

# Seed ecology of a Mediterranean perennial herb with an exceptionally extended flowering and fruiting season

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*Lobularia maritima* is a Mediterranean short-lived herb with a flowering and fruiting season that lasts for ten months. Previous studies have shown that recruitment in periods other than autumn of the flowering season has few demographic implications; that is contributes little to the population growth rate. Since environmental conditions in periods other than autumn would allow recruitment, we examined to what extent the seed ecology of *L. maritima* accounts for recruitment shortage for the greater part of the year. To this end, we studied the effects of selfing and outcrossing on seed production and germination, within- and between-year variation in seed mass and germination, seed characteristics in the soil seed bank throughout the year, and the effect of temperature as a factor controlling seed germination. Results indicate that selfing does not decrease recruitment, and thus the observed changes in visitation rate and pollinator composition throughout the year cannot account for differences in recruitment. Germinability decreases throughout the year, suggesting a possible cost in reproduction associated with extended flowering. *L. maritima* has a transient seed bank whose seeds also experience a decrease in their germination throughout the year. Finally, temperature affects seed germination patterns, indicating the existence of quiescence mechanisms that prevent germination in the months prior to the summer drought. Overall, the results obtained support and, at least partly, explain the recruitment patterns of *L. maritima* observed in the field. © 2003 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2003, 142, 273–280.

**ADDITIONAL KEYWORDS:** germination – *Lobularia maritima* – pollinators – quiescence – seed bank – seed mass – temperature requirements.

## INTRODUCTION

As a result of environmental (e.g. seasonal climatic conditions) and biotic (e.g. competition for pollinators) factors, which are accepted as primary selective forces for flowering times (Rathcke & Lacey, 1985; Marquis, 1988), the flowering seasons of many Mediterranean angiosperms last for only a few months (Kummerow, 1983; Bosch, Retana & Cerdá, 1997; Picó & Retana, 2001). There are, however, a few exceptions to this general pattern. *Lobularia maritima* (L.) Desv. is a short-lived perennial crucifer of the Mediterranean Basin, which is unusual in that it flowers and fruits uninterruptedly for ten months. The ecology (Gómez, 2000; Picó & Retana, 2000, 2001) and demographic implications (Picó, de Kroon & Retana, 2002) of

*L. maritima*'s extended flowering and fruiting have been widely investigated. The main demographic consequence of extended flowering in *L. maritima* is that the plant has the potential to recruit new individuals into the population during the whole reproductive season (Picó & Retana, 2000). Despite this important demographic feature, further studies have revealed that recruitment in autumn mostly contributes to population growth, and recruitment during the rest of the year appears to have no demographic significance (Picó *et al.*, 2002). In this sense, *L. maritima* acts as a Mediterranean annual, whose dynamics basically depend on successful recruitment in autumn (e.g. Espigares & Peco, 1993; Sans & Masalles, 1994; Rebollo *et al.*, 2001).

The lack of demographic importance for seeds produced in the periods other than autumn has been interpreted as being caused by a combination of dif-

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ferent factors. One of them is the existence of climatic constraints. Some periods are characterized by little rainfall, which leads to low recruitment. Moreover, high seed predation rates throughout the year, basically by ants of the genus *Messor* (Picó & Retana, 2000), cause major seed losses during the entire flowering and fruiting season, and only the heavy seed production in autumn exceeds seed losses (Picó & Retana, 2000). These factors are highly variable from year to year (see Cros, Cerdá & Retana, 1997 and Picó & Retana, 2000 for variability in ant activity and seed production across years, respectively), and this means that abiotic and biotic conditions in some years would allow the plant to have peak recruitment in periods other than autumn. However, recruitment peaks in winter or spring have never been observed in our study population during six years of demographic monitoring (Picó *et al.*, 2002).

