

## Temporal variation in the female components of reproductive success over the extended flowering season of a Mediterranean perennial herb

F. Xavier Picó and J. Retana

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We examined the reproductive success of the perennial herb *Lobularia maritima* during its extended flowering and fruiting season. The within- and between-year variability of the female components of reproductive success (from flower, fruit and seed production to seed survival, seed germination and seedling establishment) were analysed during four flowering seasons. All the components of reproductive success studied showed a significant within- and between-year variation. September was the period of the year with the maximum values of flower and fruit production, and the highest germination and establishment rates. Nevertheless, seed losses due to both predispersal and postdispersal seed predation during this period were also the highest, seriously reducing seed output in this period. On the other hand, in those periods in which seed production was low, i.e. January and May, the percentage of seeds lost to seed predators was the lowest. Reproductive success in each period of the flowering season was estimated using a simple demographic model, in which the information concerning all the components already calculated was integrated. The two variables used to estimate reproductive success in each period, i.e. the number of new individuals produced per plant and the probability of a seed becoming an adult plant, showed relatively small differences over the year. These results suggest a counter-balance of the different components of reproductive success in this species, with favourable and unfavourable periods for the different components being compensated during its extended flowering season.

F. X. Picó and J. Retana, Centre de Recerca Ecològica i Aplicacions Forestals (CREAF) i Unitat d'Ecologia, Facultat de Ciències, Universitat Autònoma de Barcelona, E-08193 Bellaterra (Barcelona), Spain (ibec26@blues.uab.es).

Flowering phenology may have a great influence on plant reproductive success and ultimately, fitness (English-Loeb and Karban 1992). This is because of the interaction between phenology and several ecological factors important for successful reproduction, including resources for flower and seed production, pollinators, flower and seed herbivores, seed dispersers and pathogens (Primack 1985). Competition for pollinators has often been suggested as the primary selective force determining reproductive success (Brody 1997, and references therein), but other factors, such as flower and

seed predation (Pettersson 1994, Eriksson 1995), may also be important selective forces. There are two opposing points of view that seek to determine whether or not flowering phenology has been under selective pressure. On the one hand, it has been suggested that flowering periods have evolved under the selective pressure imposed by several ecological factors, such as competition for pollinators (Schemske et al. 1978, Bawa 1983, de Jong and Klinkhamer 1991), predictability of pollination and opportunities for colonization (Bawa 1983), or flower and fruit herbivory (Bawa 1983,

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English-Loeb and Karban 1992). On the other hand, Ollerton and Lack (1992) point out that flowering phenology has not been under strong natural selection because there are other plant attributes on which natural selection could act more efficiently. Other studies (Rabinowitz et al. 1981, Rathcke and Lacey 1985, Rathcke 1988) also show that the successive flowering of species, which has been expected to be controlled by competition for pollinators, is indistinguishable from random patterns. Finally, there is also evidence that phylogenetic membership strongly influences a species' flowering time, and that seasonal limitations of flowering times are affected by phylogenetic constraints (Kochmer and Handel 1986).

In the Mediterranean regions, most plants flower during a few months, and the blooming is concentrated in spring (Mooney et al. 1974, Kummerow 1983, Bosch et al. 1997). The reproductive and vegetative cycles of Mediterranean plant species are affected by the important shifts that abiotic and biotic factors show throughout the year (Mooney et al. 1974, Kummerow 1983, Bosch et al. 1997, Cros et al. 1997). Given the role that some of these factors may play as selective pressures on flowering times (Rathcke and Lacey 1985, Pettersson 1994, Shitaka and Hirose 1998), an extended flowering season in Mediterranean environments appears to be an exception to the rule. However, the fact that an extended flowering season is rare in Mediterranean environments does not mean that it is an ineffective flowering pattern for ensuring successful reproduction. Bawa (1983) lists, as possible advantages of an extended flowering and fruiting period in tropical environments, the reduction of the risk of reproductive failure, the possibility of mating with more individuals of the population, a better control over relative investment in flowers and fruits, and the avoidance of seed predators. To investigate whether an extended flowering can represent a successful pattern in a Mediterranean environment, we have designed a 4-yr study to determine shifts in the female components of reproductive success (from flower, fruit and seed production to seed germination and seedling establishment) throughout the entire flowering season of *Lobularia maritima*. This is a polycarpic, perennial herb, living in the Mediterranean basin, which shows an unusual extended flowering season that lasts for 10 months (de Bolòs et al. 1993, Bosch et al. 1997). The following questions are addressed: 1) How do all the above components of reproductive success change throughout the extended flowering season of *L. maritima*? 2) To what abiotic and/or biotic factors can the shifts in these components be related? 3) What is the probability of a seed in a ripe fruit becoming an adult plant, and how variable is this probability throughout the entire flowering season?

