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Rainfall patterns after fire differentially affect the recruitment of three Mediterranean shrubs

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Abstract

In fire-prone environments, the "event-dependent hypothesis" states that plant population changes are driven by the unique set of conditions of a fire (e.g., fire season, climate). Climate variability, in particular changes in rainfall patterns, can be most important for seeder species, since they must regenerate after fire from seeds, and for Mediterranean shrublands, given the high yearly variability of rainfall in these ecosystems. Yet, the role of rainfall variability and its interaction with fire characteristics (e.g., fire season) on plant populations has received little attention. Here we investigated the changes in seedling emergence and recruitment of three seeder species (*Cistus ladanifer*, *Erica umbellata* and *Rosmarinus officinalis*) after fires lit during three different years and at two times during the fire season (early and late in the fire season) to account for potential changes in the soil seed-bank during the year. Three plots were burned at each season, for a total of 18 plots burned during the three years. After fire, emerged seedlings were tallied, tagged and monitored during three years (two the last burning year). Rainfall during the study period was rather variable, and in some years was well below average. Seedling emergence after fire varied by a factor of 3 to 10, depending on the species and on the burning year. The bulk of seedling emergence occurred in the first year after fire, and seedling recruitment at the end of the study period was tightly correlated with this early emergence. Seedling emergence in *E umbellata* and *R officinalis*, but not in *C ladanifer*, were correlated with precipitation in the fall and winter immediately after the fire, being *E umbellata* most sensitive to low rainfall. Fire season was generally not an important factor in controlling emergence and recruitment. We discuss how projected changes in rainfall patterns with global warming can alter the balance of species in this shrubland, and can drive some species to near local extinction.

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1 Introduction

In fire-prone environments, the "event-dependent hypothesis" states that plant population changes are driven by the unique set of conditions of a fire (e.g., fire intensity, fire season, fire area or pre-, and/or post-fire climate; Bond and van Wilgen, 1996). For a given vegetation type, the energy released during fire varies enormously, depending on the weather conditions during fire in interaction with fuel structure and composition (Bessie and Johnson, 1995). Therefore, it is not surprising that much attention has focussed on understanding the role of fire intensity and severity on plant populations (Moreno and Oechel, 1991; Pausas et al., 2003; Keeley et al., 2008). The role of fire season has equally been studied since long due, among other, to its significance for management (Trabaud and Lepart, 1981). Fire season can affect plants response to fire because, among other, the composition of the seed bank is season-dependent (Bond et al., 1984; Knox and Clarke, 2006). The effect of post-fire climate on plant population changes after fire, although potentially important, has only seldom been considered (Keeley et al., 2005). Although some studies have addressed the impact of climate and weather extremes following fire (e.g., droughts, heavy rains) (de Luis et al., 2005; Prieto et al., 2009), little is known about how inter-annual rainfall variability interacts with other components of the fire regime, namely fire season, to affect plant regeneration after fire.

The effects of post-fire rainfall and fire season on plant regeneration after fire deserve particular attention in the Mediterranean region and other Mediterranean-type climate areas of the world. These areas are characterized by warm and dry summers, and cool and moist winters; total yearly precipitation as well as the length of the rainy season are very variable from year to year and droughts are common (Lana et al., 2006). Fires, particularly very large fires, and multiple large fire-episodes tend to occur under severe fire weather, which are partly the result of reduced rainfall and drought (Trigo et al. 2006; Founda and Giannakopoulos, 2009). Therefore, large areas, which at times can amount to significant portions of a country, could be regenerating under, and be

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subject to, similar climate conditions. That is, the effects of climate variability on plant populations under regeneration could be geographically extensive and, eventually, lead to long-lasting changes. Therefore, it is essential to understand how inter-annual variability in rainfall patterns and rainfall extremes, among other climatic conditions, affect post-fire regeneration.

Seeder species are common in Mediterranean areas (Trabaud, 1987; Bond and van Wilgen, 1996). These are species with individuals dying during the fire and which depend on post-fire germination for reestablishment. Therefore, they can be particularly sensitive to the vagaries of the weather and climate after fire. Germination is commonly triggered by the first rains (Quintana et al., 2004). However, the optimum germination temperature varies among species (Baskin and Baskin, 1998), hence, the temporal pattern of rainfall and temperature can shift up to several months the time of germination. Once germination has occurred, soil moisture is probably the most limiting factor for survival (Moreno and Oechel, 1992). Mortality during the first few months, up to and including the first summer, is very high (Moreno and Oechel, 1992; Thanos et al., 1996; Lloret, 1998; Quintana et al., 2004). Consequently, climatic conditions after fire can play a significant role in triggering germination and causing mortality in seeder species. Modelling and empirical studies show that the viability of a population can be at risk due to drought following fire (Lamont et al., 1991; Maschinski et al., 2006). A differential sensitivity among coexisting species towards the post-fire climate, either for germination or for survival, could lead to shifts in the structure and composition of plant populations.

Aside from the postfire climatic conditions, the number of seedlings emerging after fire is a function of the size and dormancy state of the soil seed-bank in interaction with fire intensity. Soil seed banks in Mediterranean ecosystems are persistent, although their fluctuations from year to year and within a year have not yet been well quantified (Parker and Kelly, 1989). It can be argued that the size of the seed-bank will change during the course of the season, being highest in late summer and lowest in late spring, before seed maturation and dispersal (Bond, 1984; Bastida and Talavera, 2002). Therefore, the size of the soil seed-bank at the time of fire could vary depending on when fire occurs, and this could affect the number of germinates and subsequent recruits.

