Acta Oecologica 22 (2001) 209−217

S1146609X01011146/FLA

The flowering pattern of the perennial herb *Lobularia maritima*: an unusual case in the Mediterranean basin

F. Xavier Picó[a,b], Javier Retana[b]*

[a] Present address: Department of Ecology, University of Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands
[b] Unidad de Ecología y CREAF, Facultad de Ciencias, Universidad Autónoma de Barcelona, E-08193 Bellaterra (Barcelona), Spain

Received 29 September 2000; revised 19 August 2001; accepted 24 August 2001

Abstract – In plant communities of the Mediterranean Basin most plant species reach their blooming peak in spring and have characteristically short flowering periods of two-three months. The perennial herb *Lobularia maritima* represents an exception to these characteristics, because it flowers for almost 10 months, and has its flowering peak in autumn. In this five-year study, we describe the flowering pattern of *L. maritima* at the population and community levels. Despite the unusually extended flowering period of *L. maritima*, the species showed characteristic low among-year variability in the length of the flowering period but large interannual variation in the distribution of flowers throughout the flowering period. The flowering pattern (unimodal or bimodal) of *L. maritima* individuals differed among the five years, suggesting that *L. maritima* plants are plastic enough to tailor their flowering to variable environmental conditions. We conclude that flowering phenology of *L. maritima* represents a very particular case in the plant community studied, and the influence of abiotic and biotic factors on the phenology of this species is discussed. © 2001 Éditions scientifiques et médicales Elsevier SAS

extended flowering / Mediterranean climate / phenology

1. INTRODUCTION

The climate of the Mediterranean Basin, and to a large extent of all Mediterranean areas, is characterized by a pronounced seasonality. In the Mediterranean Basin, rainfall is concentrated in autumn and spring with a mild to severe drought in summer. Temperatures are usually mild in winter and at their highest in summer [1, 19, 21]). Reproductive cycles of plants, as well as those of animals interacting with them (pollinators, herbivores, seed predators or dispersers) are affected by these climatic variations [4, 6, 7]. Plant communities in the Mediterranean Basin show characteristic flowering phenologies especially when contrasted with tropical climate regions [15, 18]: 1) although some plant communities show uninterrupted flowering activity throughout the year [4, 12, 25], most species reach their blooming peak in spring, when temperatures are already warm, prior to limitations of summer drought [13, 19, 25]; 2) most plant species, even those that bloom in seasons other than spring, have characteristically short flowering periods of two-three months [4, 15, 19].

Nevertheless, some exceptions to this general pattern occur. Several Mediterranean shrubs flower during the transition between the wet and dry seasons [7, 12, 15, 18], and some deep-rooted perennials may flower in summer and autumn [4, 7, 13]. Examples of species with extended flowering periods are very rare [15]. *Lobularia maritima* (L.) Desv. (Brassicaceae) is a perennial herb occurring in the Mediterranean Basin, which represents an exception to both flowering characteristics mentioned above: it flowers for nearly 10 months (from September to late June), with the peak of the flowering period in autumn [4, 23]. In this five-year study, we describe and discuss the flowering patterns of *L. maritima* at the population and community levels. Our major goals are: (1) to identify the peculiarities of the flowering pattern of *L. maritima* in relation to other plant species in the community; (2) to analyse annual variability of flowering phenology in *L. maritima*; 3) to estimate within population differences in flowering phenology of *L. maritima*.

**Correspondence and reprints:* Fax: 34 - 93 581 13 12.
E-mail address: javier.retana@uab.es (J. Retana).

2. MATERIAL AND METHODS

2.1. Plant species and study area

Lobularia maritima (L.) Desv. (Brassicaceae) is a polycarpic and perennial herb, distributed throughout the Mediterranean basin, where it grows in coastal zones, dunes and scrublands [3]. The plant is a short-lived perennial with a lifespan of approximately three years. *L. maritima* plants form a basal rosette with prostrated-ascending flowering stems. Flowers are hermaphroditic and insect-pollinated [4, 11, 23], and present a high degree of self-compatibility (F.X. Picó and J. Retana unpublished data). *L. maritima* flowers are mostly visited by flies throughout the year, although beetles are also common in the months prior to summer (J. Retana and F.X. Picó unpublished data). Several biotic agents, basically in autumn, can have an important impact on *L. maritima* flower production and subsequent reproductive output. In particular, in autumn mycoplasm-like organisms (MLO) can infect plants, which die during the course of the flowering season. Also in autumn moth larvae (unidentified species) predate flowering stems of host plants but with no negative effects on plant survival (J. Retana and F.X. Picó unpublished data). Finally, ants of the genus *Messor* cause severe pre- and post-dispersal seed losses, mostly in autumn and late spring, when their activity peaks [23].

