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Original article

Lack of recruitment in *Lavandula stoechas* subsp. *pedunculata*: a case of safe-site limitation

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ARTICLE INFO

Article history:

Received 8 June 2005

Accepted 20 March 2006

Published online 4 January 2007

Keywords:

Central Spain

Mediterranean

scrubland–grassland mosaic

Seedlings

Soil seed bank

ABSTRACT

Lavandula stoechas subsp. *pedunculata* regeneration depends exclusively on the establishment of new individuals. Seed availability and seedling emergence and survival are therefore critical life stages and processes for species regeneration. In this study, seedling emergence and survival was monitored for two years in the scrub, both in clearings and adjacent to adult plants, and the surrounding perennial grassland, at 1, 3 and 5 m from the scrub. Soil seed bank spatial distribution was also studied for one year in the same two habitats, using the same sampling design. Soil seed availability in the scrub is high regardless of the distance from the adult individuals. On the contrary, the adjacent grassland shows a drastic fall in seed density, and almost no seedlings were observed there. In the scrub, seedling density was negatively related to distance from the three nearest adult plants in the clearings, and positively related to adult plant size beneath the adult *Lavandula* plants. There was also a negative relationship between seedling density and the percentage of bare soil. Only one seedling survived the first drought period, with no detection of effects of either position with respect to adult individuals or seedling density. We hypothesized that the study populations suffer a lack of appropriate safe sites within the scrubland while in the adjacent perennial grassland, observed low seed availability was added to safe-site limitation. That results in a lack of successful seedling establishments and a poor expansion potential of *Lavandula* scrublands, whose edges remain static in the short and medium term. As found in other Mediterranean scrubland, recruitment may only occur in years with particularly favourable weather, under disturbance regimes that increase seedling survival probability or when external dispersal agents increased seed availability in adequate places for *Lavandula* establishment.

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1. Introduction

Seedling establishment is the most critical life stage for the persistence of “seeder” scrub, especially in highly variable

environments (Grice and Westoby, 1987; Mesléard and Lepart, 1991; García-Fayos and Verdú, 1998; Lloret, 1998; Escudero et al., 1999, 2000; Traveset et al., 2003). Recruitment may be limited by the availability of seeds, because low seed

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doi:10.1016/j.actao.2006.03.008

production or dispersal, and/or the lack of suitable microsites for germination or establishment (Eriksson and Ehrlén, 1992; Schupp, 1995).

Recruitment of new individuals under stressful conditions only takes place when the survival probability of seedlings increases for some reason (Eriksson and Fröberg, 1996). Optimal situations for establishment are usually conditioned by spatial or temporal heterogeneity in the intensity of the limiting factor. In semiarid and Mediterranean climates, the spatial and temporal heterogeneity in water availability is the main driving factor for seedling establishment. In this sense, the proximity of adult plants can increase seedling survival (Bruno et al., 2003; Pugnaire et al., 1996), although some negative effect has been also described (Fowler, 1986; Van Auken and Bush, 1991; Vilá and Sardans, 1999). Survival and recruitment of new individuals into the population also increase during wetter years (Milton, 1994; Wiegand et al., 1995; O'Connor and Roux, 1995). Probably the most efficient strategy to counteract environmental stochasticities is the existence of a persistent seed bank, which allows exploitation of propitious conditions whenever these arise (Peco et al., 1998; O'Connor, 1995; García-Fayos and Verdú, 1998; Rey and Alcántara, 2000). Finally, establishment also depends on the disturbance pattern. In the Mediterranean Basin, the regeneration of many scrub species needs wildfires or any type of soil perturbation (Herrera, 1997; Pugnaire and Lozano, 1997; Lloret, 1998; Ferrandis et al., 1999).