The objectives of this study were to assess how post-fire seedling emergence and establishment of three seeder species changed following fires lit during three years and at two different seasons. The questions addressed were: how variable is seedling emergence and establishment following burning in different years? Is this variability related to the climatology following fire, in particular to rainfall? How does the burning season interact with the previous factors? By burning during several years and at two times during the fire season we intended to assess the variability in emergence and recruitment through the years, and to cover a period within which a large fluctuation in the soil seed-bank could occur. By allowing a long period of time within the year between burns we aimed at understanding the consequences of fires that could occur at different times during the year. This is important under the ongoing and projected changes in climate for the Mediterranean. Increased temperature, reduced total precipitation and changes in rainfall patterns (Christensen et al., 2007) are projected to lengthen the fire season (Moriondo et al., 2006; Moreno et al., 2010), hence, making fires to occur earlier and later during the year.

2 Materials and methods

The study was carried out at the Quintos de Mora Range Station (Los Yébenes, Toledo, 39°23′ N, 4°00′ W). The climate is Mediterranean (mean yearly temperature is 14.6 °C and mean precipitation is 683 mm, of which only 13.2 % fall during the summer months (June–September). An old (> 45 yr) shrubland stand was chosen in a south-facing slope, 17 % inclination, at 900 m elevation. The shrubland was composed of *Cistus ladanifer* L. (2.1 individuals m^{-2}), *Erica arborea* L. (1.5 individuals m^{-2}), *Erica umbellata* Loefl. ex L. (0.6 individuals m^{-2}), *Phillyrea angustifolia* L. (2.5 individuals m^{-2}) and *Rosmarinus officinalis* L. (0.5 individuals m^{-2}). *Cistus ladanifer*, *Erica umbellata* and

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Rosmarinus officinalis (*Cistus*, *Erica* and *Rosmarinus* from here on), are non-sprouting, seeders, i.e., all plants die after fire, and recruitment is dependent on germination. *Erica arborea* and *Phillyrea angustifolia* are resprouters. Emergence of these two species was nil during the study period and will not be treated further on.

During three consecutive years, burns (burning year 1 to burning year 3 (B1, B2 and B3)) were conducted early and late in the fire season (ES and LS, respectively). At each burn, 3 experimental plots ($13 \times 14\,m^2$) were burned, adding up to 18 experimental plots in total (3 yr × 2 seasons× 3 replicates). ES burns were conducted at the end of June, and LS burns were conducted in late September or early October. Fires were conducted by burning up-hill and downwind. All three plots per season and year were burned during the same day. Burning was always conducted on clear, sunny days, and under stable conditions. Soil surface temperatures during the fire were recorded with 10–15 K-type thermocouples placed 1 cm above soil surface and connected to a data logger (Campbell Scientific, Logan, Utah, USA) for all except the first set of burns. We calculated fire-intensity as the time-temperature integral, which can be a good estimation of the total heat reaching the soil surface during fire.

The Range Station has been used for game hunting for decades, and herbivore stocks are kept at much higher rates that would be normal. To avoid trampling and herbivory by large mammals the whole area was fenced before the first fire. In each plot, two 10 m transects were established, and along each, ten $50 \times 50\,cm^2$ quadrats were permanently set at regular intervals. These were used to monitor post-fire seedling emergence and survival. After fire, emergence and establishment were monitored regularly at monthly intervals (during active periods of seedling emergence). Emerged seedlings were tallied, tagged and monitored during the three following years except for the last set of burns (B3) in which post-fire monitoring lasted only two years. Therefore, seedling monitoring after fire lasted four years (Yr 1 to Yr 4). B1 burns were conducted in the fire season preceding Yr 1, and were monitored from the beginning of Yr 1 to the end of Yr 3. B2 burns were conducted in the fire season of Yr 1, and were monitored during Yr 2 to Yr 4, both included. B3 burns were conducted in the

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fire season of Yr 2, and were monitored during Yr 3 and Yr 4. Seedling emergence after fire occurred during a maximum of three years, and was differentiated by yearly cohorts based on the year-after-fire of emergence (cohort 1 to cohort 3). Since the burns were done in consecutive years, different cohorts overlapped over the years.

Differences in seedling emergence and recruitment at the end of the second year of monitoring in relation to burning year, fire season and cohort were analyzed by means of repeated measures ANOVA. There were two between-subjects factors and one within-subject factor, with three replicates for each treatment combination. Between subjects factors were burning year (B1, B2, and B3; $n = 3$) and fire season (ES and LS; $n = 2$). The within-subject factor was the time (year-after-fire, YAF) at which the emergence occurred (cohorts 1 and 2; $n = 2$). We did not include in this analysis the data of cohort 3 of B1 and B2 burns, since no such information was available for B3 burns. Finally, differences in the time-temperature integral (a measure of fire intensity; Keeley, 2009) between burning year and fire season were analyzed by means of two-way ANOVA.

To understand trends in recruitment and the factors controlling them, we compared recruitment at the end of YAF2 with emergence during YAF1 by means of linear regression ($n = 6$, that is, each point was the mean of the three plots burned per season and year). Similarly, we compared recruitment at the end of YAF3 with recruitment at the end of YAF2 for B1 and B2 burns ($n = 4$; B3 burns could not be included since YAF3 was not sampled in these burns). Differences in the slope of these relationships among species were examined by the ratio of the difference in slopes to the standard error of the difference between slopes. Finally, seedling emergence at the end of YAF1 was related to rainfall during fall and winter (October through February) of that year for each of the burns by ordinary least square linear regression, using the mean of the two values (ES, LS) of the dependent variable for each of the dependent variable (rainfall of each year). Statistical analyses were conducted with SPSS vs. 13 (SPSS Inc., Somers, NY).