The study area is located at Collserola Park, a protected area just beside Barcelona (NE Spain; 41°24’N, 2°6’E), 280 m above sea level on an eastern slope facing the Mediterranean coastline. The climate is Mediterranean with a strong maritime influence. Mean monthly temperatures are at a maximum in August (23.3°C) and a minimum in January (7.8°C). Mean annual precipitation is 620 mm, with variable drought severity in summer. Climatic data were obtained from the Fabra Metereological Station, 2 km away from the study site.

The community studied is a savannah-like grassland (*Hyparrhenietum hirto-pubescentis*), a typical disturbed coastal community in the Mediterranean basin [10]. The vegetation of the site is the result of a fire that occurred 20 years ago in a *Pinus pinea* L. forest. The tree layer is composed of a few *P. pinea* trees that survived the fire. There are two shrub/herbaceous layers: the upper layer (1-2 m high) is composed of herbaceous (e.g. *Hyparrenia hirta* Pers., *Foeniculum vulgare* Mill.) and shrub species (e.g. *Cistus monspeliensis* L., *Spartium junceum* L., *Daphne gnidium* L.). The lower layer (15-50 cm high) is dominated by *Brachypodium retusum* L. and other herbaceous plant species such as *L. maritima*, *Sedum sediforme* (Jacq.) Pau and *Hirschfeldia incana* Moench.

2.2. Flowering phenology of the plant community

To quantify the flowering phenology of the different plant species in the community, a 100-m-long three-m-wide transect was laid across the study area. The number of pollination units (*sensu* [8]: inflorescences or groups of flowers than can be considered as a whole by pollinators) with open flowers of each plant species was counted every fifteen days uninterruptedly for five years, from September 1993 to August 1998. To measure the consistency of the community flowering phenology across years, the monthly number of plant species in bloom in the five years of study was compared with a G test.

We studied the 15 most common plant species recorded in the transect, which represented 71% of the total number of species found (15 out of 21), and 98.3% of the flowering units encountered. Using September 1 as day 1, five variables were used to characterise the flowering phenology of each of the 15 species studied: (1) the onset of the flowering period (i.e. the first flowering date; ONSET); (2) the centre of the flowering period (i.e. the date with the median number of pollination units recorded throughout the flowering season; CFP); (3) the length of the flowering period (i.e. the number of days between the first and the last flowering dates; LFP); (4) the position of the flowering peak or date with the maximum number of pollination units in the whole flowering period (i.e. the ratio between the number of days to reach the peak and LFP; PEAK); and (5) the maximum bloom (i.e. the maximum number of pollination units counted in a single census within the flowering season; MAX). The mean and the coefficient of variation (CV) for the five years were computed for each of these variables. A principal components analysis (PCA) was used to generate a reduced coordinate system that provided information about the phenological similarities among plant species.

2.3. Flowering patterns of *L. maritima*

The flowering patterns of individual *L. maritima* plants were studied during five flowering seasons, from 1993/94 to 1997/98 on a different number of *L. maritima* plants chosen at random (25, 26, 32, 71 and 26 plants, respectively). The high mortality rates of adult plants in summer due to drought forced us to add new plants every year of the study. As a result, only a small proportion of plants sampled during the five years of study (38 plants out of 180) were monitored over two consecutive years. Those individuals that survived summer drought were used to test the consistency of individual flowering pattern from year to year (see below). The number of flowering stems per plant was counted every fifteen days from early September to early July. Survival of tagged plants was also monitored in each census, and plants that died during the flowering season (0, 7, 8, 5 and 4, respectively, in each of the five seasons considered) were excluded from analyses.

Each *L. maritima* individual sampled was characterised according to two criteria. First, plants were classified into three size classes according to the number of flowering stems borne per plant. The number of flowering stems is a good estimator of plant size because it shows a high correlation with both plant diameter and plant volume (J. Retana and F.X. Picó, unpublished data). For convenience of analysis, three size categories were identified: small individuals, with a maximum of ten flowering stems, medium individuals, with ten to twenty-five flowering stems, and large individuals, with more than twenty-five flowering stems at any moment of their flowering period. Second, plants were also characterised according to the proportion of flowering stems produced per month. We differentiated plants with an unimodal pattern, when more than 60% of the total flowering stems were produced from September to December, and plants with a bimodal pattern, when more than 50% of the total flowering stems were produced in two flowering peaks, one in autumn and one in early spring. The consistency in the proportion of individuals of the different sizes, and in flowering patterns across the five years was evaluated using a G test.

To characterise the flowering phenology of *L. maritima*, circular statistics have been used. The proportion of flowering stems per month in each individual plant was treated as a circular frequency distribution with data grouped at 30° (30° = 1 month) intervals, with 1 September as the starting point. Two circular statistics, polar co-ordinates, were computed for each plant: (1) the mean angle a which, translated into days, represents the centre of the flowering period (CFP), and (2) r, which is a measure of concentration of the circular distribution. This statistic r varies from 0, when data are completely dispersed in all directions, to 1, when all the data are concentrated in one direction. Statistical tests are based on Zar [28]. Among-year variation of a and r was tested by the Kruskal-Wallis analysis of variance, and the Nemenyi test (see [28]) was used for pairwise comparisons.

