variance); B) the model for the Building stage ($F = 0.643$, $P < 0.005$) explained 49% of the total variance (axes 1 and 2 explained 31% and 2% and the conditional variable explained 16%); C) the model for Mature stage ($F = 0.403$, $P < 0.005$) explained 22% of the total variance (axes 1 and 2 explained 21% and 1% and the conditional variable had

emergence in the autumn 2008 cohort (10–11 individuals $\cdot m^{-2}$; Table 2), which was even higher than the post-fire flush. In the other autumn cohorts, emergence ranged between 3 individuals $\cdot m^{-2}$ and 4 individuals $\cdot m^{-2}$. *Cistus* and *Ulex* preferably emerged on open micro-sites since they were negatively influenced by shrub cover (Fig. 1B). In contrast, *Rosmarinus* was not so linked to open spaces, and emerged on micro-sites near adult plants (Fig. 1B).

In the mature stage, all species had low values of seedling emergence (1–3 individuals m^{-2} , Table 2). Seedling emergence for *Cistus* was the lowest of all successional stages. *Ulex* also had the lowest values of emergence, although no significant differences were found (Table 2). Nonetheless, the emergence of *Rosmarinus* was similar to other successional stages (Table 2). Seedling emergence for all three species was negatively correlated with litter cover > 2 cm deep (Fig. 1C).

3.3. Seedling survival and establishment

In all three species, mortality was generally highest shortly after germination, a pattern clearly found during the very early establishing phase (winter–spring). After that, mortality was much lower, with only a few losses during summer (Fig. 2).

The percentages of survival in *Cistus* were the lowest of the three species studied, ranging from 5 to 15% in all successional stages at the end of our study. However, the first post-fire cohort (autumn 2006) was an exception to this pattern, as it reached 26% survival (Table 3). The Log-Rank comparisons of survival curves for the autumn 2006 cohort showed that survival in the post-fire stage was significantly different from that in the other successional stages (Fig. 2, Table 3). However, this difference disappeared in subsequent cohorts, and only differences were found between the post-fire and the building stages in the autumn 2008 cohort (Table 3). Consequently, *Cistus* establishment was practically confined to the initial post-fire cohort of 29 individuals $\cdot m^{-2}$, since neither in subsequent post-fire cohorts, nor in other successional stages did *Cistus* establishment reach more than 1 individual $\cdot m^{-2}$ (Table 4).

Rosmarinus seedlings had percentages of survival ranging from 33% to 61% in the post-fire and building stages, respectively. No significant differences in the survival curves were found between these two stages for this species (Fig. 2, Table 3). However, the survival curves in the mature stages were significantly different from those in both the post-fire and the building stages in the two cohorts studied (Fig. 2, Table 3); in the autumn 2006 and 2007 cohorts, mature-stage survival was highly reduced to 5% and 34%, respectively (note that for the building stage it was 61%). The cohort from autumn 2008 was very scarce, making it impossible to perform any analysis. The establishment of *Rosmarinus* was low (< 1 individual $\cdot m^{-2}$ in any of the studied cohorts, Table 4).

The percentage of survival of *Ulex* seedlings ranged from 25% to 47% for all cohorts and successional stages. Environmental conditions at the different successional stages did not affect seedling survival in this species, as no differences in survival curves were found between any successional stage in any cohort (Fig. 2, Table 3). There was a flush of establishment in the first post-fire cohort (autumn 2006) of approximately 2 individuals $\cdot m^{-2}$, whilst establishment in the subsequent post-fire cohorts was negligible (Table 4). However, we should highlight that, in the building stage, establishments between 1 and 5 individuals $\cdot m^{-2}$ per year were found in some cohorts. Establishment in the mature stages was virtually nil (Table 4).

no effect). Grey arrows are predictor variables, whilst emergent seedlings of the different species are shown in black. The numbers in brackets are P values (permutation test with 1000 iterations).