Despite these limitations, many shrub species are efficient colonizers after land abandonment in the northern Rim of the Mediterranean Basin. An outstanding example is *Lavandula stoechas* subsp. *pedunculata* (Miller) Rozeira (henceforth *Lavandula*), which has spread over old mainly annual grassland and cropland during the last 50 years in Central Spain. Actually the patches of *Lavandula* scrubland occupy mainly the slopes together with a matrix of annual grasslands, but do not invade the bottom lands in which perennial grassland dominates.

Lavandula seeds have no specific dispersal structures (Azcárate et al., 2002). Seed production per plant is quite variable, ranging from around 2000 to 30,000, and highly depending on plant size (Sánchez, 2001). Autochorous dispersed seeds concentrated are on the nearest 30 cm, and maximum observed dispersal distance has been 1 m (Sánchez and Peco, 2002). Effective endozoochorous dispersal by sheep has been observed, but this dispersal mechanism is not operating in the study sites at the moment (Sánchez and Peco, 2002). The seeds do not present any particular dormancy as around 75% of seeds, collected directly from the plant, germinate in a few days when sown in near-natural conditions (Sánchez, 2001). Nevertheless, this species can form short-term persistent seed banks as viable seeds have been found in deep soil layers (5–10 cm depth) although in low numbers (Traba, 2000).

Current *Lavandula* stands show very poor recruitment. Seedlings have been only observed inside the scrub patches but survival should be low as more than one-year-old seedlings are extremely rare (pers. obs.). In the adjacent perennial grassland neither seedlings nor adult individuals are present (pers. obs.). Previous experimental studies reveal that seed germination is not limited over perennial cover, however, later establishment is very poor, resulting in just 1.4% survival

probability for transplanted seedlings during the first growing period (Sánchez and Peco, 2004).

All of these information lead us to hypothesise a poor recruitment potential due to general safe-site limitation together with low seed availability immediately outside the present *Lavandula* stands.

To date, no information has been presented on *Lavandula* soil seed bank and seedling appearance and survival patterns. A detailed examination of both life stages should provide information on the factors controlling the establishment of this species in the two main habitats in the area, the actual *Lavandula* scrubland and the surrounding perennial grassland. In this study we will examine: (1) the density and distribution of *Lavandula* seeds in the soil after the post-dispersal predation and secondary dispersal processes; (2) the emergence and survival of seedlings in *Lavandula* scrubland and surrounding perennial grassland in relation to: (i) distance from adult plants; (ii) size of the adult plant; (iii) seedling density; (iv) microhabitat structure; (v) germination date. If the species fails to establish we should be able to assess whether this failure is related to a propagule limitation or to a lack of favourable sites for establishment. On the contrary, if recruitment takes place, the data recorded allow us to determine what a “safe site” is for *Lavandula* seedlings.

2. Materials and methods

2.1. Study site

The study was conducted in the Moncalvillo-Pedrezuela study area in central Iberia (40° 38'N, 3° 70'E; 900 m a.s.l.; 2000 ha). Climate is continental Mediterranean (mean annual temperature 13.2 °C; annual rainfall 540 mm). The area has a gneiss lithology and shallow acid soils. The potential vegetation is a holm oak forest (*Quercus ilex* subsp. *ballota*), although little more than small fragments and isolated trees remain in rocky places. At present the predominant vegetation is a *L. stoechas* subsp. *pedunculata* scrubland with a rich annual community in the open spaces between *Lavandula* plants (Peco et al., 2006).

Lavandula is an endemic non-clonal shrub of the Ibero-North African Region. Its fruit is a tetranuculate composed of four ellipsoid mericarps (average weight 0.91 mg, maximum length 1.79 mm; $n=50$) (Azcárate et al., 2002). In the last half of the 20th century, the species began to spread across the centre of the Iberian Peninsula over former grass and croplands due to the abandonment of traditional management. Its populations now shape a mosaic structure (Ramírez-Sanz et al., 2000) in which the *Lavandula* scrubland occupies the high and middle slope positions but not the bottom lands, which are occupied by *Agrostis castellana* perennial grassland, called *vallicares* (Rivas-Goday and Rivas-Martínez, 1963). In the study area, *Lavandula* forms almost monospecific scrublands with a mean density of 1.89 individuals/m² (S.D. = 0.65). *Vallicares* can grow to a metre in height, and their dry aerial biomass reach a mean weight of 322.5 (S.D. = 159.0 g/m²) (Sánchez, 2001).

