

RESEARCH PAPER

Age-specific, density-dependent and environment-based mortality of a short-lived perennial herb

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ABSTRACT

Density-independent and density-dependent processes affect plant mortality. Although less well understood, age-specific mortality can also play an important role in plant mortality. The goal of this study was to analyse several factors accounting for mortality in the Mediterranean short-lived perennial herb *Lobularia maritima*. We followed three cohorts of plants (from emergence to death) during 4 years in field conditions. We collected data on plant mortality of the effect of biotic agents (moth larvae and mycoplasma-like organisms, MLOs) and environmental variables. We also estimated density-dependent relationships affecting the fate of seedlings and adults. Results show that cohorts differed in their survival curves and ageing significantly increased mortality risk. Seedling mortality was density-dependent whereas adult mortality was not affected by density. MLO infection led to higher plant mortality whereas moth larvae attack did not affect plant mortality. In general, seedlings and adult plants experienced the highest mortality events in summer. We found, however, weak relationships between weather records and plant mortality. Age and size structures were not correlated. Overall, this study provides a comprehensive review of age-specific, density-dependent and density-independent factors that account for mortality of *L. maritima* plants throughout their life cycle in field conditions, highlighting the fact that age is an important factor in determining plant population dynamics.

INTRODUCTION

Mortality represents one of the four elements, along with recruitment, immigration and emigration of individuals, that accounts for changes in plant numbers through time and space (Watkinson 1997). In many plants, the highest mortality occurs among initial life-cycle stages and, following establishment, the death rate tends to be lower (Harper 1977). Two types of mortality have traditionally been studied. Density-independent mortality occurs as a result of many factors, for example harsh weather conditions (Lindkvist & Chen 1999; Keith 2002), herbivore activity (Ehrlén 1995; Scheidel & Bruelheide 2004; Wiseman *et al.* 2004) or diseases (Kison & Seemüller 2001). The extent of density-independent mortality strongly depends on environmental heterogeneity, which can be highly variable at all spatial and temporal scales. Density-

dependent mortality often occurs among early life-cycle stages of plants by killing offspring (especially when offspring density is high) that germinate near parents (Watkinson 1997), whereas adult plants represent the result of a density-dependent process. It has been shown that both types of mortality may act in concert (Rees & Brown 1992), ultimately determining the structure of plant populations from seed to adult stages and regulating plant numbers in a population (Toft & Fraizer 2003; Gratzler & Rai 2004).

In addition to density-dependent and density-independent mortality, there is another factor that may strongly influence mortality rates and can also act in concert with them: age. Ageing is related to increased oxidative stress at the cell level that leads to an accumulation of RNA and DNA mutations (Pla *et al.* 2000), so overall plant function deteriorates as plants become older. Although

plant size and developmental stage are better predictors of survival, as are growth, fecundity (Watkinson 1997; Mencuccini *et al.* 2005) and overall demographic behavior (Caswell 2001), the fate of plants also depends on their age (Roach 2001, 2003; Roach & Gampe 2004). Determining the age-dependent component in relation to the observed demographic patterns can be difficult (Roach & Gampe 2004), but it is important to understand the relationship between age, reproduction and mortality to obtain valuable insights into the evolution of plant life histories (Charlesworth 1980; Roach 2003). Age and size distributions of plant populations do not necessarily exhibit the same profile, suggesting that size structure cannot always be used to infer age structure in plants (Butson *et al.* 1987; Groot & Horton 1994; García & Antor 1995; Sano 1997). In plant populations, studies on age structure and age-dependent demographic patterns are more restricted to woody plants, in which the determination of age is more feasible, *e.g.* by using tree rings (Schweingruber 1988; Fritts & Swetnam 1989). In contrast, few such studies have been made of perennial herbs, since quantifying the effects of age on vital rates requires the monitoring of several cohorts during their entire life span (Roach 2003; Menges & Quintana-Ascencio 2004; Roach & Gampe 2004).