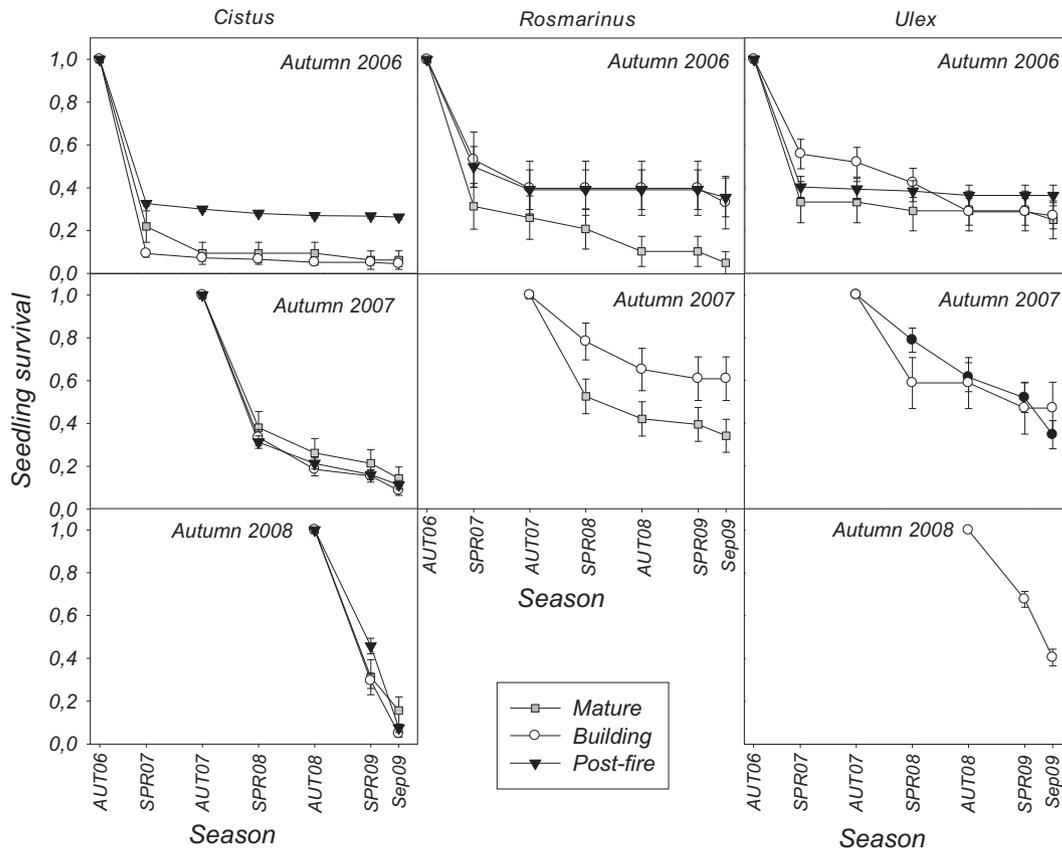


Fig. 2. Kaplan–Meier survival curves for the cohorts with the sufficient seedlings (>1 seedling \cdot m $^{-2}$). Data represent means \pm SE. AUT = Autumn, SPR = Spring, and Sep = September (early Autumn).

4. Discussion

Obligate seeder shrubs experienced a declining pattern of emergence and establishment as succession progressed to mature stages; this suggests a reduction in the availability of suitable micro-habitats for their regeneration through time. In the three species studied there was a flush of germination in the immediate post-fire cohort, which also had high levels of survival and establishment. The regeneration occurring at this first stage may be the main determinant of community composition through time, until senescence processes take place in adult individuals. This regeneration pattern may be in agreement with the tolerance mechanism proposed by Connell and Slatyer (1977). However, some shifts in species composition with respect to the initial regenerated community can occur; we found seedling establishment at least until the building stages (10–12 years after fire) in the three species studied. Therefore, we must reject our initial hypothesis that seedling establishment would be restricted only to post-fire stages. In fact, seedling recruitment processes of seeder species in inter-fire periods have previously been observed in Mediterranean Basin shrublands. Lloret (1998) found patterns of seedling establishment in a similar shrubland from NE Spain 10 years after fire, and Clemente et al. (1996) observed significant recruitment of new individuals in fire-free periods in *Rosmarinus* shrublands in Portugal. Nevertheless, our results suggest that, over the course of time, this recruitment will decrease with the decline in micro-habitats suitable for seedling establishment, until it practically ends in mature stages (22–27 years after fire). In a similar direction, Siles et al. (2008) found in shrublands in S Spain that the time required to reach a steady community dominated by *Rosmarinus*

was at least 18 years. The ability of the shrubs studied to recruit in inter-fire periods agrees with results reported for some suffruticose species from the chaparral (Keeley et al., 2006) and subshrubs in the Californian coastal sage scrub (DeSimone and Zedler, 1999), which are also able to establish uneven-aged populations after fire with recruitment linked to open gaps. These species may be classified as ‘opportunistic’ species that germinate and establish on open sites or disturbed soil following fire and/or non-fire disturbance (Ackerly, 2004). However, it is worth noting that the recruitment patterns detected in our study contrast with those described for most obligate seeder shrubs in Mediterranean regions, where germination and recruitment depend entirely on fire cues and are found almost exclusively during the first year after fire (Pierce and Cowling, 1991; Bell et al., 1993; Keeley, 1992, 1995).