## Material and methods

### Plant natural history and study site

*Lobularia maritima* (L.) Desv. (Brassicaceae) is a polycarpic, perennial herb. In the Mediterranean basin, it grows in coastal zones, dunes and scrublands (de Bolòs et al. 1993). *L. maritima* forms a basal rosette of prostrate-ascending flowering stems. The flowering and fruiting season may last, depending on climatic conditions, for nearly 11 months, from early September to early July (Picó and Retana unpubl.). Flowers are hermaphroditic and insect-pollinated, mainly by flies and most notably by syrphids (Bosch et al. 1997). *L. maritima* presents a high degree of self-compatibility and a high capacity for autogamous self-pollination (Picó and Retana unpubl.). Fruits are siliquae (2–3.5 mm length) containing two seeds (1–2 mm length).

Field work was conducted at the suburban site Sant Pere Màrtir, at Collserola Park, a protected area just outside Barcelona (NE Spain; 41°24'N, 2°6'E; elevation 280 m). The site is located on an east-facing slope facing the Mediterranean Sea. Climate is typically Mediterranean, with 620 mm of mean annual rainfall, and mean monthly temperatures with a maximum of 23.2°C in August, and a minimum of 7.8°C in January. The site is a scrubland (as a result of a fire that occurred 15 years ago) dominated by shrub species, such as *Cistus monspeliensis* L., *Spartium juncum* L., and *Ulex parviflorus* Pourr., with some bushes of *Daphne gnidium* L. There are still some sparse individuals of *Pinus pinea* L. that survived the fire. The area is quite open and the herbaceous community is mainly composed by *Brachypodium retusum* Pers., *Hyparrhenia hirta* L., *Foeniculum vulgare* Mill., *Echium vulgare* L., *Hirschfeldia incana* L., *Inula viscosa* L. and *L. maritima*, which is quite abundant.

### Division of the flowering season of *L. maritima*

To identify the variation in components of reproductive success that *L. maritima* plants might show throughout the year, the extended flowering season of *L. maritima* was divided into five different periods. Each of them (hereafter called flowering periods) lasts for two months. Their names are, consecutively, September, November, January, March and May. The September period includes data from September and October, the November period includes data from November and December, and so on. These periods differ in terms of climatic conditions (mainly precipitation and temperature) and biotic factors (such as incidence of flower and seed predation or density of competitors for seedling establishment).

## Flower, fruit and seed production

Flower and fruit production were recorded in three flowering seasons, 1993–1994, 1995–1996 and 1996–1997. A haphazard set of 20–25 plants were tagged and monitored each flowering period. Four flowering stems per tagged plant were marked with a fine cotton thread, just at the base of the flower buds. After a different number of days (from 30 to 60, depending on the length of the interval between anthesis and fruit ripening in each period), mature, aborted, and depredated fruits were counted, as well as the number of flowers still open. Aborted fruits were easily recognizable by their small size, and cut pedicels denoted fruit predation by ants of the genus *Messor*. The total flower/fruit production of each individual monitored per period was estimated as the product of the flower/fruit production per flowering stem (an average of the four tagged stems per plant) and the average number of flowering stems per individual during this period. Daily flower and fruit production rates per individual were obtained by dividing the total flower and fruit production per period by the duration of the period (59–62 d). Fruit set, i.e. the proportion of flowers that set fruit, was calculated in each period. The number of seeds per fruit was recorded during the flowering season 1996–1997. To do this, fruits from 10–16 plants were collected in each flowering period. From those, a haphazard sample of 25 fruits was chosen, and the number of seeds per fruit was counted.