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3 Results

Annual precipitation during the four years (Yr 1 to Yr 4) of monitoring following the three burning years (B1 to B3) was very variable, and covered a large portion of the long-term variability observed in the area (Fig. 1). Rainfall in Yr 1 and Yr 4 were above the long-term mean, while rainfall in Yr 3 and, particularly, during Yr 2 were well below average (Fig. 1). The experimental burns had a pattern of temperatures at the soil surface similar between burning years and seasons (Fig. 2). There were no statistically significant differences for time-integrated temperatures during fires (Burning year: $F_{2,10} = 1.59$, $p = 0.25$; Season: $F_{1,10} = 2.25$, $p = 0.16$; Burning year × Season: $F_{1,10} = 0.40$, $p = 0.54$). We thus concluded that differences in seedling emergence for the various year-season fires did not arise from differences in fire intensity.

There were large differences in total emerged seedlings between years and species. *Cistus* was the species with the greatest average seedling emergence during the three burning years, varying between burns by a factor greater than 3 (from 61 to 204 seedlings m^{-2}). *Erica* produced, on average, the second largest emergence; yet, its variability between burns was much larger (factor of 12, from 13 to 156 seedlings m^{-2}). *Rosmarinus* was the species with fewer seedlings emerged on average, and with lesser variability among burns (factor of 3, from 6 to 17 seedlings m^{-2}; Fig. 3).

Burning year was a statistically significant factor for emergence in *Cistus*, and *Erica* and non-significant in *Rosmarinus* (Table 1). Seedling emergence during the various years after fire (cohort 1 to cohort 3) changed depending on the burning year and species. Emergence following B1 burns occurred in one single cohort (cohort 1) for all three species (Fig. 3). On the contrary, emergence after B2 burns occurred during the next three years. Emergence following B3 burns occurred also at least during the next two years after fire (the third year could not be sampled).

Emergence was generally highest in YAF1 than in YAF2 or YAF3 for all burning years, although there was variability among species (Fig. 3). While this pattern was true for *Cistus* and *Rosmarinus* in all burns, it was not so for *Erica*. Indeed, in some

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burning years (B2 and B3), emergence in this species was higher in YAF2 than in YAF1. Actually, in one occasion (B2, LS) emergence in YAF3 (cohort 3) was even higher than in YAF1 (cohort 1) (Fig. 3). Time of emergence (YAF1 and YAF2 cohorts were the only two tested; see Methods) was a significant factor for the three species. Furthermore, there was a significant interaction between time of emergence and burning year for all three species, and with season for *Cistus* and *Rosmarinus*, not for *Erica* (Table 1). In absolute figures, LS burns produced greater emergence than ES ones for *Cistus* and *Rosmarinus,* while for *Erica* tended to be the opposite (Fig. 3). Nevertheless, season was a statistically significant factor only for *Cistus*. Furthermore, season in this species interacted with burning year and time of emergence, respectively (two way interaction) and jointly with the two (three way interaction; Table 1).

At the end of the third year after fire (second for B3 burns) recruitment for the three species showed similar patterns to total seedling emergence (Fig. 4). Note that the population of recruiters of *Cistus* and *Rosmarinus* was mainly composed of cohort 1 individuals (Fig. 4). That was not so for *Erica*, whose recruiter population was composed of individuals that had germinated in the first, second or even third year after fire, depending on the burning year (Fig. 4). Few effects, however, were significant in recruitment: year was a marginally significant factor in *Erica*, with a significant interaction with time of emergence. Season was also a marginally significant for *Cistus*. Time of emergence was only a significant factor for *Rosmarinus* (Table 1).

Recruitment at the end of the second year after fire was tightly correlated with seedling emergence during the first year after fire in the three species (Fig. 5). The slope of this regression was significantly ($p \leq 0.05$) different among the three species, being highest in *Rosmarinus* (0.35), intermediate in *Cistus* (0.24) and lowest in *Erica* (0.12). Furthermore, recruitment at the end of the third year was virtually the same than at the end of the second year for *Rosmarinus* and *Cistus* (we observed an intercept and a slope statistically identical ($p < 0.05$) to 0 and 1, respectively), not for *Erica* in which recruitment decreased in the third year with respect to the second one (Fig. 6). There was a significant relationship between the amount of rain fallen in autumn and winter

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(October through February) the first year after fire for *Rosmarinus* and, particularly, for *Erica* but not for *Cistus* (Fig. 7).

4 Discussion

How variable is seedling emergence and recruitment after burning in several years and in two seasons for the three species studied? The short answer is much, although variability is species-dependant, and different for emergence or recruitment. Seedling emergence across burns varied the least in *Rosmarinus,* followed closely by *Cistus*, but in *Erica* was much more pronounced. Recruitment varied also among species but there was a close relationship between emergence during the first year and recruitment three years after fire. This close relationship between emergence and recruitment (Fig. 5) indicates that the potential for variation in the population of recruits from year to year can be important, depending on what happens during the first year after fire. This supports the hypothesis that "event dependent" processes can be a major cause of population changes. Furthermore, not all three species responded equally to burning in the various years. That means that the population of recruits of each species will vary depending on the particularities surrounding and following fire, and that differences among species can occur as a result of fire.

How were emergence and recruitment patterns related to rainfall after fire? The answer is that very much, but different for each species. Rainfall during autumn and winter (October through February) in the YAF1 appeared to be the main factor in determining changes in emergence and, ultimately, recruitment for the three species (Figs. 3, 6 and 7). The burn-year that was followed by a wet fall and winter (B1 burns; Fig. 1), emergence was highest in all three species and occurred only during the first post-fire year (basically one single yearly cohort). By contrary, when the first year after fire was dry (B2 burns; Fig. 1), the three species responded with a similar pattern of reduced overall emergence and delayed emergence through the next two years. Indeed, three yearly cohorts contributed to recruitment in all three species, in particular in *Erica*. It is important to note that Yr 1 and Yr 2 were at the extreme (46 % above and 60 %

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below average autumn and winter precipitation, respectively, Fig. 1b) sides of the frequency distribution of rainfall in the area, which allows arguing that they provided us with a good representation of the range of patterns of emergence and establishment after fire in this shrubland.