The subtle differences detected in the preferential micro-habitats for germination and establishment of each species suggested a differentiation in their regeneration niche (Grubb, 1977). These differences may imply that the chance of establishment and coexistence of species varies over time because of the changing environmental conditions within succession (Bazzaz, 1979). In this context, we propose a conceptual scheme that hypothesizes how the establishment patterns vary during succession for each species and in relation to canopy development (Fig. 3). Immediately after fire, the availability of resources and/or factors needed for the regeneration of species reaches its optimum (Fig. 3A). Direct fire effects (i.e., soil temperatures and/or smoke) can enhance germination of soil-stored seeds (Bell et al., 1993; Keeley, 1995; Moreira et al., 2010), and our study species probably responded to these effects. However, the responses varied between species. The germination of species with hard-coated seeds broken by heat,

Table 3

Number of emerged seedlings and percentage of survival at the end of the study for Autumn cohorts. The effect of the successional stage on the survivorship of seedlings of each species was compared by Log-Rank tests (*P* values below 0.05 are shown in bold).

Cohort	Emerged (individuals)	Survival (%)	Log-rank comparison	
			Post-fire	Building
<i>Cistus albidus</i>				
Autumn 06				
Post-fire	1665	26.3		
Building	290	4.5	< 0.001	
Mature	32	6.2	0.008	0.395
Autumn 07				
Post-fire	252	11.3		
Building	161	8.7	0.683	
Mature	42	14.3	0.444	0.309
Autumn 08				
Post-fire	188	7.4		
Building	166	4.8	0.004	
Mature	32	15.6	0.742	0.221
<i>Rosmarinus officinalis</i>				
Autumn 06				
Post-fire	28	35.7		
Building	15	33.3	0.939	
Mature	19	5.3	0.023	0.049
Autumn 07				
Post-fire	0	–		
Building	23	60.9	–	
Mature	38	34.2	–	0.041
Autumn 08				
Post-fire	3	–		
Building	11	–	–	
Mature	6	–	–	–
<i>Ulex parviflorus</i>				
Autumn 06				
Post-fire	99	36.4		
Building	52	26.9	0.489	
Mature	24	25	0.307	0.551
Autumn 07				
Post-fire	17	47.1		
Building	52	34.6	0.706	
Mature	12	–	–	–
Autumn 08				
Post-fire	7	–		
Building	158	40.5	–	
Mature	7	–	–	–

such as *Cistus* and *Ulex* (Roy and Sonié, 1992; Baeza and Roy, 2008), showed some affinity (but not significant) with high fire severity micro-sites. Note that the severity of our fires was generally intermediate and the micro-sites suffering from more severe fire intensity probably experienced optimum temperatures for breaking the seed coat without reaching deleterious temperatures. *Rosmarinus*, in contrast, is a soft-seeded species that shows some sensitivity to high temperatures (Moreira et al., 2010), and had a negative correlation with fire severity; however, the fact that its germination is stimulated by smoke (Moreira et al., 2010) could partly explain its enhanced germination after fire. In addition, other indirect fire effects, such as the consumption of vegetation and the opening of large gaps in the canopy, can also promote species regeneration. The incidence of solar radiation can lead to higher daily fluctuations in soil temperature and contribute to rendering hard-seeded species permeable. Furthermore, the high red to far-red ratio in the light spectrum reaching the soil surface can also enhance germination. In fact, these two germination cues have previously been observed for *Ulex*, *Cistus* and other fire-prone

species (Roy and Sonié, 1992; Baeza and Roy, 2008; Santana et al., 2010a). In post-fire environments, seedling survival is expected to be enhanced both by increasing the availability of soil nutrients through ash deposition, and by increasing soil water availability due to a lack of competition (Thanos and Rundel, 1995; DeBano et al., 1998).