2.2. Soil seed bank sampling

Five sites (approx. 2 ha each) in which *Lavandula* scrubland was present were selected inside the study area (henceforth Pz1, Pz2, Pz3, C1 and C2). In each one we collected 38 soil samples, 20 inside the scrubland and 18 in the adjacent grassland. The sampling points inside the scrub were distributed at random, noting in each one the distance to the three nearest *Lavandula* plants. In the grassland, 6 × 3 random samples were collected at 1, 3 and 5 m from the *Lavandula* scrubland, and at points with a sharp contact between *Lavandula* scrubland and the adjacent vallicares.

The soil samples were extracted with a 5 cm long × 5 cm diameter metal core sampler in September 1997 before the start of autumn germination. The samples were air-dried and then stored in paper bags for a couple of months. Subsequently all samples were treated with a solution of hydrogen peroxide and sodium hexa-meta-phosphate to break down the clay, and then sieved to remove the coarse (>2 mm) and fine fraction (<5 mm), in which no *Lavandula* seeds were found. The remaining fraction was analysed under a magnifying glass to count the seed content, ignoring decayed, aborted and parasitised seeds, which were detected by finger pressure.

2.3. Seedlings sampling

During the 1997–1998 and 1998–1999 growth periods, we monitored the establishment and survival of *Lavandula* seedlings. A roughly 100 × 200 m area occupied by the species was chosen for the installation of 60 20 × 20 cm permanent plots. Thirty were inside the *Lavandula* scrubland, stratified in turn into two types of positions: clearings (open spaces among adult plants) ($n = 14$) and points under randomly chosen *Lavandula* individuals ($n = 16$). Another 30 sampling plots were arranged in the adjacent grassland at 1, 3 and 5 m from the *Lavandula* scrubland ($n = 10$, for each distance).

We measured the distance from each plot to the three closest adult *Lavandula* individuals and, in the case of those beneath *Lavandula* plants, we noted the two main diameters and height. Volume was estimated as the volume of a rectangular prism showing these three measurements. In each 20 × 20 cm plot, we also typified the microhabitat structure with data on ground cover of bare soil, lichen, moss, perennial herbs and litter, according to classes: 0, 0% of cover; 1, 0–1%; 2, 2–12.5%; 3, 13.5–25%; 4, 26–50%; 5, 51–75%; 6, 76–100%.

Each naturally emerging seedling was identified, noting its exact position on an acetate sheet, which allows individual monitoring. The plots were visited eight times between October 1997 and August 1998, and four times during the following vegetative period: mid-December, March, June and September.

2.4. Data analysis

2.4.1. Soil seed bank

The spatial structure of the seeds in each *Lavandula* site was described using the Morisita index (Elliot, 1983). This index is equal to 1 for random distributions, >1 for contagious distributions and <1 for regular distributions. Significant deviations of the random distribution were checked by a χ^2 test (Elliot, 1983).

The effect of site and position (clearing-*Lavandula* plants) was checked with an ANOVA, with the former as a random factor and the latter as a fixed factor. The dependent variable was the number of seeds found per sample transformed logarithmically. The relationship between the latter variable and the distance to the three nearest plants was also tested by regressing it onto the mean of these three distances and testing its relationship to seed number by means of a simple regression.

2.4.2. Seedling emergence

The spatio-temporal variability of seedling number per sampling plot, transformed logarithmically, was analysed using an ANOVA with the year as a repeated measure factor and the position as a two-level fixed factor (clearing-*Lavandula* plant). As no significant interannual variation in seedling number was found, seedling abundance was considered as the total of seedlings observed in each plot during the two years.