Despite the differences in emergence patterns, the tight correlation between emergence on the first year and recruitment two or three years after fire (Figs. 5 and 6) indicates that individuals emerging after the first year will have a low probability of become recruits one or two years later. Consequently, what happens during the first year is most critical, and rainfall in autumn-winter explained much of the variation in emergence for some species. Emergence in *Erica* was the most sensitive of the three species to rainfall (highest slope between rainfall during autumn-winter of YAF1 and emergence; Fig. 7b), and its survival was the lowest of the three (lowest slope between recruitment two or three years after fire and emergence during the first or second years after fire, respectively; Figs. 5b and 6b). So, in dry years, emergence during the first year will be low and so it will be recruitment three years later. Its sensitivity to rainfall was such that its regeneration can be compromised during dry years, as it happened after B2 burns, in which recruitment was so low that neared local extinction. The sensitivity of *Erica* to the rainfall patterns of the years following fire was such that each of the burning years had a different cohort dominating the recruitment population. Emergence in *Rosmarinus* was also positively related to rainfall in the autumn-winter following fire (Fig. 7c), but seedlings once emerged survived in greater proportion (higher slope, Fig. 5c) than in the other species, much regardless of the rainfall in the following years. Finally, *Cistus* had an emergence that was less sensitive to rainfall during the first year after fire (Fig. 7a), but seedlings survived at a high rate, less though than *Rosmarinus*, and much regardless of the rainfall variability in the following years (Fig. 5a). In fact, the very high coefficient of determination of these last two species indicates that only 8 % of the variance remained unexplained and due to other factors that the initial emergence, which contrasts with the nearly half of the variance that remained unexplained in *Erica*.

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So, *Cistus* and *Rosmarinus* are species that will recruit once emergence occurs, much independent of the vagaries of the rainfall following their emergence, the first summer included. That was not so for *Erica* that was more sensitive to such changes in precipitation. Consequently, the post-fire rainfall can impact the overall population of germinates and recruits, and unbalance the relative weight of the various species in the overall population of seedlings. The lack of relationship between *Cistus* recruitment and rainfall is probably the result of the significant effect of season on seedling emergence. That means that, within the season, the seed bank of *Cistus* is probably fluctuating more than that of the other two species, either because more seeds are incorporated to the soil or because those that do so are more resistant to fire (Thanos et al., 1992; Bastida and Talavera, 2002; Reyes and Trabaud, 2009). Consequently, the number of emergences fluctuates in relation to rainfall but also in regard to the soil seed bank size (see below).

How variable is emergence and establishment in relation to fire-season? The answer is that not much, although there were variations among species. In Mediterranean-type ecosystems seedling emergence has usually been found to be greater following autumn rather than early-season burns (Bond et al., 1984; Knox and Clarke, 2006). Several hypotheses have been suggested to explain why fire season may affect post-fire emergence in seasonal climates, among them the temperature threshold (Hodgkinson, 1991) and the phenology of seed dispersal (Bond, 1984) are most relevant. According to the temperature threshold argument, during the early-season fires, when the soils hold more moisture, the temperatures reaching deeper into the soil might not be sufficient to break seed dormancy of seeds requiring heat shock (Hodgkinson, 1991). Thus, germination and emergence of species with seed dormancy would be promoted after late-season fires, when soil heating might penetrate deeper into the soil.

In the present work all fires were of similar fire-intensity. Soil moisture was not measured, but the upper horizons were dry at the time of burning. It thus seems that none of these factors played a significant role on germination and emergence in this case. Following the phenology of seed dispersal hypothesis, germination would be higher

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after fires occurring just after maximum seed dispersal, the seed-bank declining thereafter until the next season due to seed attrition by predators or other causes. In our case, both *Cistus* and *Erica* produce large quantities of seeds per year, not so *Rosmarinus*. We counted in one year and for a mean-size individual 18 000, 13 500 and, 2000 seeds produced by *Cistus*, *Erica* and *Rosmarinus*, respectively (Luna, 1998). Therefore, the temporal variability of the soil seed bank must be rather great. Seed dispersal varies among species: *Rosmarinus* disperses from March to July; *Erica* disperses from July to October, with peak dispersal occurring in August; *Cistus* has an extended period of seed dispersal, from July to January in the study area, with peak dispersal occurring also in August (Luna, 1998). Nevertheless, fire season was, for the most part, not a significant factor on emergence, except for *Cistus*, whose emergence was significantly affected by season, being autumn fires the ones producing greater emergence. Season was a still marginally significant in recruitment at the end of the second postfire year.

Our results show that emergence and recruitment in each species showed a slightly different response to fire and ensuing conditions. *Cistus* emergence was sensitive to year of burning, season and year after fire of emergence. Yet, recruitment was only marginally significantly affected by season. In all cases, *Cistus* produced the most seedlings, more than enough to replace the original population before fire (see also Quintana et al., 2004). *Cistus* is a dominant species in acidic shrublands in the Western Mediterranean, and dominates postfire environments. This allows arguing that this species is not vulnerable to changes in climatology or season of burning to maintain its population through fires. By contrary, *Erica* was sensitive to post-fire year, showing a substantial reduction in emergence and recruitment when dry post-fire conditions occurred. In one of the years recruitment was minimal and it occurred mainly from seedlings germinated in the third year, not in the first year, as it happened in the other two species, which probably impairs its competitive ability with respect to the seedlings of the other coexisting species. *Cistus* and *Rosmarinus* are distributed throughout much the Central Iberian Peninsula, and throughout a large range of annual

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precipitation. By contrary, the distribution of *Erica* is more restricted, and is related to areas with higher precipitation. Indeed, the eastern limit of the distribution of *Erica umbellata* coincides roughly with the study site area (Benito Cebrián, 1948). Thus, *Erica* appeared as the most vulnerable species of the three to variations in precipitation that might occur from one year to another. Finally, *Rosmarinus* showed low emergence rates, probably a reflection of its lower soil seed bank. However, it was the species with the highest relative recruitment success, which is consistent with its larger seed-size (Moles and Westoby, 2004). Emergence of *Rosmarinus* is not linked to fire, and its germination is not dependent on fire-related cues (Reyes and Trabaud, 2009). That is, *Rosmarinus* shows low dormancy levels, thus probably a large proportion of seeds germinate as soon as the conditions required are met (Clemente et al., 2007). Opposite to *Cistus*, *Rosmarinus* appears as successful during all stages on succession and not only after fire occurrence (Clemente et al., 2007).