## Predispersal and postdispersal seed predation

Ants of the genus *Messor* were those chiefly responsible for both predispersal and postdispersal seed predation (Picó and Retana pers. obs.). Predispersal seed predation was defined as the seed predation that took place when fruits were removed directly from the flowering stems. It was recorded in 1993–1994, 1995–1996 and 1996–1997, together with flower and fruit production (see above). Postdispersal seed predation was defined as the seed predation that occurred when seeds had already dropped from ripening fruits. It was measured during the season 1996–1997. To evaluate postdispersal seed predation in each flowering period, *L. maritima* seeds were collected and dyed with red colour, which made them easily recognizable. Previous experimental tests showed that the red colour used did not induce any modification in the response of ants to seeds. Sixteen replicates of 20 seeds each were placed on the surface of Petri dishes full of soil. These Petri dishes were distributed at haphazard points over the study area and were removed a month after sowing. The remaining coloured seeds were counted under the stereomicroscope to obtain the proportion of non-depredated seeds.

## Seedling emergence

To evaluate the percentage of seed emergence from undepredated seeds in each flowering period, an experiment was performed at the Experimental Fields of the Universitat Autònoma of Barcelona (14 km from Barcelona; 41°2'N, 2°1'E; elevation 150 m), where environmental conditions (mainly temperature and precipitation) were very similar to those found at the Sant Pere Màrtir study area. We did not carry out this experiment at the study site for two reasons: a) the experimental pots could not be distributed throughout the area during the duration of this experiment (ca one year) because of the extreme risk of their total or partial removal due to human vandalism; and b) we tried to avoid the interference of seeds produced in the area and dispersed on the pots in the estimation of the seed germination rate. To obtain cohorts of seeds in each of the five flowering periods, seeds were harvested from haphazardly chosen plants (20–30 different plants in each period) in the study area of Sant Pere Màrtir. Ten replicates of 50 seeds each were buried in flowerpots (15 cm diameter × 17 cm height), filled with soil collected at the Sant Pere Màrtir site. These pots were placed in the open. New cohorts of seeds were sown each flowering period. Every month after the respective sowings, seedlings emerging from each flowerpot were counted for each cohort. Survival of already-emerged seedlings was also recorded every month after sowing during the following 12 months.

## Seedling survival

Seedling survival in the field was evaluated during three flowering seasons (1994–1995, 1995–1996, and 1996–1997). Twelve (eight in 1994–1995) 1 × 1 m<sup>2</sup> plots were haphazardly placed in the study area of Sant Pere Màrtir. *L. maritima* seedlings emerging at the end of each month (from September to June) in each plot were marked with differently coloured tags. Tagged seedlings were monitored throughout the year. All seedlings that survived the next summer were considered as adult plants at the beginning of the next flowering season, because they behaved as adult plants, producing flowering stems, flowers and fruits.

## Data analysis

The effect of year and flowering period on flower and fruit production rate per individual, fruit set, and predispersal seed predation was analysed using two-way ANOVA models. The influence of flowering period on data recorded during only one year, such as postdispersal seed predation, number of seeds per fruit, and the percentage of germinating seeds, was analysed using

Table 1. Simple main effects, testing the significance of flowering period separately for the different years, for flower and fruit production rates, fruit set, and predispersal seed predation.  $F$  values of the test are given for each year. Significance: \*,  $P < 0.0001$ ; ns, not significant. Mean ( $\pm$ SE) values for the same variables in each period of each season are given below. Means with different letters in the significant seasons differ significantly from one another (Student-Newman-Keuls test,  $P < 0.05$ ).