Hence, other factors must account for low contributions of recruitment to population growth recorded in winter and spring months. Among these other factors, features of *L. maritima*'s seed ecology might determine this shortage of recruitment. For instance, constraints between extended reproduction and seed quality might operate in such a way that seed quality could decrease throughout the season, as found in other plant species with a shorter flowering season (Wolfe, 1995; Vaughton & Ramsey, 1998). Furthermore, seeds produced throughout the season might differ strongly in terms of dormancy, since parental plants encounter different environmental conditions (water and nutrient availability, pollinators, etc.) that could affect subsequent seed characteristics and fate (Fenner, 1985). This paper aims to determine whether seed ecology limits recruitment of *L. maritima* during most of its reproductive season. In particular, the following questions are addressed: (1) what are the effects of self- and cross-pollination on seed production, seed mass, and germination? Also, related to this, what are the flower visitation patterns that might determine the relative importance of selfing and outcrossing in different periods of the year? (2) What is the temporal variability in seed mass and germinability between and within flowering seasons? (3) What are the characteristics of the soil seed bank throughout the year? and (4) what are the temperature requirements for *L. maritima* seeds to germinate?

## MATERIAL AND METHODS

### PLANT LIFE HISTORY AND STUDY SITE

*Lobularia maritima* is a short-lived perennial herb of three to four years maximum lifespan, although most of the plants live for one to two years. First flowering of new plants occurs after their first summer, although

some early autumn seedlings can flower in their first spring. Flowering stalks (10–30 cm height) produce flowers, fruits, and seeds uninterruptedly over ten months. Each flowering stalk lasts for several months and the largest plants can bear up to a few hundred stalks. Fruits are siliques (2–3.5 mm long) containing two seeds (1–2 mm long) that lack primary dispersal mechanisms. The period of time between anthesis and seed dispersal ranges from 15 to 60 days depending on weather conditions. Seed production peaks strongly in autumn, decreases in winter, and peaks again in spring prior to the end of the flowering season. Germination rates also peak in autumn but remain low throughout the rest of the flowering season.

The study was conducted in a Mediterranean shrubland at Collserola Park, a protected area near Barcelona, north-east Spain (41°24'N, 2°6'E; elevation 280 m). Climate is Mediterranean with 620 mm of mean annual rainfall. Maximum and minimum mean monthly temperatures are 23.2°C in August and 7.8°C in January, respectively. These shrublands are quite abundant in the western Mediterranean Basin. A shrub (e.g. *Cistus monspeliensis* L. and *Spartium junceum* L.) and a herbaceous layer (e.g. *Brachypodium retusum* L.) can be identified in this plant community (see Picó & Retana, 2000, 2001 for a detailed description of the study site).

### HAND-POLLINATION EXPERIMENTS AND NATURAL POLLINATORS

In autumn 1994, a total of ten *L. maritima* plants with 25–30 flowering stalks each were randomly selected for hand-pollination experiments. We tested for autogamy (bagging flowering stalks to avoid pollinator visits), selfing (hand-pollination with pollen from the same plant), outcrossing (hand-pollination with pollen from several donors), and natural pollination (no bagging and no hand-pollination) on each sampled plant. Two flowering stalks per plant and treatment were selected and 4–5 flowers per flowering stalk were used in the experiment. Flowering stalks were tagged at the base of the flower buds just before anthesis and bagged (except for natural pollination). Flowers were not emasculated due to small flower dimensions and because flowers can be easily damaged. Selfing and outcrossing treatments were repeated on the same flowers over two days to ensure successful pollination. For each treatment, we estimated fruit set (the proportion of flowers that set fruit) and seed set (the proportion of ovules that set seed) including data from all flowers and fruits per treatment. Immediately after collection, all seeds were first weighed individually to the nearest 100 µg with a precision balance (MC1, Sartorius AG) and then placed on moistened paper

filter in Petri dishes to monitor germination. Germination experiments were conducted in a dark germination chamber at 15°C and monitored over three weeks. The effects of the four pollination treatments on fruit set, seed set, seed weight, and germination were tested with a one-way ANOVA. When necessary, and after graphically examining the residuals, variables were transformed for normality, homoscedasticity and linearity, using arc-sine transformation for proportions and log transformation for all other variables (this applies for all analyses presented throughout the paper).