The relationship between the number of seedlings per plot and the distances to the three closest *Lavandula* plants, their diameters and volume, were calculated by simple regression. We also designed multiple regression models with the same dependent variable. Independent variables were distances to the three closest *Lavandula* plants for the plots in the clearings, and volume of the closest individual for the plots beneath the *Lavandula* plants.

For microhabitat structure data (bare soil, lichen, moss, perennial herbs and litter), the intervals' mid-point was regarded as cover for each class. The relationship between these variables and seedling number was also analysed by means of simple regression.

2.4.3. Seedling survival

The survival functions were estimated by the Kaplan–Meier method, while the Gehan generalization of the Wilcoxon test was used to compare two survival functions (1997/1998–1998/1999; clearing-*Lavandula* plant). To compare more than two group functions (germination timing: autumn, winter and spring) we used a generalization of the Gehan, Peto and Peto test and the log-rank test. The effect of the seedling number established in each sampling plot on mortality was analysed with the Cox proportional risk regression (Lee, 1992).

The Statistica programme (StatSoft, 1998) was used for all statistical analyses.

3. Results

3.1. Soil seed bank

The number of seeds per sample ranged between 0 and 10 (Fig. 1, Table 1). This resulted in an overall mean of 1.95 ± 0.85 (S.D.) seeds per sample and a density of 976.4 ± 382.8 (S.D.) seeds/m². In the grassland we observed a much lower seed availability. Seeds were only found in 10.4% of the samples, and the mean density was 104.4 ± 87.6 , 50.6 ± 62.4 , 44.6 ± 46.0 seeds/m², at 1, 3, and 5 m from the *Lavandula* scrubland, respectively.

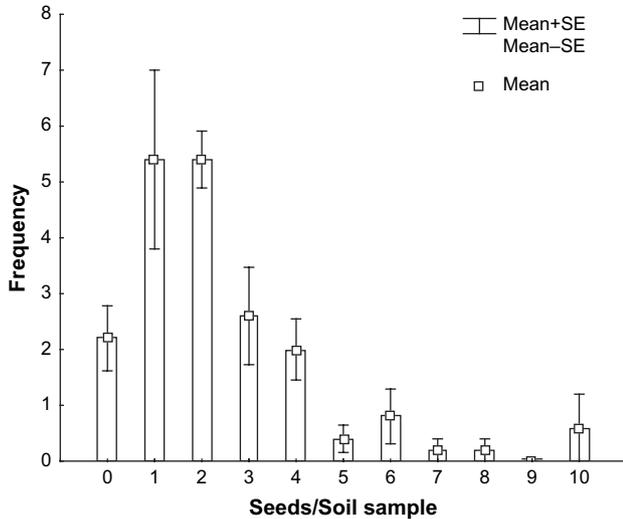


Fig. 1 – Number of seeds frequency distribution (mean values for the five *Lavandula* sites) observed in the soil samples ($n = 20 \times 5$) collected inside the scrub.

Seed distribution inside the scrubland was not consistent. The Morisita index suggests a significantly non-random clustered distribution in three *Lavandula* sites, while the others did not deviate from random (Table 2). Seed number related significantly to the site (Table 3), but we only found a marginally significant relationship between seed number and position with respect to the adult individuals (Table 3). The relationship between mean distance from the nearest three individuals and the number of seeds ($r = -0.05$; $n = 20 \times 5$) was not significant.

3.2. Space-time variability of seedling emergence

Over the two study years, we recorded a total of 145 seedlings. Mean density in the scrub was 65.8 ± 69.3 and 50.8 ± 44.3 seedlings/m² for the 1997/1998 and 1998/1999 growth periods, respectively. In the grassland we recorded a total of five seedlings (Table 4).