In the subsequent building stage, the availability of suitable micro-habitats for species regeneration declines as the direct and indirect effects of fire decrease through time. Open gaps in the canopy left among the building individuals, and the absence of a thick litter layer, are the main requirements for achieving seedling emergence in hard-coated seeds (i.e., *Cistus* and *Ulex*). The seeds that remain ungerminated in the soil after fire or those produced by the new individuals can be stimulated by temperature fluctuations, and by high levels of light and radiation affecting the soil in open gaps. Moreover, *Cistus* produce a fraction of soft-coated seeds that are not dormant and germinate readily under favourable conditions (Thanos et al., 1992). However, the existence of seedling emergence did not translate into establishment for all species; emerging seedlings of *Cistus* had high mortality rates and its establishment in the building stages was very low (≤ 1 individuals·m⁻²). This suggests that the regeneration of *Cistus* could be tied to those environments created immediately after a disturbance (Fig. 3B), where the high availability of soil resources is the only way to counterbalance its high mortality rate. *Ulex* was the only species with a significant recruitment in open gaps in our study (Fig. 3B). In contrast, the germination of *Rosmarinus* differed from that of the hard-seeded species in that it was more related to the proximity of adult individuals than to canopy gaps. This may have several explanations. For example, the scarce abundance of *Rosmarinus* individuals could mean that seed availability was low and seedlings emerged near seed-producing adults. It is also possible that the germination and establishment of *Rosmarinus* are not so linked to open gaps as to safer sites next to parent plants (Ellner and Shmida, 1981; Escudero et al., 1999). *Rosmarinus* had a low number of established individuals in the building stages, but this was probably due to its low number of emergent seedlings, as it showed high survival rates. Our findings contrast with Lloret (1998), who did not find any relationship between seedling germination and open gaps. This discrepancy could be the result of the differences in the analyses among studies, as this author analysed all the species together.

As the succession progresses towards mature stages (22–27 year after fire), the established individuals grow (Fig. 3A), and the availability of resources needed for germination, such as temperature and light fluctuations, declines. The production of litter through time, and the individuals of short-lived species in senescent phases, can increase the cover and thickness of the litter layer, impeding seedling emergence. In fact, litter depth can influence recruitment by decreasing the surface suitable for germination (Facelli and Pickett, 1991; Lloret, 1998; Baeza and Roy, 2008). Besides, the production of new pools of seeds can be reduced as consequence of the senescent phase experienced by *Cistus* and *Ulex*. For *Rosmarinus*, the high density of adults may have a negative effect on seedling establishment because of competition for light and soil resources. This fact could be suggested by the high mortality rates experienced in *Rosmarinus* seedlings at mature stages in comparison with previous stages. However, further studies are needed to confirm this observation. We must note that the scheme depicted in Fig. 3 is based on the monitoring of few cohorts, and more observations throughout time are needed to validate it completely.

Traditionally, obligate seeder species in the Mediterranean basin have been globally regarded as pioneer species at early successional stages due to their high production of small seeds and their high

Table 4
Seedlings established at the study for each cohort and successional stage. Data represent mean \pm SE (ind m^{-2} ; $n = 3$). Values in the same row with different lowercase letters indicate that cohorts differ significantly within the same successional stage. Values in the same column with different capital letters indicate differences between successional stages in the same cohort (Kruskal–Wallis test, $P < 0.05$, HSD Tukey test). P values below 0.05 are shown in bold.