It is worth noting that density-dependent and environmental factors may interact with age in a complex manner, hence studies on plant population biology should aim to discern the effects of these factors on plant mortality. The goal of this study was to analyse density-dependent, density-independent and age-specific mortality of the Mediterranean perennial herb *Lobularia maritima* (L.) Desv. (Brassicaceae) by following natural cohorts in their environment for their entire life span and identifying the factors that cause mortality at different life-cycle stages. These empirical data can be relevant to the development of models that will illustrate the relationship between age and critical demographic parameters in the context of life history evolution in plants. We address the following questions: (i) What are the cohort dynamics of *L. maritima* from which insights on age-specific mortality can be obtained? (ii) What is the impact of density-dependent factors on mortality of *L. maritima* during its entire life cycle? and (iii) What abiotic and biotic factors account for mortality in *L. maritima*?

METHODS

Plant species and study site

Lobularia maritima is a small, short-lived, polycarpic perennial herb. Its geographical range includes the entire Mediterranean basin, where it grows in coastal areas, including dunes and scrublands. The plant consists of a rosette of ascending flowering stems. Flowering and fruiting occur throughout the year, from early September to late June (Picó & Retana 2000). Flowers are hermaphrodite and insect-pollinated, mainly by flies and ants (Bosch

et al. 1997; Gómez 2000; Picó & Retana 2003). The species is self-compatible and self-fertile, showing a high fruit:flower ratio when isolated from pollinators (Picó & Retana 2003). The fruit is a silique with two seeds in each part. In summer, under extreme heat combined with drought, adult *L. maritima* plants become dormant and lose aboveground biomass (Picó *et al.* 2002).

We undertook this study at the Collserola Metropolitan Park of Barcelona, NE Spain (41°24' N, 2°6' E; elevation 280 m). The study site is a typically open coastal scrubland, and its complete description can be found elsewhere (Picó & Retana 2001). Climate is typically Mediterranean, with a marked seasonality in the precipitation regime and a summer drought. Mean annual rainfall is about 620 mm and mean monthly temperatures range between 7.8 °C in January and 23.2 °C in August.

Mortality data and analysis

Data required to study different mortality causes in *L. maritima* were obtained from the same sampling plots used to study the demography of the species over 6 years (see Picó *et al.* 2002). The sampling design consisted of 12 1 × 1-m² plots randomly placed in the study area over five flowering seasons (from 1994–1995 to 1998–1999). *Lobularia maritima* seedlings emerging in each plot during the flowering season were marked with coloured tags and monitored every 2 months throughout the year (six censuses per year). During the five flowering seasons considered, we monitored three different cohorts from emergence to death (those that emerged as seedlings in 1994–1995, 1995–1996 and 1996–1997). The fate of a total of 583, 153 and 631 seedlings, respectively, per cohort was monitored during the entire sampling period. Seedling survival in each plot and year was estimated as the proportion of surviving seedlings at the beginning of the next flowering season related to the total number of seedlings emerging during the whole flowering season. All plants surviving at the end of the first year were monitored across years until they died.

The effects of plant age and cohort on plant mortality were analysed with a Generalized Linear Model with a binomial error and a logit link function (Crawley 2002). All plants from all plots were pooled together. As in the model we did not detect signs of overdispersion, we did not need to incorporate plot as a random variable in the analysis. This statistical analysis was performed with the GENMOD procedure of the SAS package. We also analysed the temporal dynamics of mortality for each *L. maritima* cohort by adjusting a log-linear model (Healy 1988; González-Astorga & Núñez-Farfán 2000). The linear coefficient of the model reports on how constant mortality is through time, whereas the quadratic, non-linear coefficient of the model is related to the intensity of mortality through time.

Mortality of seedlings, *i.e.* the number of seedlings dying from the beginning of a flowering period to the beginning of the following period, was divided in two

components: mortality in autumn/spring (from September through June), and mortality in the summer period (July and August). Differences among years in mortality in autumn/spring, summer mortality and overall mortality were tested with chi-square tests. All seedlings that survived their first summer became reproductive plants at the beginning of the next flowering season. As seedlings of each flowering season were different cohorts and the number of adult plants also differed among years (depending on adult mortality), we considered the values of the same plot for the three flowering seasons as different replicates (see Picó *et al.* 2002; Retana *et al.* 2004). The relationships between seedling survival and seedling and adult density, and between adult survival and adult density were analysed using linear regression models.