The seasonal germination and survival patterns of seedlings closely coincided in the two monitoring years. Most seedlings germinated in autumn, 61% on average for the two years, while the rest appeared in winter (25%) and spring (14%). Seedling mortality monitoring showed that 55% died in summer while 31% and 13% died in spring and winter, respectively.

Table 1 – Seed content per sample found in five *Lavandula* sites (Pz1, Pz2, Pz3, C1, C2)

	N	Mean	Std. dev.	Sum	Min.	Max.
Pz1	20	1.12	1.01	22	0	4
Pz2	20	3.09	3.24	61	0	10
Pz3	20	2.19	1.73	44	0	5
C1	20	2.29	1.88	46	0	7
C2	20	1.08	1.01	22	0	4

Table 2 – Morisita index ($I\delta = 1$, random distribution; $I\delta > 1$ contagious distribution; $I\delta < 1$ regular distribution) and χ^2 for distribution of seeds number found in five *Lavandula* sites (Pz1, Pz2, Pz3, C1, C2)

	χ^2 critical ($n = 20, \alpha = 0.05$) = 30.144				
	Pz1	Pz2	Pz3	C1	C2
Morisita	0.93	1.66	0.95	1.74	1.23
χ^2	19.48	31.09	18.76	53.27	110.43

Neither the position (clearing-*Lavandula* plant), nor the year showed a significant effect on the observed number of seedlings (Fig. 2). We did note a significant negative relationship between distance from the three nearest *Lavandula* plants and seedling number in the sampling plots situated in the scrub clearings. These three distances explain a little more than 50% of the variance observed in seedling number ($R^2 = 0.53$, $F(3,10) = 3.70$, $p = 0.05$).

The observed number of seedlings in plots beneath adult plants increased ($r = 0.54$; $p = 0.04$) with the volume of the plant above the sampling plot and with its area ($r = 0.56$; $p = 0.03$), calculated from the two main plant diameters. The model designed on the basis of volume was more explanatory, with 32% explained variance ($F(1,13) = 0.03$, $p = 0.03$). Finally, only bare soil cover seemed to be significantly related ($r = -0.37$, $p = 0.04$) to seedling number.

3.3. Seedling survival

Over the two study years only one seedling survived its first summer. Mortality causes could not be ascertained in all cases, but generally seem to be winter frost and water stress in spring and in summer.

The differences between the seedling survival functions in the two growth periods were not significant (Gehan's Wilcoxon = -1.69, $p = 0.09$), and thus the data for the two years are considered together (Fig. 3a).

The effect of position, when comparing the survival function between the seedlings under adult individuals and those in clearings, did not yield significant differences (Gehan's Wilcoxon = -1.48, $p = 0.14$) (Fig. 3b).

No significant relationship was found between seedling density and survival ($\chi^2 = 0.11$, d.f. = 1, $p = 0.7$). On the contrary, seedlings that emerged in spring had lower survival likelihood than those that emerged in autumn ($\chi^2 = 20.23$, d.f. = 2, $p < 0.001$) (Fig. 3c).

Table 3 – ANOVA results showing the effect of site and position (plots under adult plants-plots in open spaces among adult plants) on the log number of seeds observed per soil sample inside the *Lavandula* scrubland

	M.C.	d.f.	F	P
Site	0.82	4	2.75	0.03
Position	0.52	5	1.73	0.13

Table 4 – Seedling number recorded per 20 × 20 cm quadrat in scrub and grassland during the two growth periods

		Total	Mean	Range	Std. dev.
1997/1998	Scrub (n = 30)	79	2.63	0–10	2.79
	Grassland (n = 30)	4	0.13	0–1	0.35
1998/1999	Scrub (n = 30)	61	2.03	0–6	1.77
	Grassland (n = 30)	1	0.03	0–1	0.18

4. Discussion

4.1. Seed bank spatial distribution

Seed density diminished from scrub to grassland, coinciding with the exponential negative distribution observed for autochorously dispersed seeds (Friedman and Orshan, 1975; Parker, 1982; Auge and Brandl, 1997; Sánchez and Peco, 2002), and also with the high granivore ant predation rates recorded in the ecotones between scrub and grassland (Sánchez and Peco, 2006).