To investigate whether the pattern of flowering stem production at the population level could be related to changes in weather conditions throughout the year, the relationships between monthly flowering stem production and temperature and precipitation monthly regimes were investigated. Three different 12×12 matrices were constructed. The elements of each matrix were the pairwise differences between months in monthly flowering stem production, mean monthly temperature and mean monthly precipitation. The matrices were named PHENOLOGY, TEMPERATURE, and PRECIPITATION, respectively. The correlation between the PHENOLOGY matrix and the other two matrices was estimated by computing the Mantel test with the MANTEL program of the R package [16].

3. RESULTS

3.1. Flowering phenology of the plant community

In all five years, there were plant species in bloom throughout the year, with a maximum in spring (*figure 1A*). The number of plant species in bloom each month showed no significant differences from year to year (G test, $p = 0.826$), indicating that the overall phenological pattern of the plant community was highly consistent among years. *L. maritima* largely outnumbered all other entomophilous species in the community in both absolute and relative abundance from October to March (*figures 1B and 1C*) None of the other plant species reached 5 pollination units m^{-2} at any time of the year, but a few reached values above 20% relative abundance in the months of the year when *L. maritima* bloom was lowest. Thus, two shrubs and one herbaceous species reached their maximum relative abundance in succession: *Cistus monspeliensis* in April, *Spartium junceum* in June, and *Sedum sediforme* in July. Another species, *Foeniculum vulgare*, showed the highest relative abundance in the community from July to September.

The flowering periods of the 15 plant species studied are represented in *figure 2*. The means and coefficients of variation of the different phenological variables for each of the species are given in *table I*. *L. maritima* was the first species to start flowering after the summer, while most species in the community started flowering in spring or early summer (*figure 2*). The centers of the flowering period (CFP) of most species were also concentrated in April and May, and only *L. maritima* and *Inula viscosa* had their CFP in autumn. Most species in the community flowered for 1 to 4 months. *L. maritima* was the plant species with the longest flowering period, with a mean of 242.8 days (*table II*), followed by *H. incana* (5 months). *L. maritima* also had by far the largest number of pollination units in a single census (MAX) (*table II*). *L. maritima* expressed the largest coefficient of variation (CV) for ONSET (*table II*), and intermediate to high CV for CFP and PEAK, indicating that there was large among-year variation in the distribution of *L. maritima* flowers over the flowering period. Conversely, *L. maritima* had a low CV value for LFP, confirming that this species expressed a similarly-long flowering period every year. *L. maritima* also showed low inter