To identify changes in the spectrum of flower visitors throughout the entire flowering season of *L. maritima*, we divided it into five different periods of two months each. Their names are, consecutively, September, November, January, March and May. The September period includes September and October, the November period includes November and December, and so on. In each period, we sampled four 1 m<sup>2</sup> plots, laid across the study area over three days per period. On each sampling day, the total number of flowering stalks was counted. Four insect counts of 20 min each were made from 11:00 to 16:00 hours. In each count, all insects observed foraging on the flowers were identified by sight and recorded. The number of flowering stalks visited by each insect was also counted. Visitors were determined to family level. For each period, we added together the number of floral visitors over all sampling dates and plots. The effects of period on the visitation rate (number of insects per 100 flowering stalks per minute) were tested with a one-way ANOVA, and the spectra of visitors of the different periods were compared with a  $\chi^2$  test.

#### TEMPORAL VARIATION IN SEED WEIGHT AND GERMINATION

We collected seeds from 15–20 randomly chosen *L. maritima* plants in each period of the flowering season in 1994–95, 1995–96, and 1996–97. Immediately after collection, subsamples of 100 seeds were weighed individually to obtain seed weight estimates at each sampling period, and additional subsamples of 500 seeds were placed in ten Petri dishes (50 seeds each) to monitor germination over three weeks in a dark germination chamber at 15°C. Effects of year and period on seed weight and germination were tested with a two-way ANOVA.

#### SOIL SEED BANK

The seed bank study was carried out during the 1995–96 season. To identify changes in the seed bank throughout the entire *L. maritima* flowering season, we randomly collected 16 soil samples (100 cm<sup>2</sup> area × 1 cm

depth each) across the study site in each of the five periods described above. We also collected soil samples in summer when the plant does not flower. Soil samples were sieved (1 mm mesh), weighed and a subsample of the total soil was used. All seeds found in subsamples were counted and immediately placed in Petri dishes to monitor germination over three weeks in a dark germination chamber at 15°C. Effects of period on seed density in the soil seed bank and seed germination were tested with a one-way ANOVA.

#### EFFECT OF TEMPERATURE ON SEED GERMINATION

Using a temperature-controlled incubator, we tested the effect of six temperatures (5, 10, 15, 20, 25 and 30°C) on seed germination. This temperature range includes the naturally occurring temperatures in the study area throughout the year (see above). In autumn 1996, we collected seed from at least 30 *L. maritima* plants. A total of 50 seeds were placed in each of ten Petri dishes at each of the six temperatures. Petri dishes with seeds incubated in darkness were monitored over three weeks. Because only one incubator was available, the whole experiment lasted for 18 weeks and seed was dry-stored at room temperature. Under these conditions, viability of *L. maritima* seeds does not decrease after 1 year ( $N = 5$ ,  $F_{1,8} = 0.08$ ,  $P = 0.8$ ; one-way ANOVA), assuming that seed remained capable of germinating throughout the experiment. The effect of temperature on seed germination was tested with a one-way ANOVA.

## RESULTS

#### HAND-POLLINATION EXPERIMENTS AND NATURAL POLLINATORS

Neither fruit set nor seed set differed among pollination treatments ( $F_{3,36} = 1.33$  and  $2.31$ ,  $P = 0.28$  and  $0.09$  for fruit set and seed set, respectively). Fruit set was very high in all four treatments with mean percentages above 63%, while seed set showed lower values (although non-significant) for selfing and autogamy treatments than for outcrossing and natural pollination treatments (Table 1). For both seed weight and seed germination, differences among the four treatments were not significant ( $F_{3,36} = 1.35$  and  $0.88$ ,  $P = 0.27$  and  $0.46$  for seed weight and seed germination, respectively). Mean seed weight ranged 209–258  $\mu\text{g}$  and mean germination was above 95% in all treatments (Table 1).