Factors determining adult mortality of *L. maritima* plants were monitored during five flowering seasons (from 1993–1994 to 1997–1998). At the beginning of each season, 25–71 additional adult *L. maritima* plants were randomly selected, marked with numbered plastic tags, and mapped. Every 15 days throughout the entire flowering season, the state (dead or alive) and the number of flowering stalks per tagged plant were recorded. The maximum number of flowering stalks during the flowering period was used as a measure of plant size, given the particular architecture of the plant that has no basal rosette of leaves but only flowering stalks. In fact, the maximum number of flowering stalks showed a significant correlation with maximum plant volume (calculated as $\pi \times \text{radius}^2 \times \text{height}$; $R^2 = 0.69$, $P < 0.0001$, $n = 50$). To evaluate mortality in the summer period, tagged plants were monitored again in mid-September, at the beginning of the following growing season. The number of flowering stalks of *L. maritima* plants decreased due to two biotic causes: (i) moth larvae that attacked some flowering stalks, grazing all flowers and buds and (ii) mycoplasma-like organisms (MLOs), which caused proliferation of flower buds and originated flowering heads with a form of a witches' broom. As in the case of seedlings, overall mortality of adult *L. maritima* plants, *i.e.* the number of individuals that died from the beginning of a flowering period to the beginning of the following period, was divided in two components: mortality in autumn/spring (during the flowering period) and mortality in the summer period (when *L. maritima* plants were dormant). Differences among years in autumn/spring mortality, summer mortality and overall mortality were tested with chi-square tests. Differences in plant status (dead or alive) in each of these periods in the total number of stalks, the percentage of stalks grazed by moth larvae and the percentage of stalks infected by MLOs were analysed using one-way ANOVA models. Data for individuals sampled in the five sampling seasons were pooled.

The strong seasonality in weather conditions that characterises Mediterranean climates is expected to affect plant population dynamics. For this reason, we analysed potential effects of weather on mortality. Meteorological data, including mean temperature and total rainfall from

September to August (the whole year) and from June to early September (the summer), of the study years were obtained from the Fabra Meteorological Station. The relationship between these weather records and mortality of *L. maritima* seedlings or adult plants was analysed using linear regression models.

When necessary, variables were transformed for normality, homoscedasticity and linearity, using arcsine transformation for proportions and log transformation for all other values. Statistical analyses were based on Zar (1996) and performed using SPSS statistical software (SPSS Inc. 2003).

RESULTS

Age-specific mortality

We found significant differences in mortality among cohorts (Table 1) because cohort 1996–1997 exhibited high mortality (Fig. 1). Mortality also varied among plant ages (Table 1), with lower values for seedlings (54.8%) and for 1-year old plants (63.3%) than for 2-year old plants (87.4%). The interaction between age and cohort was also significant (Table 1): there were differences in plant mortality among cohorts for seedlings and for 1-year old plants, but not for 2-year old plants (Fig. 1).

The linear coefficients of the log-linear model were not significant for any of the cohorts (b -values = -0.17 , 0.09 and 0.25 for cohort 1994–1995, 1995–1996 and 1996–1997).

Table 1. GLM model analysing the effects of plant age (seedling, 1- and 2-year old plants) and cohort (1994–1995, 1995–1996 and 1996–1997) on plant mortality; $n = 1843$.

factor	df	F
cohort	2	144.4**
age	2	23.2**
cohort x Age	4	13.3*

* $P < 0.01$; ** $P < 0.0001$.

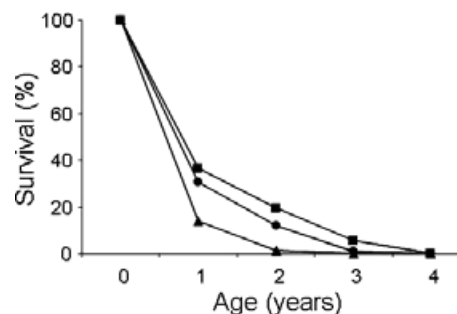


Fig. 1. Yearly survival of three *Lobularia maritima* cohorts. The season of seedling emergence was: 1994–1995 for cohort 1 (squares), 1995–1996 for cohort 2 (circles), and 1996–1997 for cohort 3 (triangles). $n = 583$, 153 and 631 initial seedlings in cohorts 1, 2 and 3, respectively. All plots have been pooled.