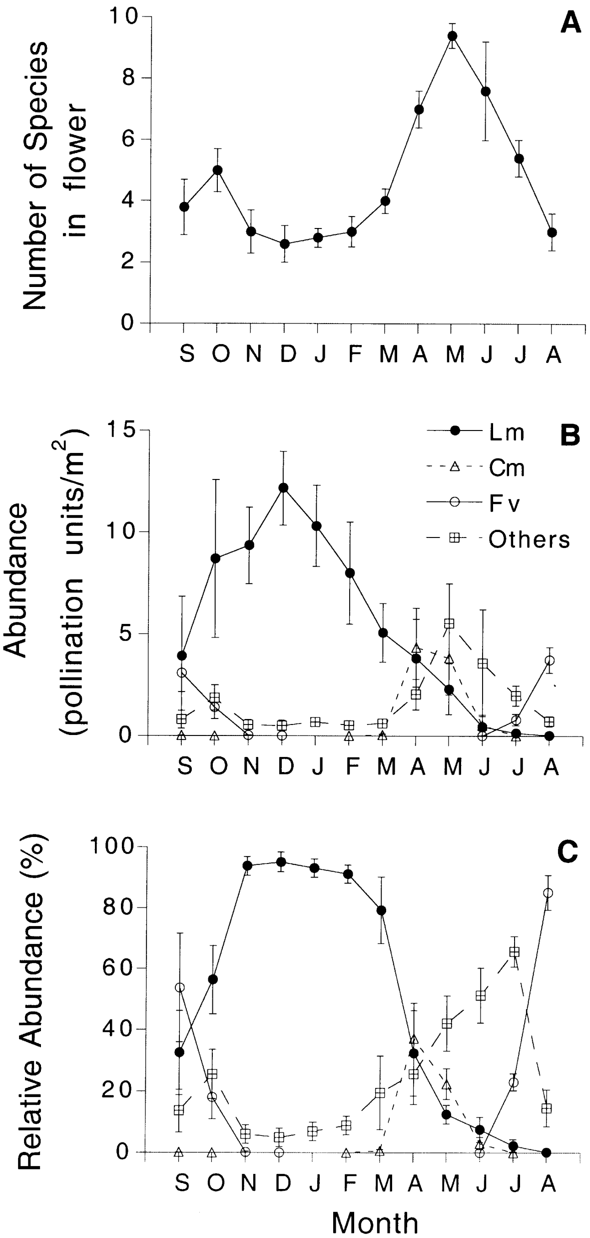

Figure 1. Mean (± SE) phenological features of the Collserola plant community: number of plant species in bloom per month **(A)**; abundance **(B)**, and relative abundance (in % of total pollination units) **(C)** of the most common plant species in the study area. Lm, *Lobularia maritima*; Cm, *Cistus monspelliensis*; Fv, *Foeniculum vulgare*; others, all other species. $N = 5$ years.

annual variation in MAX, compared to other plant species in the community.

By means of ordination and classification analysis, plant species were grouped first according to the means, and then according to the CVs of the five phenological variables studied. The first two axes obtained in the PCA for means accounted for 78% of the variance. Principal component I (54% of the variance) separated CFP and ONSET from LFP and MAX, that is, species with late ONSET and CFP were located on one side of the axis, while species with a long flowering season and high MAX values, mainly *L. maritima* due its unique phenological pattern, were located on the other side (*figure 3A*). The first two axes identified in the PCA for CVs explained 78% of the total variance. Principal component I accounted for 48% of the variance and was determined by CVs of ONSET, CFP and MAX. Principal component II accounted for 30% of the variance and was determined by the CV of LFP. In this case, *L. maritima* was also placed apart from the other plant species, except for *E. vulgare* and *H. incana* given their intermediate to high CVs for almost all variables considered, because its medium to high CV in CFP and PEAK, and low CV in LFP and MAX (*figure 3B*).

3.2. Flowering patterns of *L. maritima*

Mean circular statistics *a* (measuring central tendency) and *r* (measuring concentration) were obtained for each yearly flowering period (*table II*). The mean angle *a* varied significantly among years (Kruskal-Wallis ANOVA, $H = 11.9$, $p = 0.0017$), which indicates that there was interannual variation for the centre of the flowering period (CFP). Thus, mean CFPs, estimated by back-transforming the mean angles to dates, occurred on 30 December (1993/94), 19 December (1994/95), 9 December (1995/96 and 96/97), and 30 January (1997/98). The mean vector *r* also showed significant interannual variation (Kruskal-Wallis ANOVA, $H = 92.9$, $p < 0.0001$). Nevertheless, all *r* values were relatively close to 0, indicating that the mean angle was poorly defined, and that there was no clear mean direction. Thus, at a population level, *L. maritima* plants had flowering stems more or less regularly over the whole flowering season, although some individuals had their flowering peak in autumn (see below).

The size distribution of *L. maritima* plants showed significant variability from year to year (G test, $p < 0.0001$): the proportion of large individuals was high in 1993/94 and 1995/96, intermediate in 1994/95 and 96/97, and very low in 1997/98 (*table II*). There were also among-year differences in the proportion of individuals expressing unimodal and bimodal flowering patterns (G test, $p < 0.0001$). In 1997/98, most individuals expressed bimodal flowering patterns (*table II*). *Figure 4* illustrates the flowering phenology of the *L. maritima* individuals sampled in 1993/94. Individuals changed their flowering patterns from year