Visitation rate varied significantly between periods ( $F_{4,126} = 16.6$ ,  $P < 0.001$ ), being higher in September and, to a lesser extent, in May than in the other three periods (Table 2). Diptera was by far the most abundant flower visitor from September to March, while

**Table 1.** Means ( $\pm$ SE) for fruit set (%), seed set (%), seed weight ( $\mu$ g), and seed germination (%) of *L. maritima* in each hand-pollination treatment

Treatment	Fruit set	Seed set	Seed weight	Seed germ.
Autogamy	75.4 $\pm$ 6.8	64.1 $\pm$ 6.8	252.7 $\pm$ 22.9	95.5 $\pm$ 3.6
Self-pollination	63.0 $\pm$ 6.9	56.0 $\pm$ 6.7	208.6 $\pm$ 21.3	96.4 $\pm$ 1.6
Cross-pollination	74.7 $\pm$ 4.1	72.5 $\pm$ 4.0	247.1 $\pm$ 19.5	97.5 $\pm$ 2.6
Natural pollination	78.2 $\pm$ 5.7	75.4 $\pm$ 5.0	257.5 $\pm$ 20.9	94.9 $\pm$ 1.2

**Table 2.** Mean ( $\pm$ SE) visitation rate (number of visitors per 100 flowering stalks per minute) and spectra of pollinators in each period of the flowering season of *L. maritima*. Means with different letters differ significantly from one another (Bonferroni test,  $P < 0.05$ )

Period	Visitation rate	Spectra of pollinators			
		Flies	Beetles	Small bees	Ants
September	2.46 $\pm$ 0.52a	79.7	13.5	1.5	5.3
November	0.16 $\pm$ 0.03b	86.6	3.1	10.3	0.0
January	0.21 $\pm$ 0.10b	100.0	0.0	0.0	0.0
March	0.07 $\pm$ 0.02b	75.0	0.0	7.5	7.5
May	0.88 $\pm$ 0.16a	15.7	74.5	9.8	0.0

**Table 3.** Two-way ANOVA testing for year and period effects on seed weight and seed germination of *L. maritima* seeds. *F*, *P*-values and degrees of freedom are given

Factor	Seed weight			Seed germ.		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Year	2	11.93	<0.0001	2	21.68	<0.0001
Period	4	27.85	<0.0001	4	62.03	<0.0001
Year $\times$ Period	8	20.50	<0.0001	8	9.71	<0.0001
Error	1485			129		

Coleoptera was the predominant group in May (Table 2). Differences among spectra in the different periods were highly significant ( $\chi^2 = 315.0$ ,  $P < 0.001$ ).

#### TEMPORAL VARIATION IN SEED WEIGHT AND GERMINATION

Effects of year, period, and the year–period interaction on seed weight and germination of *L. maritima* were all significant (Table 3). Seed weight was always high at the onset of the flowering season. From September onwards, different patterns of variation between periods emerged in each study year (Table 4a). In particular, seed weight peaked again in the May and June

periods (1994–95), was relatively constant throughout the rest of the year (1995–96), or decreased progressively until the end of the flowering season (1996–97). Seed germination was high in the September period and decreased progressively throughout the year in all years of study, but the way in which seed germination decreased across periods differed greatly among years (Table 4b). Germination percentage remained high up to the January period (1994–95), sharply decreased in the November period and remained low until the end of the season (1995–96), or decreased progressively throughout the year (1996–97). It must be noted that germination percentages in this experiment are lower than those of the hand-pollination experiments

**Table 4.** Means ( $\pm$ SE) for (a) weight ( $\mu\text{g}$ ) and (b) germination (%) of *L. maritima* seeds in each period of each study year. Means with different letters differ significantly from one another (Bonferroni test,  $P < 0.05$ )