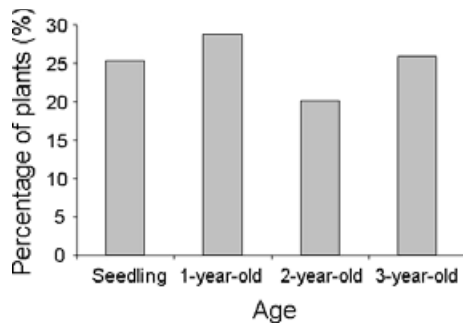


Fig. 2. Percentage of *Lobularia maritima* plants of different ages in November 1997. $n = 174$ individuals. All plots have been pooled.

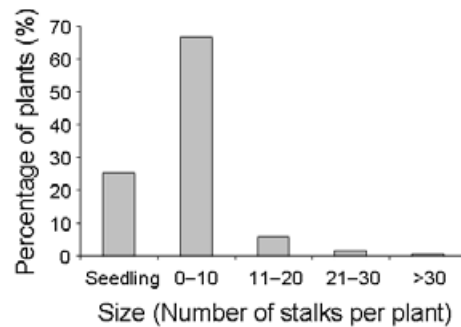


Fig. 3. Percentage of *Lobularia maritima* plants of different sizes in November 1997. $n = 174$ individuals. All plots have been pooled.

1997, respectively, $P > 0.76$ in all cases), indicating that mortality rate was not constant through time (see also Fig. 1). The quadratic coefficients were not significant (c -values = 2.16, 0.91 and 0.08 for cohort 1994–1995, 1995–1996 and 1996–1997, respectively, $P > 0.60$ in all cases), so no conclusions could be reached on the intensity of mortality through time.

Maximum lifespan of *L. maritima* individuals was 4 years (Fig. 1). In November 1997, the only year when all plants in the study within plots were of known age, the age structure of the population indicated that the proportion of individuals in the four different ages present was similar (Fig. 2). In order to compare age and size structures in 1997, a size structure was built using the maximum size reached by each tagged individual in 1997. Results show that the population was mainly represented by seedlings and small reproductive plants, whereas large plants were poorly represented (Fig. 3). Size of plants of known age in 1997 did not show significant differences among cohorts ($P = 0.27$; mean \pm 1 SE number of stalks per individual: 4.6 ± 5.4 , 4.8 ± 5.4 and 6.6 ± 8.2 for 1-, 2- and 3-year old plants, respectively).

Density-dependent mortality

Seedling survival depended on both the number of seedlings and adult *L. maritima* neighbouring plants. Seedling survival at the beginning of the next flowering season significantly decreased with the total number of seedlings and adult plants in the plot (Fig. 4A,B; linear regression; $R^2 = 0.43$, $P < 0.001$, $n = 32$, and $R^2 = 0.20$, $P = 0.012$, $n = 32$ respectively). In contrast, adult survival was not significantly affected by density of adult neighbouring plants (Fig. 4C; $P = 0.95$).

Mortality caused by abiotic and biotic factors

Overall mortality of seedlings from the beginning of a flowering period to the beginning of the following period was very high, ranging from 63.5 to 100% (Table 2A). Seedling mortality in autumn/spring (from September to June) was lower (mean \pm 1 SE: $29.8 \pm 9.7\%$) than in summer ($53.0 \pm 16.5\%$) (Table 2A). Differences among