Inside the *Lavandula* scrubland, however, seed availability was high. In this habitat, seed density did not vary predictably with distance from the nearest adult individuals. The clustered patterns found in some *Lavandula* sites and the lack of significant differences in seed number in clearings versus below adult plants may therefore be caused by secondary dispersal processes (Chambers and MacMahon, 1994; Aguiar and Sala, 1997) or post-dispersal predation (Andersen, 1989; Castellanos and Molina, 1990; Hulme, 1994; Harrington and Driver, 1995). Indeed, the number of seeds found in the seed bank was much lower than the number reaching the soil in the seed rain (Sánchez and Peco, 2002). Granivorous ants actively collect *Lavandula* seeds in the scrub zone (Sánchez and

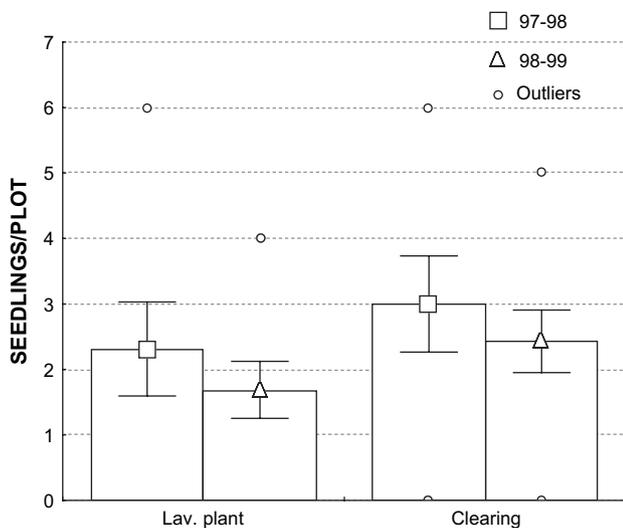


Fig. 2 – Number of *Lavandula* seedlings per plot observed inside the scrubland and clustered according to position (Lav. plant: plots under adult plants; clearing: open spaces among adult plants) for two study years.