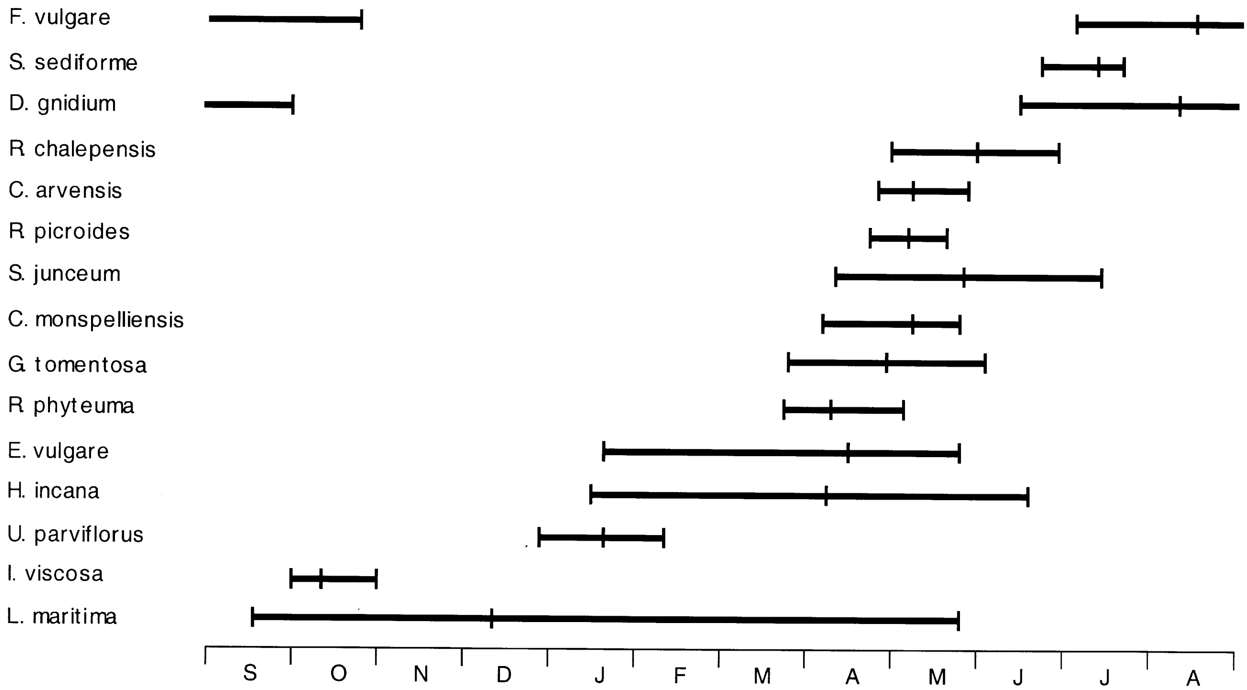

Figure 2. Flowering periods of the plant species studied. Vertical lines indicate the onset, blooming peak and end of each flowering period. Flowering periods represent an average for the years of study.

Table I. Means and coefficients of variation (CV) of the different phenological variables for each plant species. ONSET (first flowering date), CFP (center of the flowering period) and LFP (length of the flowering period) are measured in days from 1st September, PEAK (position of the flowering peak) is measured in %, and MAX (maximum bloom) is measured in number of flower units per square metre and per census.

	Mean					CV				
Plant species	ONSET	CFP	PEAK	LFP	MAX	ONSET	CFP	PEAK	LFP	MAX
Lobularia maritima (L.) Desv	20.4	106.4	35.6	242.8	23.1	79.8	18.3	51.7	17.1	38.2
Inula viscosa (L.) Ait.	33.6	43.3	36.2	27.6	3.0	21.0	16.6	53.0	2.9	39.6
Ulex parviflorus Pourr	118.0	139.7	31.2	45.6	0.4	18.5	9.3	101.4	73.8	98.1
Hirshfeldia incana Moench	138.6	221.6	48.8	148.0	4.2	64.2	25.8	70.4	44.8	71.2
Echium vulgare L.	139.2	227.0	58.7	118.0	2.6	77.7	28.0	41.0	86.5	117.3
Reseda phyteuma L.	205.2	217.7	25.8	37.8	1.1	9.0	4.6	60.5	81.8	58.6
Galactites tomentosa Moench	206.4	240.0	70.7	67.4	2.2	5.5	4.6	34.1	32.0	69.6
Cistus monspelliensis L.	214.2	231.4	50.3	47.4	14.8	3.5	3.6	34.4	18.9	52.3
Spartium junceum L.	221.8	259.0	48.1	88.2	5.1	7.1	3.0	19.2	16.6	41.4
Reichardia picroides (L.) Roth	231.8	243.2	53.4	21.4	1.0	4.0	4.0	63.0	52.8	74.0
Convolvulus arvensis L.	235.3	249.7	66.1	37.8	2.9	4.7	4.2	32.8	73.5	88.6
Ruta chalepensis L.	240.8	265.2	49.6	51.2	2.1	16.0	4.6	53.4	59.9	98.2
Daphne gnidium L.	288.7	339.7	38.5	110.2	0.9	5.1	3.7	29.6	51.9	52.8
Sedum sediforme (Jacq.) Pau	296.2	307.7	70.2	18.6	2.0	2.4	1.3	53.7	94.2	33.0
Foeniculum vulgare Mill.	309.6	352.0	49.2	110.4	6.7	1.6	1.3	25.6	9.0	28.7

Table II. Flowering features of the *Lobularia maritima* population in the five seasons considered. Circular statistics (*a*, mean angle, and *r*, parameter of concentration), and the percentages of individuals showing each size and each flowering pattern are given. Values of a and *r* sharing the same letter are not statistically different according to the Nemenyi test ($p = 0.05$). *N*, number of plants monitored. Only plants that survived during the flowering period of *L. maritima* were considered.

Year	*N*	Circular statistics				Plant size (%)			Flowering pattern (%)	
		a		*r*		small	medium	large	bimodal	unimodal
1993/94	25	121.2	c	0.020	a	4.0	8.0	88.0	36.0	64.0
1994/95	19	110.9	a	0.036	b	21.0	21.0	58.0	21.0	79.0
1995/96	24	100.9	b	0.020	a	8.3	16.7	75.0	29.2	70.8
1996/97	66	100.7	ab	0.009	c	18.2	30.3	51.5	30.3	69.7
1997/98	22	152.6	d	0.028	d	50.0	36.4	13.6	81.8	18.2

to year. Of 38 individuals sampled in two consecutive years, only 42.9% (12 out of 28) maintained the unimodal pattern and 40% (4 out of 10) maintained the bimodal pattern the following year.