Period	Year		
	1994–1995	1995–1996	1996–1997
(a) Weight			
September	206.4 $\pm$ 5.07a	229.7 $\pm$ 7.30a	315.2 $\pm$ 8.36a
November	177.6 $\pm$ 5.24bc	191.9 $\pm$ 5.82b	192.1 $\pm$ 6.87b
January	180.8 $\pm$ 8.65bc	239.9 $\pm$ 7.06a	251.6 $\pm$ 6.63c
March	242.1 $\pm$ 9.64a	223.3 $\pm$ 5.96a	192.2 $\pm$ 6.97b
May	208.6 $\pm$ 8.52ac	222.2 $\pm$ 6.53a	168.0 $\pm$ 6.90d
(b) Germination			
September	39.20 $\pm$ 2.97a	35.60 $\pm$ 2.93a	58.60 $\pm$ 11.33a
November	41.60 $\pm$ 2.83a	9.00 $\pm$ 1.09b	32.90 $\pm$ 6.43b
January	40.44 $\pm$ 2.02a	8.60 $\pm$ 1.23b	25.00 $\pm$ 1.20b
March	21.78 $\pm$ 2.34b	0.60 $\pm$ 0.31c	1.20 $\pm$ 0.80c
May	2.00 $\pm$ 0.73c	7.60 $\pm$ 0.98b	1.40 $\pm$ 0.52c

**Table 5.** Means ( $\pm$ SE) for seed density (seed  $\text{cm}^{-3}$ ) and seed germination (%) in the soil seed bank in each period of the flowering and fruiting season of *L. maritima*. Means with different letters differ significantly from one another (Bonferroni test,  $P < 0.05$ )

Period	Seed density	Seed germ.
September	0.38 $\pm$ 0.10a	64.99 $\pm$ 10.49a
November	0.15 $\pm$ 0.04ab	42.03 $\pm$ 10.87b
January	0.07 $\pm$ 0.02b	33.48 $\pm$ 10.03b
March	0.17 $\pm$ 0.05ab	29.82 $\pm$ 10.03b
May	0.11 $\pm$ 0.03ab	6.19 $\pm$ 4.14c

(Table 1), probably because of the large differences in sample size between the two experiments.

#### SOIL SEED BANK

The period of the flowering season had a significant effect on seed density in the soil seed bank ( $F_{4,71} = 2.72$ ,  $P = 0.036$ ) and germination of seeds found in the soil ( $F_{4,50} = 4.13$ ,  $P = 0.006$ ). Seed density in the soil seed bank reached a maximum in the September period and a minimum in the January period (Table 5). The proportion of seeds found in the soil seed bank that germinated also peaked at the onset of the flowering season and decreased progressively throughout the year (Table 5).

#### EFFECT OF TEMPERATURE ON SEED GERMINATION

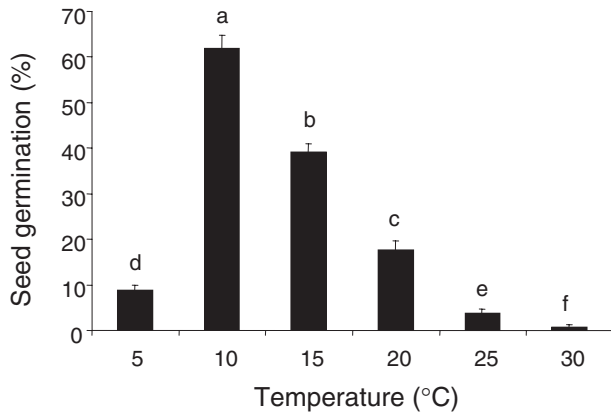
Germination of *L. maritima* seeds significantly differed among the temperatures tested ( $F_{5,54} = 156.25$ ,

$P < 0.0001$ ). Thus, seed germination peaked at 10°C, and decreased progressively at higher temperatures and at 5°C (Fig. 1). Seeds tested at 30°C were not destroyed by heat, as seeds first tested at 30°C reached germination values up to 65% when placed at 10°C.