Climate models project an overall reduction in annual precipitation for the Iberian Peninsula, with stronger reductions in summer precipitation than in winter precipitation (Giorgi and Lionello, 2008). Plant recruitment after fire was mainly driven by emergence, which in turn was related to autumn-winter precipitation, at least in *Erica* and *Rosmarinus* (Fig. 7). This implies that rainfall determining emergence is important, not that causing mortality once emergence has occurred. This indicates that an intensification of the summer drought may not be as critical for plant regeneration after fire as is usually assumed, although further studies need to confirm this. Changes in the seasonal amount of precipitation, and particularly fall and winter precipitation, have the potential to change plant demography and community composition and, eventually, other ecological relationships in fire-shrublands, such as the one studied here. In this case, we witnessed how one species (*Erica*) was much more sensitive to the varying climate conditions from year to year than the other two, and that, in some years, its recruitment after fire was compromised. The fact that *Erica* is at our study site at the end of its range towards the interior of the Peninsula shows how changes in the recurrence of certain events (dry years) can compromise its local persistence after fire. The effects

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reported here for *Erica* were similar to those found earlier, in an experiment carried out several years before this one, and in which the first year after fire was also particularly dry (Quintana et al., 2004). These two experiments document the difficulties that *Erica* has for establishing after fire in dry years. This leads us to argue that the persistence of this species in this part of Spain is seriously compromised in the case of fire and future increases in drought (Alcamo et al., 2007), a trend that has been occurring in the Iberian Peninsula (Esteban-Parra et al., 1998).

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References

Alcamo, J., Moreno, J. M., Nováky, B., Bindi, M., Corobov, R., Devoy, R. J. N., Giannakopoulos, C., Martin, E., Olesen, J. E., and Shvidenko, A.: Europe, in: Climate Change, 2007: Impacts, Adaptation and Vulnerability, Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Parry, M. L., Canziani, O. F., Palutikof, J. P., van der Linden, P. J., and Hanson, C. E., Cambridge University Press, Cambridge, 541–580, 2007.

Baskin, C. M. and Baskin, J. M.: Seeds. Ecology, Biogeography, and Evolution of Dormancy and Germination, Academic Press, San Diego, 1998.

Bastida, F. and Talavera, S.: Temporal and spatial patterns of seed dispersal in two Cistus species (Cistaceae), Ann. Bot.-London, 89, 427–434, 2002.

Benito Cebrián, N.: Brezales y brezos, Boletín Instituto Forestal de Investigaciones y Experiencias, 19, 5–67, 1948.

Besie, W. C. and Johnson, E. A.: The relative importance of fuel and weather on fire behavior in subalpine forests, Ecology, 76, 747–762, 1995.

Bond, W. J.: Fire survival of Cape Proteaceae-influence of fire season and seed predators, Vegetatio, 56, 65–74, 1984.

Bond , W. J. and van Wilgen, B. W.: Fire and Plants, Chapman and Hall, London, 1996.
Bond, W. J., Vlock, J., and Viviers, M.: Variation in seedling recruitment of cape Proteaceae after fire, J. Ecol., 72, 209–221, 1984.
Christensen, J. H., Hewitson, B., Busuioc, A., Chen, X., Gao, I., Held, R., Jones, R. K., Koli, W. T., Kwon, R., Laprise, V. M., Rueda, L., Mearns, C. G., Menéndez, J., Räisänen, A., Rinke, A., Sarr, A., and Whetton, P.: Regional climate projections, in: Climate Change, 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller, H. L., Cambridge University Press, Cambridge, 847–940, 2007.
Clemente, A. S., Rego, F. C., and Correia, O. A.: Seed bank dynamics of two obligate seeders, Cistus monspeliensis and Rosmarinus officinalis, in relation to time since fire, Plant. Ecol., 190, 175–188, 2007.
de Luis, M., Raventos, J., and Gonzalez-Hidalgo, J. C.: Fire and torrential rainfall: effects on seedling establishement after fire in Mediterrranean gorse shrublands, Int. J. Wildland Fire, 14, 413–422, 2005.
Esteban-Parra, M. J., Rodrigo, F. S., and Castro-Diez, Y.: Spatial and temporal patterns of precipitation in Spain for the period 1880–1992, Int. J. Climatol., 18, 1557–1574, 1998.
Founda, D. and Giannakopoulos, C.: The exceptionally hot summer of 2007 in Athens, Greece – a typical summer in the future climate? Global Planet. Change, 67, 227–236, 2009.
Giorgi, F. and Lionello, P.: Climate change projections for the Mediterranean region, Global Planet. Change, 63, 90–104, 2008.
Hodgkinson, K. C.: Shrub recruitment response to intensity and season of fire in a semiarid woodland, J. Appl. Ecol., 28, 60–70, 1991.
Keeley, J. E.: Fire intensity, fire severity and burn severity: a brief review and suggested usage, Int. J. Wildland Fire, 18, 116–126, 2009
Keeley, J. E., Fotheringham, C. J., and Baer-Keeley, M.: Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California, Ecol. Appl., 15, 1515–1534, 2005.
Keeley, J. E., Brennan, T., and Pfaff, H.: Fire severity and ecosystem responses following crown fires in California shrublands, Ecol. Appl., 18, 1530–1546, 2008.
Knox, K. J. E. and Clarke, P. J.: Fire season and intensity affect shrub recruitment in temperate sclerophyllous woodlands, Oecologia, 149, 730–739, 2006.