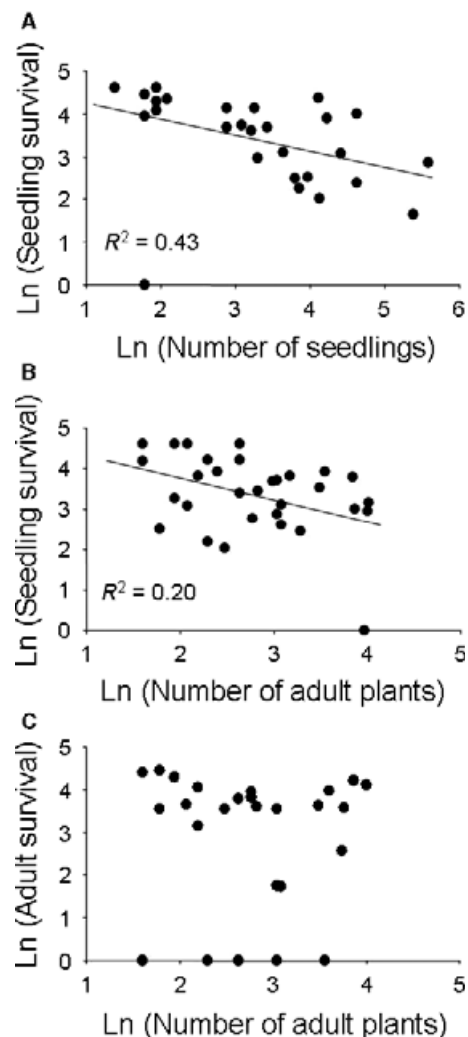


Fig. 4. Relationship between (A) seedling survival (%) and number of seedlings, (B) seedling survival (%) and number of adults, and (C) adult survival (%) and number of adults. Significant linear regressions are depicted and R^2 values given.

Table 2. Mortality (%) of *Lobularia maritima* seedlings (A) and adult plants (B) in autumn/spring (during the flowering period, from September to June), in summer (July and August) and overall (flowering period plus summer) in the 5 years of study.

flowering period	n	mortality in autumn/spring	mortality in summer	overall mortality
(A) seedlings				
1994–1995	583	29.7	33.8	63.5
1995–1996	153	28.1	41.2	69.3
1996–1997	631	23.0	63.4	86.4
1997–1998	151	44.4	50.3	94.7
1998–1999	105	33.5	66.5	100.0
(B) adult plants				
1993–1994	34	0	91.2	91.2
1994–1995	26	23.1	15.4	38.5
1995–1996	32	25.0	34.4	59.4
1996–1997	71	7.0	57.8	64.8
1997–1998	26	26.9	65.5	92.4

The number n of seedlings or adult plants monitored in each flowering period is given.

years were significant for autumn/spring mortality ($\chi^2 = 57.3$, $P < 0.0001$), summer mortality ($\chi^2 = 197.9$, $P < 0.0001$) and overall mortality ($\chi^2 = 150.9$, $P < 0.0001$).

Table 3. ANOVA tests analysing the effects of plant size, percentage of stalks infected by mycoplasma-like organisms (MLOs) and percentage of stalks grazed by moth larvae on plant status (dead or alive) in autumn/spring (from September to June), in summer (July and August) and overall.

Factor	df	F		
		plant size	stalks infected by MLOs	stalks grazed by moth larvae
autumn/Spring	175	19.5**	22.4**	2.0 ns
summer	154	1.0 ns	5.3*	0.0 ns
overall	175	3.1 ns	8.5*	0.1 ns

Size was log-transformed, while the percentage of stalks grazed by moth larvae and those infected by MLOs were arc-sin square-root transformed.

* $P < 0.05$; ** $P < 0.0001$; ns = not significant.

Table 4. Mean (± 1 SE) values for plant size (given by the maximum number of stalks), plants infected by mycoplasma-like organisms (MLOs) and those grazed by moth larvae, of individuals that survived and individuals that died in autumn/spring, in summer and overall (i.e. the whole year, including the autumn/spring and summer periods).

factor	plant size		plants infected by MLOs		plants grazed by moth larvae	
	Live	Dead	Live	Dead	Live	Dead
autumn/spring	35.1 \pm 3.2 (154)	89.4 \pm 24.1 (21)	5.9 \pm 1.4 (154)	30.0 \pm 9.0 (21)	11.4 \pm 1.3 (154)	6.0 \pm 2.6 (21)
summer	31.0 \pm 4.9 (58)	37.6 \pm 4.1 (96)	1.7 \pm 1.0 (58)	8.4 \pm 2.2 (96)	11.2 \pm 2.0 (58)	11.6 \pm 1.8 (96)
overall	31.0 \pm 4.9 (58)	46.5 \pm 5.6 (117)	1.7 \pm 1.0 (58)	12.2 \pm 2.5 (117)	11.2 \pm 2.0 (58)	10.5 \pm 1.6 (117)

Samples sizes are given in parentheses. In bold, significantly different values between live and dead plants. Overall and summer values for live plants coincide because individuals surviving the summer period are also those surviving throughout the whole year.