Weather conditions were significantly related to the phenology of flowering stem production in *L. maritima* plants. In particular, temperature and flowering stem production were correlated in 1993/94 (Mantel standardised statistic between PHENOLOGY and TEMPERATURE was $r = 0.59$, $p = 0.0004$), 1994/95 ($r = 0.43$, $p = 0.0158$), and 1996/97 ($r = 0.81$, $p < 0.0001$), but not in 1996/97 and 1997/98 ($p > 0.10$). Precipitation and flowering stem production were also correlated in 1996/97 (Mantel standardised statistic between PHENOLOGY and PRECIPITATION was $r = 0.68$, $p = 0.0003$), but not in the other 4 years ($p > 0.20$ in all cases).

4. DISCUSSION

The crucifer *Lobularia maritima* is one of the most abundant species in the plant community studied, greatly out-numbering other entomophilous species from October to March in both absolute and relative abundance of flowers (*figure 1*). Although the flowering pattern in early successional communities, such as the one studied here, is expected to be very similar among species [22], the flowering pattern of *L. maritima* was unique in the community. The most striking feature was the long flowering period, in agreement with results of other studies [4, 11]. Unlike most species in the study area of Collserola and in other Mediterranean plant communities [4, 19], which restrict their blooming to spring time, *L. maritima* maintains flower production from September to late June. Moreover, only *L. maritima* and *I. viscosa* in Collserola started flowering and had the center of their flowering peaks in autumn (*figure 2*). As a result of

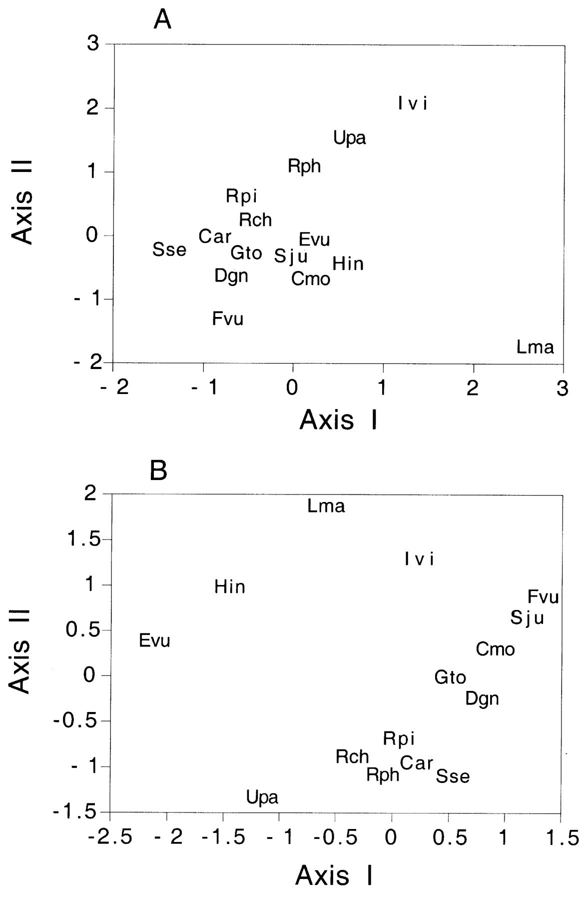

Figure 3. Representation of plant species of the plant community studied on the first two axes of the principal component analysis based on means **(A)**, and coefficients of variation **(B)** of the phenological variables considered. Abbreviations of plant species: Lma (*Lobularia maritima*), Ivi (*Inula viscosa*), Upa (*Ulex parviflorus*), Hin (*Hirshfeldia incana*), Evu (*Echium vulgare*), Rph (*Reseda phyteuma*), Gto (*Galactites tomentosa*), Cmo (*Cistus monspelliensis*), Sju (*Spartium junceum*), Rpi (*Reichardia picroides*), Car (*Convolvulus arvensis*), Rch (*Ruta chalepensis*), Dgn (*Daphne gnidium*), Sse (*Sedum sediforme*), Fvu (*Foeniculum vulgare*).