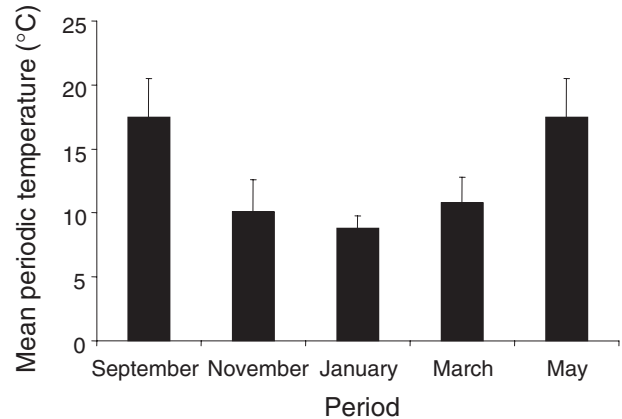
#### DISCUSSION

The low recruitment of *L. maritima* outside of the autumn period has been related to the combination of low precipitation and high seed predation activity (Picó & Retana, 2000; Picó, 2000). Results reported in the present paper show that seed ecology characteristics also account for recruitment limitation in *L. maritima*, although the plant has a huge potential to continuously recruit new plants into the population. In particular, self-pollination does not significantly decrease either the reproductive output or germinability of the resulting seeds. As a result, the remarkable changes in visitation rate and pollinator composition throughout the flowering season do not explain between-period differences in total recruitment. Hence, there is no evidence for the existence of either pollinator limitation or inbreeding depression accounting for a decrease in recruitment at any period of the flowering season of *L. maritima*.

Shifts in seed density in the soil seed bank over the year fit well with the general pattern of variation in seed production throughout the flowering season of *L. maritima*: heavy seed production in autumn followed by a progressive decrease throughout the year, finally slightly peaking in spring (Picó & Retana, 2000). Although only September and January periods differ significantly in seed density, due to the great



**Figure 1.** Mean ( $\pm$ SE) of seed germination (%) for each temperature tested on *L. maritima* seeds. Bars with different letters differ significantly from one another (Bonferroni test,  $P < 0.05$ ).



**Figure 2.** Mean ( $\pm$ SE) of average temperatures per period during the study years (1994–97) from Fabra Meteorological Station, which is located 2 km from the study site. Periods of the year in which *L. maritima* is blooming include two months each (see text for details).

heterogeneity of the soil, the seed bank study indicates that seeds in the soil basically come from current seed production at each period of the flowering season and that seeds do not remain for a long time in the seed bank, probably as a result of depletion due to high post-dispersal seed predation rates by ants recorded throughout the year (Picó & Retana, 2000). In fact, the longer seeds stay in the soil, the higher their risk of being predated (Howe & Smallwood, 1982; Hulme, 1998), as occurs in *L. maritima*. As a result, seeds buried in the soil seed bank throughout the year do not make important contributions to recruitment and subsequent population growth, as previously quantified by demographic models (Picó *et al.*, 2002).

Germination of seeds buried in the soil clearly decreased throughout the entire flowering season. An explanation for such a decrease in the germination of *L. maritima* seeds over the year can be found in results from the other two experiments reported in this paper. First, seed weight peaked in autumn and then sharply decreased in winter (Table 4), but increased again late in the season in two out of the three years of the study. However, the relationship between seed mass and germination is not clear for *L. maritima*, because seed germination clearly decreased throughout the flowering season (Table 4). This suggests that extended flowering is costly in terms of seed germination. It has been demonstrated that *L. maritima* embryos are active in obtaining resources from their mothers (Prabhakar & Vijayaraghavan, 1983), while in many other plants embryo growth takes place at the expense of endosperm reserves (Haig & Westoby, 1991). If mother

plants of *L. maritima* are affected by resource limitation throughout the flowering season, then embryos can also be negatively affected, leading to decreasing seed germination by increasing embryo mortality.