0.0001). Seedling mortality in autumn/spring marginally decreased with total rainfall during this period ($R^2 = 0.75$, $P = 0.06$, $N = 5$). Seedling mortality in summer was not correlated with mean temperature and total rainfall throughout the year or during the summer period ($P > 0.40$ in all cases).

In the case of adult plants, overall mortality was quite high, ranging from 38.5 to 92.4% (Table 2B). As in the case of seedlings, adult mortality in autumn/spring was low (mean ± 1 SE over 5 years: 16.4 \pm 5.4%) in comparison with summer mortality, which affected over half of the population (58.4 \pm 15.5%) (Table 2B). Differences among years were significant for autumn/spring mortality ($\chi^2 = 14.8$, $P = 0.0052$), summer mortality ($\chi^2 = 39.2$, $P < 0.0001$) and overall mortality ($\chi^2 = 30.3$, $P < 0.0001$). Neither summer mortality nor autumn/spring mortality of adult plants was correlated with mean temperature and total rainfall throughout the year or during the summer period ($P > 0.20$ in all cases).

Adult plant size affected autumn/spring mortality, but had no effect on summer mortality or overall mortality (Table 3). Mean and variance in size of dead plants were larger than those of live plants (Table 4). From 12.0–28.8% of adult plants were infected by MLOs during the study years. MLO infection strongly increased adult mortality. Overall, 86.5% of individuals affected by MLO diseases died before the start of the following season. There were significant differences in the percentage of stalks infected by MLOs for individuals that survived and individuals that died in autumn/spring, in summer or overall (Table 3). The percentage of stalks grazed by moth larvae had no impact on plant mortality (Table 3). Seedlings were not affected by MLO infection or grazing by moth larvae.

DISCUSSION

Lobularia maritima is a short-lived plant with a life span of up to 4 years. A comparative analysis of cohorts allowed us to assess the fate of *L. maritima* plants of known age over time, and indicates that mortality progressively increased from seedlings to 1- and 2-year old plants. Other studies on comparative analysis of cohorts (from germination to death of all plants of each cohort) of the short-lived perennial herbs *Plantago lanceolata*

(Roach 2003; Roach & Gampe 2004) and *Hypericum cumulicola* (Menges & Quintana-Ascencio 2004) also found differences in the mortality patterns of plants of known age. Overall, these results agree with a review of published life tables in plants, which indicated that over half of species have higher mortality at later ages (Silvertown *et al.* 2001). This emphasises the fact that population dynamics of plants are also determined by the demographic history of individuals (Roach 2003). Other studies demonstrated that historical effects at the individual level (based on past measures of plant performance that reflect costs of reproduction and/or ageing) may add explanatory power to models that simulate the dynamics of populations over time and determine the demographic importance of vital rates (Ehrlén 2000; Menges & Quintana-Ascencio 2004).

The density-dependent relationships found in this study are consistent with other studies showing that early stages of development have strong density-dependent mortality in plants (Nilsson 1995; Matos *et al.* 1999; Gustafsson & Ehrlén 2003). Given that density-dependent factors did not affect adult plants, recruitment is the key parameter that chiefly determines the dynamics of *L. maritima* populations (Picó *et al.* 2002): low mortality among recruits in a given year will lead to higher population growth rates and *vice versa*. It is worth noting that the age-specific mortality patterns of the three cohorts in the study agree well with the expected demographic patterns given by the population growth rates (λ) obtained for the same years of the study (Picó *et al.* 2002): low mortality and high λ for cohort 1 (year 1994–1995; $\lambda = 4.81$), intermediate mortality and λ for cohort 2 (year 1995–1996; $\lambda = 2.78$) and high mortality and lower λ for cohort 3 (year 1996–1997; $\lambda = 1.50$). Based on this study and results published elsewhere, the recruitment and establishment processes in *L. maritima* can be described as follows: for each cohort, after peak seedling emergence in autumn (Picó & Retana 2000), populations maintain a seedling bank throughout winter and spring, when seedlings have low mortality rates in comparison with those in summer. Although density-dependent seedling mortality is not apparent throughout the year, density dependence determines the number of resulting adult plants from each cohort of seedlings after the summer. Seedling weakening due to competition for resources at high densities could make plants less resistant to stress imposed by the hot, dry climate of the Mediterranean summer. It has been demonstrated for other Mediterranean perennial herbs that seedling survival during the drought period is strongly correlated with root allocation and the species ability to use belowground resources (Lloret *et al.* 1999).