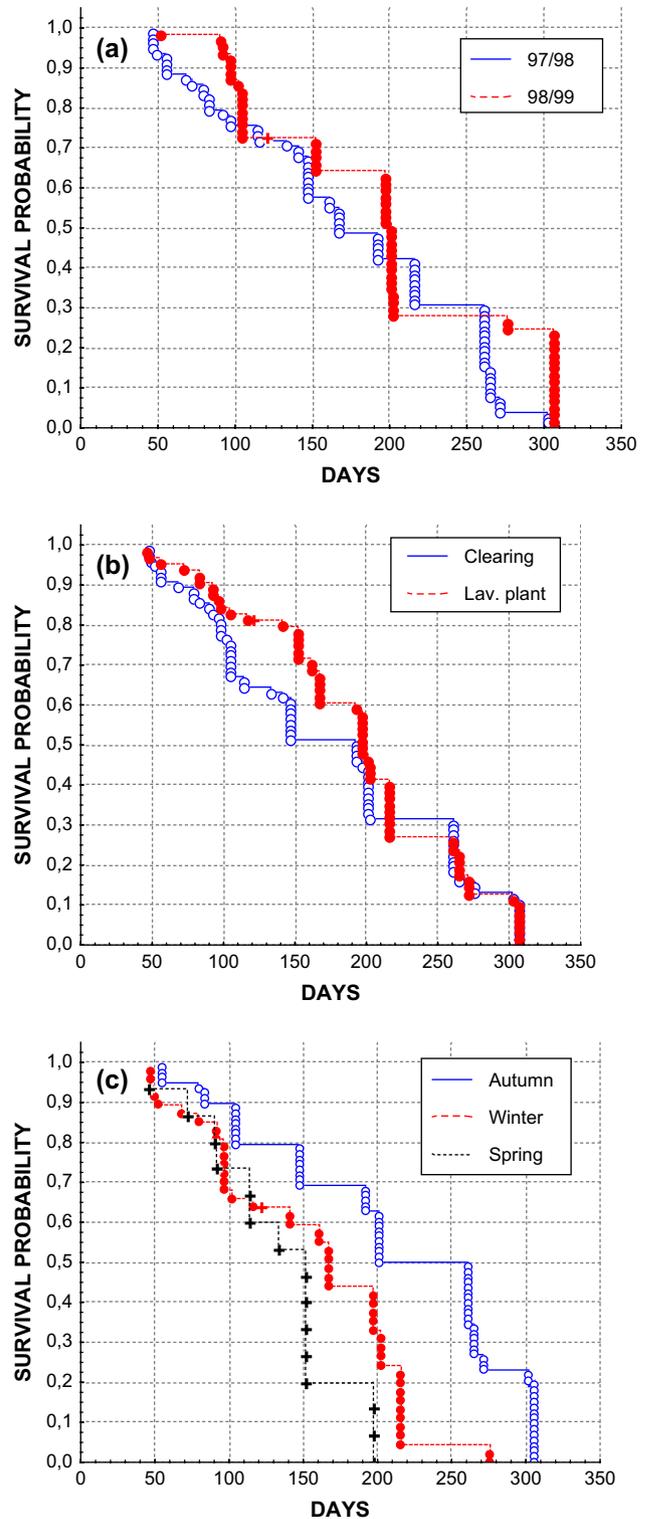


Fig. 3 – Kaplan-Meier survival functions of recorded seedlings, clustered according to year (a), position: Lav. plant = plots under adult plants; clearing = open spaces among adult plants (b) and germination timing (c).

Peco, 2006), suggesting that predation is the main cause of seed disappearance between the dispersal period and autumn (Andersen, 1989; Castellanos and Molina, 1990; Maron and Simms, 1997; Hulme, 1994).

4.2. Seed-seedling relationship

Despite high ant predation, there is a large and persistent (Traba, 2000) seed bank that showed low germination during the study period. However, the number of detected seedlings in the scrub was still higher than those observed in related (Herrera, 1997) and unrelated Mediterranean shrubs (Lloret, 1998; Verdú and García-Fayos, 1998; Rey and Alcántara, 2000).

In the grassland, on the contrary, almost no germination was observed, probably due to the scarcity of seeds and also to the negative interference caused by the grassland during *Lavandula* first life stages. A previous study has shown that perennial grassland largely diminish establishment, growth and survival of *Lavandula* seedlings (Sánchez and Peco, 2004).

4.3. Seedling establishment and distribution patterns in scrub

Seed germination primarily takes place in autumn, as with most annuals that form the herbaceous layer of this scrubland (Espigares and Peco, 1993). Autumn seedlings have a longer growth period than spring ones, which could give them a higher likelihood of surviving the drought period (Fowler, 1988).

Seedling distribution data in relation to adult *Lavandula* plants position coincide with those for the seed bank. In the case of the seedlings, there are also no differences between the observations in the clearings and those under adult individuals, a pattern often noted in other shrub species (Auge and Brandl, 1997; Pugnaire and Lozano, 1997; García-Fayos and Verdú, 1998; Verdú and García-Fayos, 1998). Considering seedling density in the clearings separately, however, there is a negative relationship with the distance from the nearest adult individuals. The same pattern is noted in the seed bank estimates, although in this case it is not statistically significant.