| Year             | Flower production rate | Fruit production rate | Fruit set       | Predispersal seed survival |                 |                 |                 |                  |                  |                 |                  |
|------------------|------------------------|-----------------------|-----------------|----------------------------|-----------------|-----------------|-----------------|------------------|------------------|-----------------|------------------|
| 1993–1994        | 21.5*                  | 21.9*                 | 0.8 ns          | 7.7*                       |                 |                 |                 |                  |                  |                 |                  |
| 1995–1996        | 11.3*                  | 13.5*                 | 2.0 ns          | 0.5 ns                     |                 |                 |                 |                  |                  |                 |                  |
| 1996–1997        | 12.2*                  | 14.1*                 | 20.8*           | 20.7*                      |                 |                 |                 |                  |                  |                 |                  |
| Flowering period | 1993–1994              | 1995–1996             | 1993–1994       | 1995–1996                  | 1993–1994       | 1996–1997       | 1995–1996       | 1996–1997        |                  |                 |                  |
| September        | 66.3 $\pm$ 22.6a       | 44.9 $\pm$ 6.7a       | 20.9 $\pm$ 4.1a | 43.5 $\pm$ 12.2a           | 36.4 $\pm$ 5.2a | 17.0 $\pm$ 3.3a | 0.90 $\pm$ 0.02 | 0.95 $\pm$ 0.01a | 0.08 $\pm$ 0.02a | 0.04 $\pm$ 0.01 | 0.20 $\pm$ 0.02a |
| November         | 27.8 $\pm$ 5.6a        | 4.1 $\pm$ 1.8b        | 6.7 $\pm$ 1.9b  | 17.8 $\pm$ 3.8b            | 3.6 $\pm$ 1.6b  | 5.1 $\pm$ 1.4c  | 0.86 $\pm$ 0.04 | 0.99 $\pm$ 0.01  | 0.10 $\pm$ 0.03a | 0.03 $\pm$ 0.03 | 0.12 $\pm$ 0.03b |
| January          | 7.6 $\pm$ 2.3b         | 6.0 $\pm$ 1.0b        | 13.3 $\pm$ 3.7b | 4.7 $\pm$ 1.4b             | 3.9 $\pm$ 0.7b  | 10.7 $\pm$ 3.3b | 0.90 $\pm$ 0.03 | 0.86 $\pm$ 0.04  | 0.13 $\pm$ 0.06a | 0.03 $\pm$ 0.02 | 0.02 $\pm$ 0.01c |
| March            | 31.4 $\pm$ 6.9a        | 12.9 $\pm$ 4.8b       | 3.4 $\pm$ 0.7c  | 25.3 $\pm$ 6.2ab           | 9.5 $\pm$ 3.4b  | 2.4 $\pm$ 0.5d  | 0.86 $\pm$ 0.02 | 0.90 $\pm$ 0.03  | 0.16 $\pm$ 0.04a | 0.05 $\pm$ 0.02 | 0.14 $\pm$ 0.04b |
| May              | 4.0 $\pm$ 1.3b         | 15.2 $\pm$ 8.2b       | 2.1 $\pm$ 0.4c  | 2.4 $\pm$ 0.7b             | 12.1 $\pm$ 6.7b | 1.4 $\pm$ 0.3d  | 0.80 $\pm$ 0.06 | 0.86 $\pm$ 0.04  | 0.01 $\pm$ 0.01b | 0.03 $\pm$ 0.01 | 0.04 $\pm$ 0.02c |

one-way ANOVA models. The effect of year and flowering period on seedling emergence and seedling establishment under field conditions was analysed using repeated-measures ANOVAs. All ANOVAs were run on log or arcsine transformed data. Whenever the period  $\times$  year interaction was significant in these analyses, simple main effects were computed following Pedhazur (1982), i.e. the significance of flowering period was tested separately for the different years. When an  $F$  ratio for a simple main effect was significant, it was followed up by multiple comparisons using the Student-Newman-Keuls test.

Data obtained from the experiment performed at the Universitat Autònoma of Barcelona and the monitored plots at Sant Pere Màrtir were used to calculate the probability of establishment  $P_i$  of *L. maritima* seedlings. This probability was estimated as the product of the proportion of germinating seeds ( $G$ ) times the proportion of surviving seedlings ( $S$ ). Since seeds only germinated in their corresponding period ( $i$ ) or after the next summer ( $is$ ), the probability of establishment  $P_i$  of the seedlings emerged from the cohort  $i$  is given by

$$P_i = (G_i \times S_i) + (G_{is} \times S_{is}) \quad i = \text{September to May}$$

### The demographic model

To integrate the above reproductive steps of *L. maritima* plants and to obtain a measure of reproductive success in each period of the flowering season, the probability of a single ovule becoming an adult plant was estimated for each period. Thus, all consecutive stages in the recruitment process were put in a demographic model where the probability of an ovule in a flower becoming an established adult plant was estimated as the product of four elemental transition probabilities between consecutive stages in the recruitment process. The probability of reproductive success  $t_1$  is computed as the product of fruit set times the relation seeds/fruit.  $t_2$  and  $t_3$  are the fractions of the seeds that escape predispersal and postdispersal seed predation, respectively. Finally,  $t_4$  considers the above-computed probability of germination and establishment of the seeds remaining in the soil,  $P_i$ , to determine the fraction of surviving seeds that became established as adult plants. From these probabilities and the total number of flowers produced in each period, the absolute (i.e. the number of ovules becoming adult plants) and relative (i.e. the probability of an ovule in a flower becoming an adult plant) recruitment expectancies were calculated for each period.