Species and successional stage	Cohort						χ^2	P
	Autumn 06 (36 months)	Spring 07 (30 months)	Autumn 07 (24 months)	Spring 08 (18 months)	Autumn 08 (12 months)	Spring 09 (6 months)		
<i>Cistus albidus</i>								
Post-fire	29.3 \pm 20.1 aA	1.9 \pm 1.4 b	1.9 \pm 0.4 b	0.6 \pm 0.2 b	0.8 \pm 0.5 b	0.7 \pm 0.7 b	13.54	0.019
Building	1.1 \pm 0.3 B	0.3 \pm 0.3	1.0 \pm 0.7	0.7 \pm 0.7	0.7 \pm 0.3	0.2	9.31	0.097
Mature	0.1 \pm 0.1 B	0	0.4 \pm 0.2	0	0.3 \pm 0.2	0	8.38	0.136
χ^2	7.26	4.59	3.32	4.59	1.10	5.60		
P	0.027	0.101	0.19	0.101	0.576	0.061		
<i>Rosmarinus officinalis</i>								
Post-fire	0.7 \pm 0.3 a	0.3 \pm 0.2 ab	0 b	0 b	0.1 \pm 0.1 b	0 b	12.18	0.032
Building	0.4 \pm 0.2	0.1 \pm 0.1	0.9 \pm 0.5	0.3 \pm 0.2	0.1 \pm 0.1	0.3 \pm 0.2	3.49	0.625
Mature	0.1 \pm 0.1	0.1 \pm 0.1	0.9 \pm 0.7	0.1 \pm 0.1	0	0.2 \pm 0.1	4.68	0.456
χ^2	3.65	1.21	2.88	1.21	1.14	3.15		
P	0.161	0.546	0.237	0.546	0.565	0.207		
<i>Ulex parviflorus</i>								
Post-fire	2.4 \pm 1.5	0.2 \pm 0.1	0.5 \pm 0.1	0.2 \pm 0.2	0.2 \pm 0.2 B	0.1 \pm 0.1	10.54	0.061
Building	0.9 \pm 0.3	0.1 \pm 0.1	1.5 \pm 0.7	0.2 \pm 0.2	5.1 \pm 2.3 A	0.4 \pm 0.4	9.98	0.076
Mature	0.4 \pm 0.3	0.1 \pm 0.1	0.3 \pm 0.2	0.1 \pm 0.1	0 B	0	6.14	0.293
χ^2	2.57	1.15	3.31	1.15	6.17	1.17		
P	0.276	0.564	0.191	0.564	0.046	0.558		

In brackets the age of seedlings at the end of the study.

growth rates (Verdú, 2000; Pausas et al., 2004). Nevertheless, our findings suggest that the differences in the regeneration niches of these species, together with other life-history traits (e.g. life-span), may point to the existence of tradeoffs that make them more competitive in a particular set of environmental conditions during succession (Parrish and Bazzazz, 1982; Silvertown, 2004). Some species generate a large number of seeds whose establishment is very dependent on post-fire conditions (i.e., heat, open gaps, high soil resource levels). This seems to be the case of *Cistus* and other short-lived shrubs that generate a large offspring after fire, become dominant in recurrently perturbed environments and replenish their seed bank rapidly (Fig. 3; Roy and Sonié, 1992; Baeza et al., 2007; Clemente et al., 2007; Santana et al., 2010b). In contrast, species like *Ulex* and *Rosmarinus*, whose recruitment is not so

linked to fire, may take advantage of building stages to colonise open gaps and expand their abundance through time. The life-span of these species would also be determinant, as the longest-lived species, e.g., *Rosmarinus*, occupy the later successional stages (Fig. 3; Baeza et al., 2007; Clemente et al., 2007; Santana et al., 2010b). Therefore, although the response of a species to post-fire environmental conditions (i.e., sensitivity to fire severity, survival, seed dispersal mode and distribution of the seed bank) would be the main factor determining species establishment and possible spatial coexistence (Moreno and Oechel, 1992; Quintana et al., 2004; De Luis et al., 2008), the ability of a species to establish in inter-fire periods may also be an important factor driving seeder-species coexistence through the successional process in the western Mediterranean Basin.