Moss, lichen and perennial cover are neither an impediment nor of assistance to seedling establishment in the study area. The same can be said of the leaf litter, which nowhere reaches high values that could interfere with seedlings establishment as noted in other studies (Facelli and Pickett, 1991; Facelli, 1991; Pugnaire and Lozano, 1997; Lloret, 1998). Seedling establishment decreases with increasing cover of bare soil, as previously found for seedlings of other Mediterranean scrublands (Lloret, 1998; Rubio and Escudero, 2000; Maestre et al., 2003). In these kinds of habitats, especially in cases involving sandy soil and a paucity of organic matter such as in the study area, the lack of vegetation can considerably worsen the moisture and temperature conditions, hindering seed hydration and the subsequent seedling emergence.

4.4. Seedling mortality in scrubland

High seedling mortality rates are found widely amongst woody species in zones with dry periods (Harrington, 1991; O'Connor, 1995; O'Connor and Roux, 1995; García-Fayos and Verdú, 1998; Owens et al., 1995; Paynter et al., 1998; Rey and Alcántara, 2000). This had a generalised effect on *Lavandula* seedlings in all the analysed situations and made it impossible to detect spatial patterns linked to the likelihood of recruitment.

No evidence was found for possible facilitation under the adult individuals. This type of interaction is widespread in

arid and semiarid communities (Pugnaire et al., 1996; Flores and Jurado, 2003), but under extremely stressful conditions a shift from facilitation to competition may occur (Maestre and Cortina, 2003).

Survival in scrub clearings, areas of low competition for resources with adult individuals (Milton, 1994, 1995; Auge and Brandl, 1997), was not higher, either. The heavy degree of soil desiccation in the summer months causes the death of seedlings regardless of their position in the scrub. In addition, the distance between individuals and their radial, extremely superficial root growth should make competition high, even in the free areas between individuals (Reichenberger and Pyke, 1990; Cahill and Casper, 2000).

No relationship was found between *Lavandula* seedling mortality and density. These relationships may be either negative, due to the scarcity of a resource (Owens and Norton, 1989), or positive, as the high seedling densities may occur at favourable points where resource availability compensates for the presence of neighbouring plants (Fowler, 1988). Again, the heavy water stress responsible for the death of practically all the *Lavandula* seedlings makes it impossible to detect this type of pattern, which is possibly more important in episodes with a higher level of recruitment.

Only germination timing seems to affect survival probability, as seen in the comparison of functions of the different seedling cohorts established on the basis of the germination season. This difference would have led autumn seedlings to a greater likelihood of surviving the drought if the local weather conditions were less severe.

5. Conclusion

This study shows that there is a clear difference in seed and seedling density between the two analysed habitats. The scrubland is characterized by high seed availability and the establishment of a large number of seedlings, although they were incapable of surviving the first drought in any of the study situations. We may therefore consider *Lavandula* regeneration in the scrubland to be safe-site limited which, in the absence of disturbances, causes a gradual ageing process in the populations. In the adjacent grassland the practical absence of seedlings could be explained by (1) the low density of seeds and (2) safe-site limitation as a consequence of the negative effect of perennial grassland on early establishment (Sánchez and Peco, 2004). This has a considerable effect on the expansion potential of *Lavandula* scrublands whose edges are regarded as static in the short and medium term. This is a clear contrast with the colonising nature of *Lavandula*, which should be associated with certain disturbance regimes (Herrera, 1997), the presence of dispersal agents (Sánchez and Peco, 2002; Sánchez and Peco, 2006) and/or the occurrence of years with unusually benign weather conditions (Milton, 1994; Wiegand et al., 1995; O'Connor and Roux, 1995).

Acknowledgements

F.M. Azcárate and A. Escudero helped to organize ideas and information. Financial support was received from the Spanish

Science and Technology Commission (CICYT, Project AMB 990382 and REN2003-01562/GLO) and the Spanish Education and Culture Ministry (F.P.I. for A. M. Sánchez).

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