## Results

### Flower, fruit and seed production

Both flower and fruit production rates per individual showed significant variation among periods (two-way

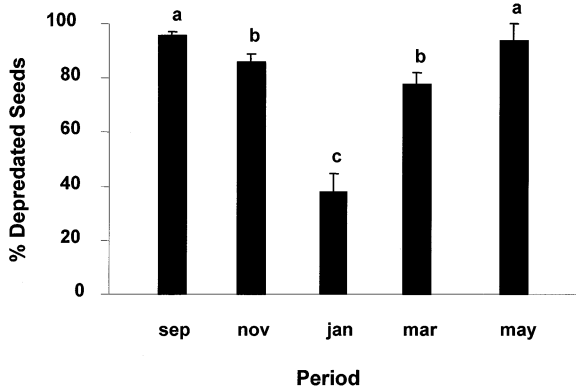


Fig. 1. Mean (+ SE) percentages of postdispersal seed predation in each period of the whole flowering season of *L. maritima*. Different letters on the top of bars indicate significant differences among periods according to Fisher's PLSD post hoc test ( $P < 0.05$ ).

ANOVA;  $F = 31.9$  and  $F = 34.7$ , respectively,  $P < 0.0001$  in both cases) and among years ( $F = 11.8$  and  $F = 10.1$ , respectively,  $P < 0.0001$  in both cases). There was also a significant interaction between factors ( $F = 5.5$  and  $F = 5.9$ , respectively,  $P < 0.0001$  in both cases). The analyses of simple main effects showed, for both variables, significant differences among periods in the three years (Table 1). Thus, September showed the highest values (not significantly different from November and March in 1993–1994), and May the lowest (also in some cases similar to those of other periods). Fruit set also showed significant differences among periods (two-way ANOVA;  $F = 9.8$ ,  $P < 0.0001$ ) but not among years ( $P > 0.05$ ), and the period  $\times$  year interaction was also significant ( $F = 4.6$ ,  $P < 0.0001$ ). The test of simple main effects showed that only the season 1996–1997 had significant differences: fruit set was highest in September, November and January, intermediate in March, and lowest in May (Table 1).

The number of seeds per fruit was variable among periods (one-way ANOVA;  $F = 18.3$ ,  $P = 0.0001$ ). The maximum number of seeds per fruit was recorded in May (Mean  $\pm$  SE =  $1.78 \pm 0.04$  seeds/fruit), and the minimum values were recorded in March ( $1.24 \pm 0.05$  seeds/fruit) and in November ( $1.36 \pm 0.05$  seeds/fruit), while January ( $1.61 \pm 0.04$  seeds/fruit) and September ( $1.67 \pm 0.05$  seeds/fruit) showed intermediate values.

### Predispersal and postdispersal seed predation

Predispersal seed predation showed significant differences among years (two-way ANOVA;  $F = 7.2$ ,  $P = 0.0009$ ) and among periods ( $F = 10.2$ ,  $P < 0.0001$ ). The interaction between factors was also significant ( $F = 4.1$ ,  $P < 0.0001$ ). The simple main effects for this variable indicated significant differences in 1993–1994 and 1996–1997, but not in 1995–1996 (Table 1). Thus,

predispersal seed predation was highest in May in 1993–1994, and in May and January in 1996–1997. In 1995–1996, seed predation was similarly high in the five periods considered (Table 1). Postdispersal seed predation was much more important than predispersal seed predation. It also showed great variability among periods (one-way ANOVA;  $F = 26.1$ ,  $P = 0.0001$ ): the heaviest postdispersal seed predation was recorded in September and in May, and the lowest in January (Fig. 1).