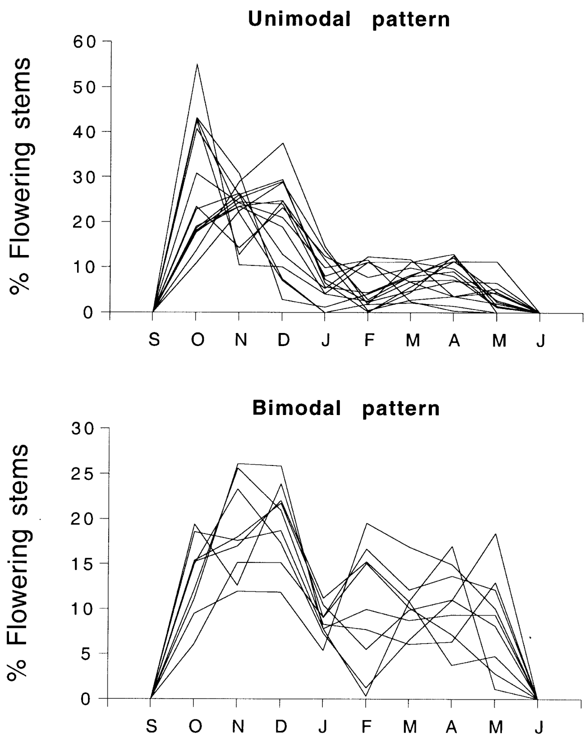

Figure 4. Flowering phenology of 25 *L. maritima* individuals monitored in 1993/94. Plants with unimodal (16 individuals), and bimodal (9 individuals) flowering patterns are shown separately. Data were standardised by defining the total number of flowering stems of each individual over the year as 100%. X-axis, month of the year. Y-axis, proportion of flowering stems per month.

these differences, *L. maritima* was clustered completely apart from all other plant species in the reduced coordinate system based on flowering phenology characteristics (*figure 3*).

L. maritima showed low among-year variability in the length of the flowering period, and the largest variability in the onset of the flowering period (*table II and figure 3*). It also showed medium to high variability in the center and the peak of its flowering period. That is, *L. maritima* showed large interannual variation in the distribution of flowers throughout its consistently long flowering period. These patterns of temporal variability might be season-dependent, while the consistency in the length of the extended flowering in *L. maritima* might be explained by the generally mild winters occurring in the Mediterranean basin that do not disrupt photosynthetic systems in evergreen plants [5, 9, 19]. Thus, *L. maritima* and other species starting to flower in autumn, such as *I. viscosa* in this study, have an extended period of time with adequate conditions for flower production. As a result, their flowering onset and peak vary depending on the environmental conditions of each particular year. Conversely, flowering time in species starting to bloom in spring is limited by an often severe summer drought, with high temperatures that cause evaporative stress to peak. For this reason, the onset and peak of spring-flowering plants are less variable (*table I*).

Flowering in *L. maritima* extends over much of the year because *L. maritima* individuals produce flowering stems more or less regularly over the whole flowering season (*figure 4*), not because different individuals flower at different times. Nevertheless, the flowering pattern showed large intrapopulation variation, both within and among years. At the population level, the proportion of individuals displaying unimodal or bimodal patterns differed among the five study years. It is well known that a wide variety of abiotic factors (and also biotic ones, see below), such as photoperiod, temperature or moisture, can interact in a complex way to determine flowering patterns in many plant species [24]. In the case of *L. maritima*, temperature was significantly correlated with flowering in three of the five years sampled, but we only found a significant relationship between flowering and precipitation in one of the five years of study. Other studies also find no significant correlation between flowering at the population level and the amount of monthly rainfall [17]. Some studies have reported significant genetic variability for flowering phenology [26, 27], but variation in flowering patterns in *L. maritima* is better attributed to phenotypic plasticity in response to environmental variation than to genotype: more than half of the *L. maritima* individuals monitored changed flowering patterns over consecutive years. The plasticity of flowering patterns in *L. maritima* is further evidenced by the pronounced intrapopulation variation in timing of flowering peak. Individual differences in flowering peak of the order of weeks, rather than days, have been reported for only a few plant species [20].

Although we discuss phenological patterns as being function of abiotic factors, there are other factors that might also affect reproduction and survival of *L. maritima* plants. According to Kochmer and Handel [14], phylogenetic constraints may be very important in determining community-level patterns of phenology because phylogenetic membership strongly influences a species' flowering time. Moreover, biotic factors (either pollination, disease, herbivory -including seed predation-, or seed dispersal) could be also important for explaining the differences in reproduction and growth of *L. maritima* plants in the different flowering periods of the year. Retana and Picó (in preparation) have observed that flowering time has a large impact on herbivory and disease in *L. maritima* : stalk and flower losses attributed to herbivores affect *L. maritima* plants in September and November, while disease by mycoplasm-like organisms occurs from September to January. There was also variation throughout the flowering period of *L. maritima* in the number and types of pollinators (Picó and Retana, unpublished data), and in pre- and post-dispersal seed losses, which are maximum in autumn and late spring when activity of granivorous ants peaks [23]. Thus, extended flowering of *L. maritima* might act as a mechanism to compensate for reproductive failure in some parts of the season. However, we have not enough information to conclude whether or not these biotic and abiotic factors, either individually or in interaction, have acted as selective forces to determine extended flowering in *L. maritima*.