Lamont, B. B., Connell, S. W., and Bergl, S. M.: Seed bank and population-dynamics of Banksia-Cuneata – the role of time, fire, and moisture, Bot. Gaz., 152, 114–122, 1991.
Lana, X., Martínez, M. D., Burgueño, A., Serra, C., Martín-Vide, J., and Gómez, L.: Distributions of long dry spells in the Iberian Peninsula, years 1951-1990, Int. J. of Climatol, 26, 1999–2021, 2006.
Lloret, F.: Fire, canopy cover and seedling dynamics in Mediterranean shrubland of Northeastern Spain, J. Veg. Sci., 9, 417–430, 1998.
Luna, B.: Fenología y esfuerzo reproductivo de las especies arbustivas de un jaral-brezal del centro de la Península Ibérica, Tesina de Licenciatura, Madrid, 1998.
Moles, A. T. and Westoby, M.: Seedling survival and seed size: a synthesis of the literature, J. Ecol., 92, 372–383, 2004.
Moreno, J. M. and Oechel, W. C.: Fire intensity effects on germination of shrubs and herbs in Southern California chaparral, Ecology, 72, 1993–2004, 1991.
Moreno, J. M. and Oechel, W. C.: Factors controlling postfire seedling establishment in Southern California chaparral, Oecologia, 90, 50–60, 1992.
Moreno, J. M., Zavala, G., Martín, M., and Millán, A.: Forest fire risk in Spain under future climate change, in: Atlas of Biodiversity Risks, edited by: Settele. J., Penev, L., Georgiev, T., Grabaum, R., Grobelnik, V., Hammen, V., Klotz, S., Kotarac, M., and Kühn, I., Pensoft, Sofia and Moscow, 72–73, 2010.
Moriondo, M., Good, P., Durao, R., Bindi, M., Giannakopoulos, C., and Corte-Real, J.: Potential impact of climate change on fire risk in the Mediterranean area, Clim. Res., 31, 85–95, 2006.
Parker, V. T. and Kelly, V. R.: Seed banks in California chaparral and other Mediterranean climate shrublands, in: Ecology of Soil Seed Banks, edited by: Leck, M. A., Parker, V. T. and Simpson, R. L., Academic Press, San Diego, 231–256, 1989.
Pausas, J. G., Ouadah, N., Ferran, A., Gimeno, T., and Vallejo, R.: Fire severity and seedling establishment in Pinus halepensis woodlands, Eastern Iberian Peninsula, Plant. Ecol., 169, 205–213, 2003.
Prieto, P., Penuelas, J., Lloret, F., Llorens, L., and Estiarte, M.: Experimental drought and warming decrease diversity and slow down post-fire succession in a Mediterranean shrubland, Ecography, 32, 623–636, 2009.
Quintana, J. R., Cruz, A., Fernández-González, F., and Moreno, J. M.: Time of germination and establishment success after fire of three obligate seeders in a Mediterranean shrubland of Central Spain, J. Biogeogr., 31, 241–249, 2004.

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Reyes, O. and Trabaud, L.: Germination behaviour of 14 Mediterranean species in relation to fire factors: smoke and heat, Plant Ecol., 202, 113–121, 2009.
Thanos, C. A., Daskalakou, E., and Nikolaidou, S.: Early post-fire regeneration of a Pinus halepensis forest on Mount Párnis, Greece, J. Veg. Sci., 7, 273–280, 1996.
Thanos, C. A., Georghiou K., Kadis C., and Pantazi C.: Cistaceae – a plant family with hard seeds, Israel J. Bot., 41, 251–263, 1992.
Trabaud, L.: Fire and survival traits of plants, in: Role of Fire in Ecological Systems, edited by: Trabaud, L., SPB Academic Publishing, The Hague, 65–89, 1987.
Trabaud, L. and Lepart, J.: Floristic changes in a Quercus coccifera L. garrigue according to different fire regimes, Vegetatio 46, 105–116, 1981.
Trigo, R. M., Pereira, J. M. C., Pereira, M. G., Mota, B., Calado, T. J., Dacamara, C. C., and Santo, F. E.: Atmospheric conditions associated with the exceptional fire season of, 2003 in Portugal, Int. J. Climatol., 26, 1741–1757, 2006.

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Table 1. Main effects and interactions of the repeated measures ANOVA for burning year, fire season and time of emergence (yearly cohorts) on emergence and recruitment at two years after fire of three seeder species growing in a Mediterranean shrubland in Central Spain. Fire year and fire season were between subject factors, and time of emergence (cohorts 1 and 2) was a within subject factor. Species were: *Cistus ladanifer* (*Cistus*), *Erica umbellata* (*Erica*) and *Rosmarinus officinalis* (*Rosmarinus*). $N = 3$ plots per fire season and year.