### Seed germination and seedling establishment

The percentage of seed germination in the corresponding period showed significant variation among periods (one-way ANOVA;  $F = 29.2$ ,  $P = 0.0001$ ). The cohort of seeds produced in September showed the highest percentage of germination in this period, whereas the percentage of germination of the cohorts from the other periods did not reach 1% (Table 2). Germination rate of the cohorts of *L. maritima* seeds after the summer, i.e. in the next September period, also showed significant variation among periods (one-way ANOVA;  $F = 14.0$ ,  $P = 0.0001$ ). In this case, the cohorts of seeds produced in March and in May showed the highest percentage of germination after the summer, whereas the lowest percentage was obtained for the September cohort (Table 2).

Density of new seedlings and establishment of adults (i.e. seedlings that had survived during one summer) varied significantly among periods (repeated-measures ANOVA;  $F = 5.8$ ,  $P = 0.0003$  for new seedlings,  $F = 15.9$ ,  $P = 0.0001$  for adult establishment) but not among years (repeated-measures ANOVA;  $P > 0.10$  in both cases), although there was an interaction between factors (repeated-measures ANOVA;  $F = 2.7$ ,  $P = 0.009$  for new seedlings,  $F = 7.1$ ,  $P = 0.0001$  for adult establishment). The simple main effects carried out for these two variables only showed significant differences in 1994–1995, but not in the other two seasons (Table 3). Thus, in 1994–1995 seedling emergence and establishment were high in September and November, lower in January and nil in March and May (Table 3).

Table 2. Mean percentage ( $\pm$  SE) of germinated seeds within each period and after the summer at the experimental area during the 1995–1996 season. The values represent the percentages of the cohort of seeds in each period that germinate. Means with different letters in each column differ significantly from one another (Fisher's PLSD post hoc test,  $P < 0.05$ ).

| Period    | % germination within each period | % germination after the summer |
|-----------|----------------------------------|--------------------------------|
| September | $12.4 \pm 1.5a$                  | $0.3 \pm 0.3c$                 |
| November  | $0.2 \pm 0.2b$                   | $2.2 \pm 1.3b$                 |
| January   | $0.6 \pm 0.3b$                   | $1.4 \pm 0.9b$                 |
| March     | $0 \pm 0b$                       | $8.2 \pm 1.8a$                 |
| May       | $0 \pm 0b$                       | $7.8 \pm 1.1a$                 |

Table 3. Simple main effects, testing the significance of flowering period separately for the different years, for emerged seedlings and recently established adults (number of individuals/m<sup>2</sup> in both cases). *F* values of the test are given for each year. Significance: \*, *P* < 0.0001; ns, not significant. Mean (± SE) values for the same variables in each period of each season are given below. Means with different letters in the significant seasons differ significantly from one another (Student-Newman-Keuls test, *P* < 0.05).

| Year             | Emerged seedlings |           |             | Established adults |           |           |
|------------------|-------------------|-----------|-------------|--------------------|-----------|-----------|
| 1994–1995        | 7.2*              |           |             | 12.7*              |           |           |
| 1995–1996        | 0.1 ns            |           |             | 0.3 ns             |           |           |
| 1996–1997        | 1.8 ns            |           |             | 1.9 ns             |           |           |
| Flowering period | 1994–1995         | 1995–1996 | 1996–1997   | 1994–1995          | 1995–1996 | 1996–1997 |
| September        | 46.2 ± 23.2a      | 3.0 ± 0.7 | 18.4 ± 10.3 | 12.9 ± 5.4a        | 1.1 ± 0.6 | 4.2 ± 1.5 |
| November         | 20.6 ± 6.3ab      | 3.7 ± 1.9 | 15.5 ± 5.4  | 6.5 ± 2.2ab        | 0.6 ± 0.3 | 1.5 ± 0.6 |
| January          | 6.0 ± 1.6b        | 7.0 ± 2.8 | 3.3 ± 1.5   | 1.9 ± 0.7b         | 2.4 ± 1.0 | 0.4 ± 0.3 |
| March            | 0.0 ± 0.0c        | 3.7 ± 1.8 | 14.4 ± 3.7  | 0.0 ± 0.0b         | 1.2 ± 1.0 | 2.9 ± 0.8 |
| May              | 0.0 ± 0.0c        | 0.0 ± 0.0 | 0.0 ± 0.0   | 0.0 ± 0.0b         | 0.0 ± 0.0 | 0.0 ± 0.0 |

### Recruitment probabilities in each flowering period

Fig. 2 shows the relative importance of each component of reproductive success in each period. September was the period of the year with the maximum values of flower and fruit production, and the highest germination and establishment rates. Nevertheless, seed losses due to both predispersal and postdispersal seed predation during this period were also the highest, seriously reducing the seed output in this period. On the other hand, in the two periods in which seed production was low, i.e. January and May, the percentage of seeds that escaped seed predators was the highest.