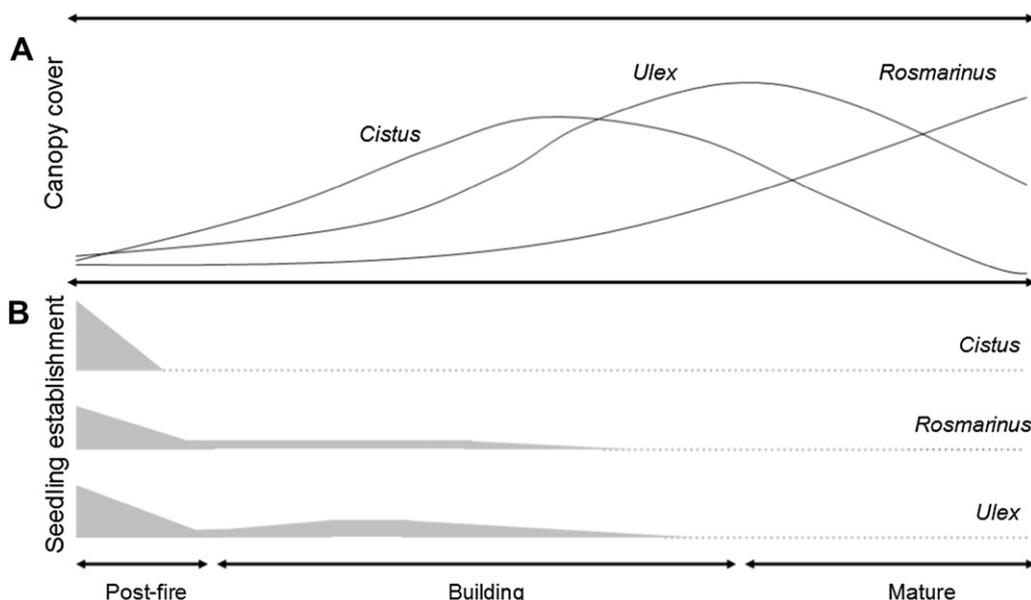


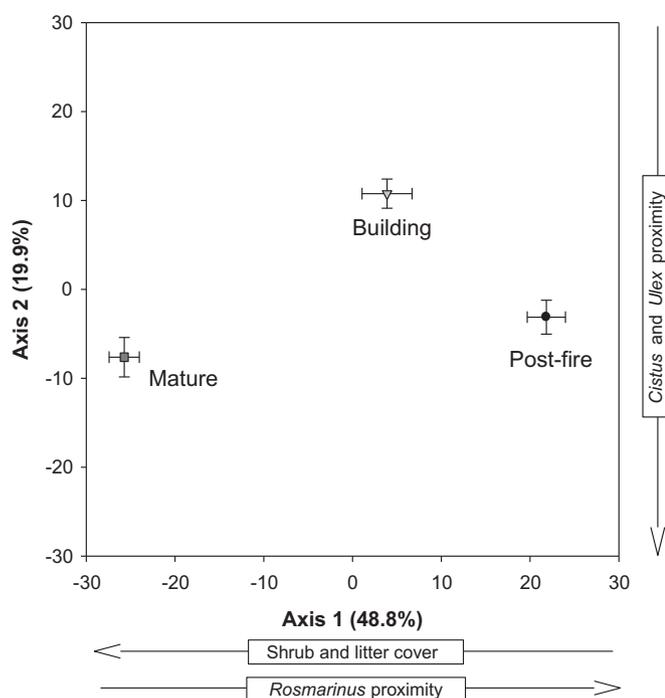
Fig. 3. Conceptual scheme showing A) canopy development along succession for the three main species, and B) patterns of seedling establishment.

Acknowledgements

We thank two anonymous reviewers for their considerable help with the manuscript. We thank J. Scheiding for the revision of the English text and the Font Roja Natura-UA Scientific Station for fieldwork support. V.M. Santana was supported by a FPU grant awarded by the Spanish Ministry of Education and Science. F.T. Maestre is supported by the European Research Council under the European Community's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement n° 242658 (BIOCOM). This research was carried out within the FIREMED (AGL200/8-04522/FOR) and Consolider-Ingenio 2010 (GRACCIE CSD2007-00067) projects. CEAM is supported by the Generalitat Valenciana and Fundació Bancaja.

Appendix A

Principal-coordinate analysis (PCO) of the environmental conditions characterising the different successional stages. Data represent means \pm SE ($n=60$). Arrows represent environmental conditions significantly correlated ($|\rho| \geq 0.6$) with the first two axes.



Appendix B

Shrub cover of stands at different successional stages. Data represent means \pm SE ($n=3$).

Shrub cover (%)	Successional stage		
	Post-fire	Building	Mature
<i>Cistus albidus</i>	0.2 \pm 0.2	30.1 \pm 2.3	2.7 \pm 1.9
<i>Rosmarinus officinalis</i>	0.1 \pm 0.1	2.2 \pm 0.5	55.3 \pm 4.7
<i>Ulex parviflorus</i>	0	21 \pm 5.8	5.1 \pm 1.1
<i>Cistus</i> dead	7.3 \pm 1.7	3.2 \pm 1.9	0.2 \pm 0.2
<i>Ulex</i> dead	5.2 \pm 0.9	2.7 \pm 1.2	42 \pm 4.3
Other shrubs	3.2 \pm 1.3	20.8 \pm 5.5	16.7 \pm 4

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