	Emergence		Recruitment	
	F	p	F	p
Cistus				
Time of emergence	188.48	< 0.001	2.09	0.17
Year	5.27	0.02	2.70	0.11
Season	12.01	< 0.01	3.30	0.09
Year × Season	5.22	0.02	2.56	0.12
Time × Year	7.90	< 0.001	0.24	0.79
Time × Season	120.60	< 0.001	0.20	0.67
Time × Year × Season	30.46	< 0.001	0.21	0.82
Erica				
Time of emergence	12.20	< 0.01	0.10	0.75
Year	3.79	0.05	2.91	0.09
Season	0.57	0.46	1.25	0.28
Year × Season	0.43	0.66	0.68	0.52
Time × Year	3.85	0.05	4.55	0.03
Time × Season	< 0.01	0.98	0.40	0.54
Time × Year × Season	1.87	0.20	1.95	0.18
Rosmarinus				
Time of emergence	56.94	< 0.001	8.20	0.01
Year	2.76	0.10	2.14	0.16
Season	0.73	0.41	0.26	0.62
Year × Season	0.11	0.90	0.02	0.98
Time × Year	36.82	< 0.001	1.80	0.21
Time × Season	14.23	< 0.01	1.84	0.20
Time × Year × Season	7.88	< 0.01	0.07	0.93

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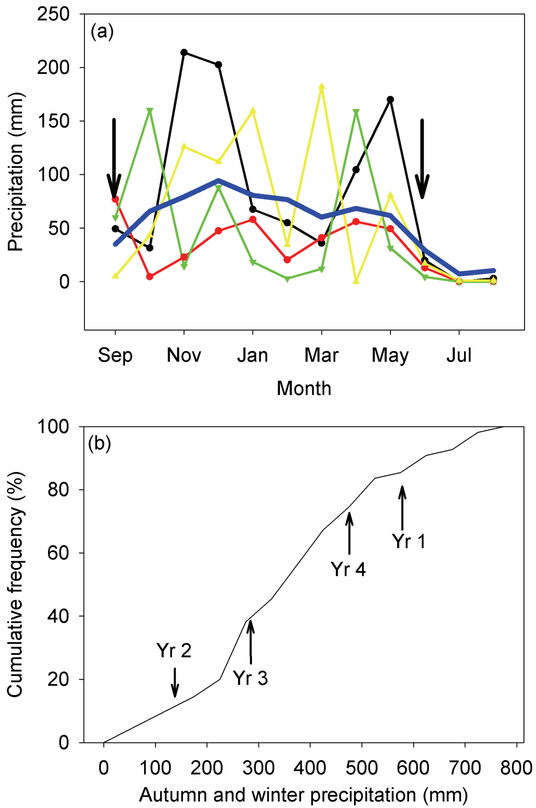

Fig. 1. (a) Precipitation on years one (Yr 1, black), two (Yr 2, red), three (Yr 3, green) and four (Yr 4, yellow) of the postfire monitoring period and 40 yr mean (blue). Arrows indicate when fires were conducted. **(b)** Cumulative frequency distribution of winter and fall precipitation (October through February), with arrows indicating the amount of precipitation of each year.

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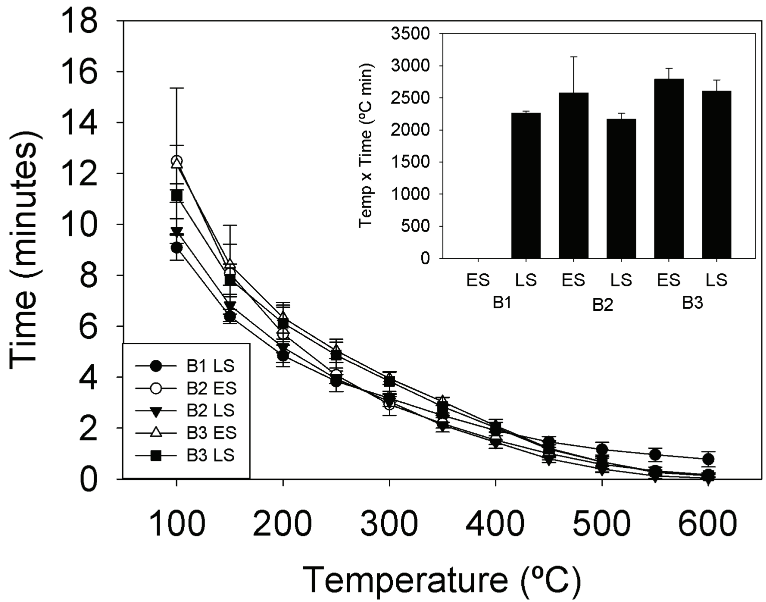

Fig. 2. Residence time of temperatures from 100 °C to 600 °C during experimental burns early (ES) and late (LS) in the fire season and in each of the three consecutive burning years (B1 to B3). Inset figure show the means and standard errors for temperature-time (in °C min). Temperature for the B1 ES burns was not available.

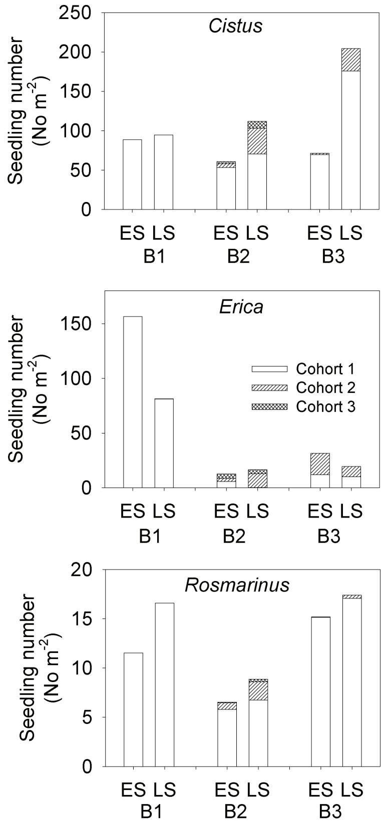

Fig. 3. Seedling emergence of three seeder species (*Cistus ladanifer, Erica umbellata and Rosmarinus officinalis*) after experimental burning early (ES) and late (LS) in the fire season during three consecutive years (B1, B2 and B3 burns) at a shrubland in Central Spain. Shown are total seedling emergence during the first (Cohort 1), second (Cohort 2) and third (Cohort 3) year after fire. Note that B3 burns were monitored only during two years.