The demographic model summarises these processes and gives a measure of the reproductive success of *L. maritima* plants in each period of the flowering season. The output of the model can be expressed in absolute (the average number of new individuals recruited from a single plant in each period) or in relative (the probability of an ovule in a flower becoming an adult plant) recruitment values (Fig. 3). Absolute recruitment values higher than 1 occurred in September (2.19 new individuals recruited per single plant), March (1.93 individuals), and January (1.07 individuals), while in the other two periods, the absolute recruitment values were lower than 1 (0.57 for November, and 0.28 for May) (Fig. 3a). Relative recruitment values also showed differences between periods (Fig. 3b). On average, the higher probabilities corresponded to the periods of March and January, both with a relative recruitment value of 0.24%, while the lowest probabilities were recorded for September (0.10%), November (0.08%), and May (0.08%).

### Discussion

Several phenological traits, such as the timing of anthesis or the length of the flowering season of plant species, can be limited by unfavourable weather condi-

tions (de Jong et al. 1992, Boaz et al. 1994, Rose et al. 1998) or by different biotic factors (Delph 1993, Biere and Honders 1996, Crawley 1997). In the case of *L. maritima*, plants show low between-year variation in the length of the flowering season in comparison with other plant species of the same community (Picó and Retana unpubl.). However, seasonality has a marked effect on the biological processes affecting the reproductive cycle of this species. According to Fig. 2, the different components of reproductive success showed their highest values in different periods throughout the flowering season. Thus, the maximum values of flower and fruit production were reached in September, fruit set was highest from September to January, the number of seeds per fruit was highest in May, the proportion of seeds surviving predation was highest in January, while seed germination and seedling establishment were highest in September.

This pattern of variation in the components of reproductive success throughout the year suggests a compensatory effect of this extended flowering period on overall reproduction. The most clear suggestion that there is a counter-balance of the different components of reproductive success is that seed production and seed predation showed opposite patterns. On the one hand,

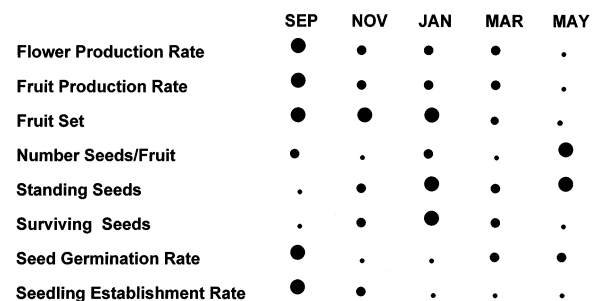


Fig. 2. Graphic representation of the relative importance of each biological process monitored in the periods of the *L. maritima* flowering season. Dot size categorisation is relative to each biological process and comparisons between dots of different biological processes are meaningless.