The second explanation for the decrease in germination and subsequent recruitment is that changes in temperature shaped the germination pattern of *L. maritima* seeds. The experiment performed to assess the effects of temperature on seed germination clearly demonstrated that 10°C maximized seed germination. According to Baskin & Baskin (1998: 54), non-dormant seeds exhibit quiescence or environmental inhibition of germination when environmental conditions are unfavourable. Given the pattern of temperature effects on seed germination and the temperatures recorded in each period at the study site during the study years (Fig. 2), this seems to be the case for *L. maritima*. Temperature records show that, according to the results presented in Figure 1, mean temperatures in November, January, and March should enhance germination of *L. maritima* seeds while those of September and May should reduce it. The September period includes two very different months: September can be still part of the summer drought in some years, while in October precipitation usually peaks, temperature drops, and massive recruitment takes place. Because of such high variability between months within the September period, mean temperature for this period does not correspond to the observed germination pattern. For November, January and March periods, lower seed production and irregular precipitation can account for low germination, although temperature would enhance seed germination. Finally, low seed production and

temperature-mediated effects would act in concert to reduce germination in the May period.

In general, the germination characteristics of a seed are determined during the course of its development, and the environmental conditions experienced by parent plants during seed production and maturation can strongly influence the degree and type of dormancy in the seed (Fenner, 1985: 79; Kegode & Pearce, 1998; van Hinsberg, 1998; Orozco-Segovia *et al.*, 2000). In the case of *L. maritima*, the environmental inhibition of germination might have been under selection, as responses of seeds to various environmental factors have a genetic basis (Baskin & Baskin, 1998: 186; Foley & Fennimore, 1998). The reason for this is that germination events late in the season, and prior to the summer drought, have few chances of successful recruitment into the population. Thus, those genotypes that produce quiescent seeds might have been selected for, as they can prevent fatal germination events. This kind of adaptation to protect seeds against harsh environmental conditions has also been reported for some other plant species (Fenner, 1985; Vázquez-Yanes & Orozco-Segovia, 1993; Vleeshouwers, Bouwmeester & Karssen, 1995; Baskin & Baskin, 1998; Arndt *et al.*, 2001; Tomback *et al.*, 2001). Although *L. maritima* shows extended flowering and fruiting, seeds produced throughout the season have the means to avoid germination in unfavourable periods of the year. Because seasonal climatic conditions may change from year to year, consequently affecting seed germination, *L. maritima* keeps the potential for peaking recruitment in winter and spring, although this event has never been observed in the field.

We conclude that, apart from the weather limitations and seed predation effects reported in previous studies, the recruitment shortage in periods outside of autumn of the extended flowering and fruiting season of *L. maritima* can also be attributed to: (1) a decrease in germinability, possibly due to the cost associated with the extended flowering season, and (2) temperature-mediated mechanisms to produce quiescent seeds that avoid germination prior to the hot Mediterranean summer. The recent study on *Ochradenus baccatus* Del. (*Resedaceae*), a common shrub in the Middle East that is in flower throughout the year, shows that seed production, recruitment and offspring quality are much higher in particular months (i.e. winter) than during the rest of the year (Wolfe & Burns, 2001). In contrast, germination experiments on the continuously flowering Mediterranean semi-desert shrub *Launaea arborescens* (Batt.) Murb. (*Asteraceae*) show that this plant has no means of preventing immediate germination, and successful recruitment totally depends on favourable weather conditions (Schutz & Milberg, 1997). All these case studies (including *L. maritima*) indicate that Mediterranean plant spe-

cies with unusually extended flowering and fruiting patterns (i.e. more than ten months) might maintain the same fitness with concentrated flowering seasons. Why then do they show such extended phenological patterns? Herrera (1988) and Picó *et al.* (2002) suggest that strong phylogenetic constraints might explain such patterns in the Mediterranean Basin, but this hypothesis has not yet been tested.

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