Lobularia maritima adult plants also died as a result of biotic agents, such as infections caused by MLOs. MLOs produce a wide array of effects on infected plants (*e.g.* stunted growth, excessive bud sprouting and inhibition of flowering) that may increase mortality risk (Kison & Seemüller 2001). Some MLOs have been reported to alter root respiration rates and protein concentrations, which

coincide with the appearance of necrosis (Isla-Flores *et al.* 1999), which might increase mortality risk. On the other hand, mortality of *L. maritima* plants was not affected by grazing by moth larvae, which only reduced the number of flowering stems of damaged plants.

With respect to abiotic variables, we can assert that summer drought is a crucial environmental factor in the *L. maritima* life cycle, given that mortality events in summer are very high. This is a common result in Mediterranean plant ecology (Picó *et al.* 2002; Groom *et al.* 2004; Quintana *et al.* 2004). It is widely accepted that a strong seasonality in environmental conditions acts as a selective pressure that shapes phenological patterns of Mediterranean plant species (Mooney *et al.* 1974; Kummerow 1983). We found, however, little correlation with weather records, since only seedling survival was marginally related to precipitation during the flowering season.

In general, plant size had a minor effect on plant mortality. Interestingly, larger plants had a higher mortality, but only during the flowering period when overall mortality was low. The positive relationship between plant size and mortality risk during the flowering season found in this study could be attributed to the cost of reproduction that resulted in increased mortality. Another study on the seed ecology of *L. maritima* also indicated a cost of reproduction in terms of seed germination (Picó & Retana 2003). *Lobularia maritima* produces seeds during a 10-month flowering and fruiting season, but seeds produced early in the flowering season are heavier and have higher germination rates than those produced later in the season, which is interpreted as a cost of the species extended reproduction (Picó & Retana 2003). Overall, these results indicate that flowering and fruiting during such a long period of time is costly in terms of important fitness components, such as recruitment and survival.

The comparison between age and size structures deserves attention. We have shown that the *L. maritima* population in the study in 1997 was dominated by seedlings and small reproductive plants. This is normal in this short-lived perennial herb, whose population dynamics strongly depend on yearly recruitment (Picó *et al.* 2002). It is remarkable that the age structure of plants in 1997 was fairly balanced among age classes, providing additional support to the fact that size and age structure in plants are poorly related (García & Antor 1995). Changes in size structure of plant populations over time may be related to changes in population dynamics (Hegland *et al.* 2001), but we do not know yet whether changes in age structure may also have demographic implications. Given the significant effect of age on plant survival in *L. maritima*, variability in age structure might play a very important role in determining population fluctuations and, ultimately, persistence. Gaining new insights into this issue would require the monitoring of plant cohorts over several years, since a complete age structure in *L. maritima* required three cohorts followed over 4 years.

Overall, this study has provided data on factors (age-specific, density-dependent and density-independent

factors) that account for mortality of *L. maritima* plants throughout their life cycle in field conditions. We conclude that the *L. maritima* population is mainly regulated by density-dependent factors at the seedling state, by age-specific effects whose importance increases as plants age, and by the effects of the summer drought on both seedlings and adult plants. Biotic agents, such as MLOs, are also important, although the proportion of infected plants in the population was rather low. This study allowed us to assess the effect of a diverse array of factors on the *L. maritima* mortality schedule in field conditions. As noted by other authors (Roach 2003; Roach & Gampe 2004), we also believe that the accumulation of data on traditionally analysed causes of mortality (*i.e.* density-dependent and environmental-based mortality), plus age-specific mortality of plants in field conditions, will contribute to increase our understanding of population dynamics as well as life-history evolution in plants.

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