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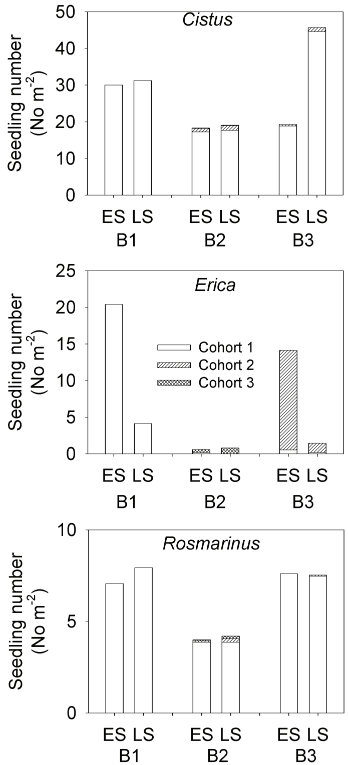

Fig. 4. Recruitment (No. m^{-2}) at the end of the study for three seeder species (*Cistus ladanifer, Erica umbellata and Rosmarinus officinalis*) after experimental burning early (ES) or late (LS) during the fire season during three consecutive years (B1, B2 and B3 burns) in a shrubland in Central Spain. Recruitment is shown distinguishing among the cohorts that germinated during the first (Cohort 1), second (Cohort 2) and third (Cohort 3) year after fire. Note that B3 burns were monitored only during two years.

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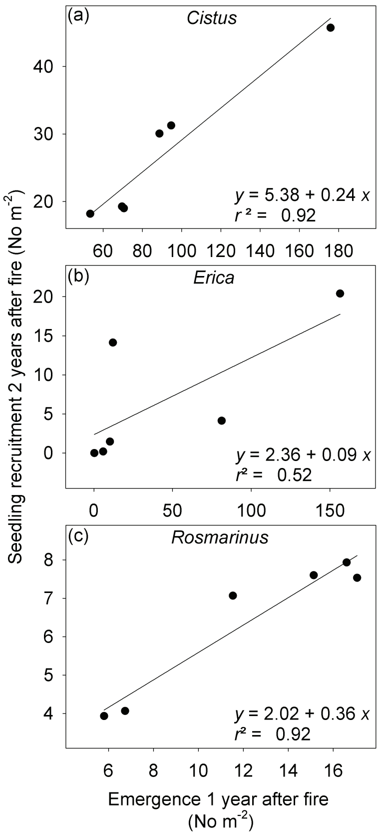

Fig. 5. Recruitment as a function of emergence one year after fire for *Cistus ladanifer* **(a)**, *Erica umbellata* **(b)** and *Rosmarinus officinalis* **(c)**. The line is the ordinary least squares best fit line. Each point is the mean of three plots.

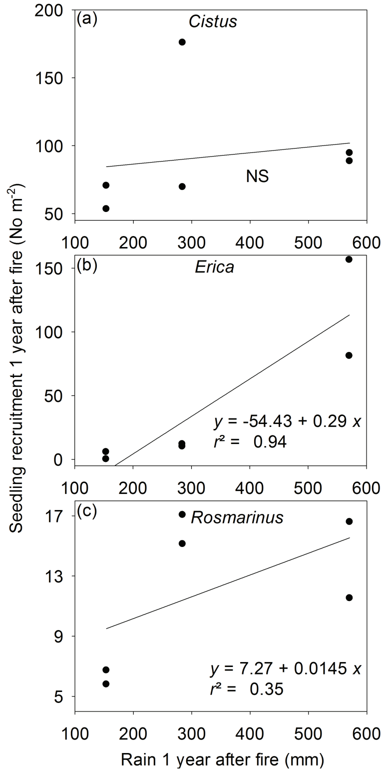

Fig. 6. Seedling emergence during the first year after fire as a function of autumn and winter (October through February) precipitation one year after fire for *Cistus ladanifer* **(a)**, *Erica umbellata* **(b)** and *Rosmarinus officinalis* **(c)** after experimental burning. The line is the ordinary least squares best fit line (see Methods) and NS indicates a non-significant model.

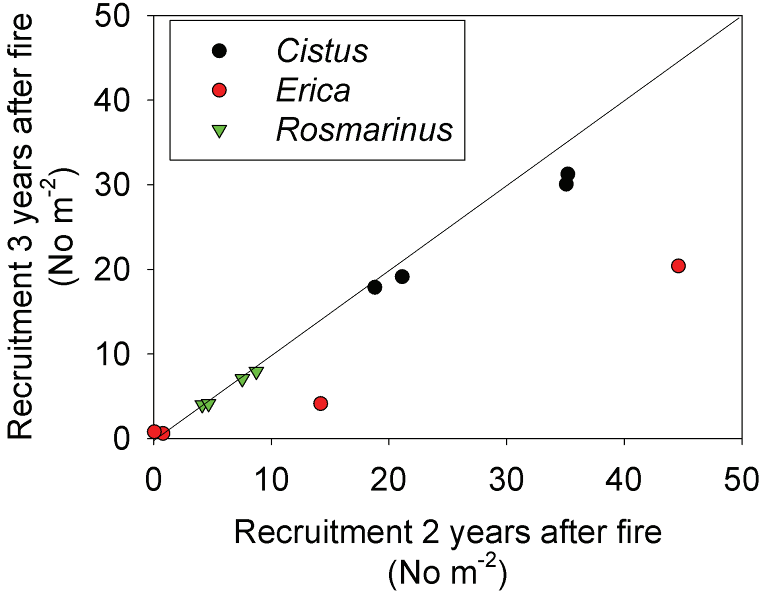

Fig. 7. Recruitment 3 yr after fire as a function of recruitment 2 yr after fire for three seeder species (*Cistus*, *Erica* and *Rosmarinus*). Note that while *Cistus* and *Rosmarinus* the relationship lies along the 1-to-1 line, for *Erica* it lies below that line, indicating mortality of 2 yr-old recruiters during the third year after fire.

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