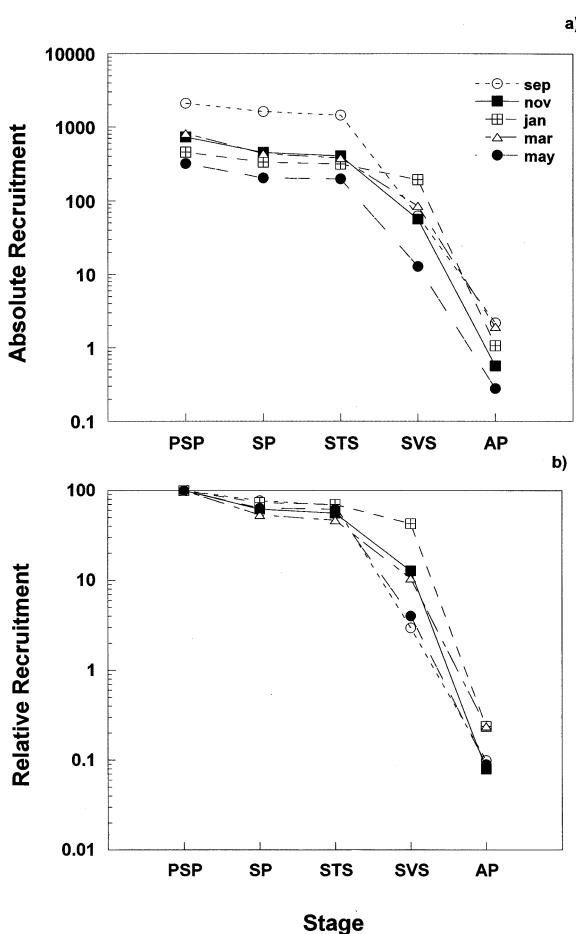


Fig. 3. Reproductive success of *L. maritima* in each period of the flowering season. (a) Absolute and (b) relative recruitment expectancies for *L. maritima* plants in each stage of the reproductive cycle. Absolute recruitment represents the number of ovules becoming adult individuals per *L. maritima* plant. For relative recruitment, potential seed production has been arbitrarily set at 100%. PSP, potential seed production; SP, real seed production; STS, standing seeds; SVS, surviving seeds; AP, adult plants.

the amount of seeds dispersed in each period was mainly determined by flower production. Seed losses due to reproductive failure (a low fruit or seed set) had a negligible importance in determining predispersal seed output. *L. maritima* is fully self-compatible (Picó and Retana unpubl.), and pollen limitation probably makes a minor contribution to final fruit set. Other studies that have dealt with the factors for individual variation in plant fecundity also found that fruit and seed set are poor predictors of individual variation in absolute seed production (Herrera 1991). On the other hand, seed predation was more abundant on fruits produced after the major flowering peak in autumn than on those from winter or early spring. Off-peak *L. maritima* fruits may escape more easily from seed predators than peak fruits because maximum seasonal activity of granivorous

*Messor* ants, which are the main predators of *L. maritima* seeds, occurs at the end of summer and beginning of autumn (i.e. the peak of production of *L. maritima* seeds), while their activity almost ceases completely in winter and early spring (Cerdá and Retana 1994).

Several studies have demonstrated that the final effect on fitness cannot be predicted by considering all the reproductive components separately (Herrera et al. 1994, Sans and Masalles 1994, Traveset 1994, Noy-Meir and Briske 1996), and that it is not possible to assign more importance to one or another process unless the net result of all of them is known. The present study has faced this last point by calculating the recruitment probabilities per period throughout the entire flowering season. The values shown in Fig. 3 should be regarded with caution, since there are no standard errors of the estimates of reproductive success, since it was not possible to use the same sampling units (i.e. individual plants) to estimate all components of reproductive success. The absolute (i.e. the number of new individuals recruited per single plant) and the relative (i.e. the probability of an ovule becoming an adult plant) recruitment values showed slightly different patterns (Fig. 3). Thus, differences between flowering periods in absolute recruitment followed the pattern observed in flower production (but note the higher decrease observed in November compared to March and, to a lesser extent, January), while the highest relative recruitment values were those of January and March. Nevertheless, neither the absolute nor the relative recruitment values differed markedly between periods. This suggests that the final recruitment of *L. maritima* throughout its flowering season results from all these processes, and that it may not be explained exclusively by only one of them.

The results obtained in this study indicate that *L. maritima* plants have a huge potential constantly to recruit new individuals throughout almost the whole flowering season. However, this result should be interpreted carefully due to the significant year  $\times$  period interaction found for many of the biological processes monitored. Thus, contrast analyses have shown that ecological factors that cause within-year variability on some of these components in certain years, may have a much lower effect on the same components in other years. These significant interactions denote inconsistencies between years in the differential reproductive outcome of flowering at different times. On a population basis, this potential variability can be regarded as advantageous compared with other plant species with flowering seasons concentrated in a few months. Unpredictable rain and drought episodes in different periods of the year may have a disproportionate importance for the reproductive success of Mediterranean plant species. Plant species with concentrated flowering seasons can be more seriously affected by the effects of this environmental unpredictability than spe-

cies with extended flowering seasons. In *L. maritima*, the unusual persistence of the flowering season could perhaps be due to such between- and within-year variability, which could be regarded as a mechanism to buffer environmental stochasticity. Only further studies, using more precise integration methods of the different stages in the life cycle, e.g. population matrix models, can highlight the effect of this variation, not only on the components of reproductive success, but on the population dynamics as a whole.

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