The flowering phenology pattern of *L. maritima* represents a very particular case in the plant community studied and in Mediterranean environments in general. The characterization and comparison of the flowering phenology of *L. maritima* with that of other species of the same community has allowed us to highlight the particularity of this flowering pattern in the Mediterranean area. Bawa [2] lists some of the advantages of extended flowering patterns in tropical environments: better control of investment in flowers, increase in outcrossing fecundity rates, reduction in the level of geitonogamy, and decreased risk of reproductive failure. The question that arises is to know what are the advantages for plants with long flowering periods in environments completely different to tropical ones. In this sense, the existence of plant species with such unusually extended flowering periods in the Mediterranean is of great biological and ecological interest. Further studies focussing on (1) the possible advantages of extended flowering in Mediterranean environments, and (2) the factors that could influence selection for such extended flowering, are called for.

Acknowledgments. We are very grateful to Jordi Bosch, Xavier Sans and Carlos Herrera for their very helpful comments on an earlier draft of the manuscript, and to Jordi Bosch and Carles Castell for their help in field work. This research was supported by the Comissionat per a Universitats i Recerca de la Generalitat de Catalunya grant 1997FI-00854 to F.X. Picó.

REFERENCES

[1] Aschmann H., Distribution and peculiarity of Mediterranean ecosystems, in: di Castri F., Mooney H.A. (Eds.), Mediterranean-type Ecosystems. Origin and Structure, Springer-Verlag, Berlin, 1973, pp. 11–19.

[2] Bawa K.S., Patterns of flowering in tropical plants, in: Jones C.E., Little R.J. (Eds.), A handbook of experimental pollination ecology, Van Nostrand, New York, 1983, pp. 394–410.

[3] Bolós O. de, Vigo J., Masalles R., Ninot J.M., Flora dels Països Catalans, Editorial Barcino, Barcelona, 1993.

[4] Bosch J., Retana J., Cerdá X., Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community, Oecologia 109 (1997) 583–591.

[5] Castell C., Terradas J., Tenhunen J.D., Water relations, gas exchange, and growth of resprouts and mature plant shoots of *Arbutus unedo* L. and *Quercus ilex* L, Oecologia 98 (1994) 201–211.

[6] Cros S., Cerdá X., Retana J., Spatial and temporal variations in the activity patterns of Mediterranean ant communities, Ecoscience 4 (1997) 269–278.

[7] Dafni A., O'Toole C., Pollination syndromes in the Mediterranean: generalisations and peculiarities, in: Arianoutsou M., Groves R.H. (Eds.), Plant-Animal interactions in Mediterranean-type ecosystems, Kluwer Academic Publishers, The Netherlands, 1994, pp. 125–135.

[8] Faegri K., van der Pijl L., The principles of pollination ecology, Pergamon Press, Oxford, 1966.

[9] Fleck I., Díaz C., Pascual M., Iñiguez F.J., Ecophysiological differences between first-year resprouts after wildfire and unburned vegetation of *Arbutus unedo* and *Coriaria myrtifolia*, Acta Oecol. 16 (1995) 55–59.

[10] Folch R., La vegetació dels països catalans, Ketrés Editora, Barcelona, 1986, p. 541.

[11] Gómez J.M., Effectiveness of ants as pollinators of *Lobularia maritima*: effects on main sequential fitness components of the host plants, Oecologia 122 (2000) 90–97.

[12] Herrera J., Flowering and fruiting phenology in the coastal shrublands of Doñana, south Spain, Vegetatio 68 (1986) 91–98.

[13] Herrera C.M., Individual flowering time and maternal fecundity in a summer-flowering mediterranean shrub: making the right prediction for the wrong season, Acta Oecol. 13 (1992) 13–24.

[14] Kochmer J.P., Handel S.N., Constraints and competition in the evolution of flowering phenology, Ecol. Monogr. 56 (1986) 303–325.

[15] Kummerov J., Comparative phenology of Mediterranean type plant communities, in: Kruger F.J., Mitchell D.L., Jarvis J.U.M. (Eds.), Mediterranean plant ecosystems, Springer Verlag, Berlin, 1983, pp. 300–317.

[16] Legendre P., Vaudor A., The R package: multidimensional analysis, spatial analysis, Departement de sciences biologiques, Université de Montreal, Quebec, 1991.

[17] Marquis R.J., Phenological variation in the neotropical understory shrub *Piper arielanum*: causes and consequences, Ecology 69 (1988) 1552–1565.

[18] Mooney H.A., Parsons D.J., Structure and function of the California Chaparral – an example from San Dimas, in: di Castri F., Mooney H.A. (Eds.), Mediterranean-type Ecosystems. Origin and Structure, Springer-Verlag, Berlin, 1973, pp. 83–109.

[19] Mooney H.A., Parsons D.J., Kummerow J., Plant development in Mediterranean climates, in: Lieth H. (Ed.), Phenology and seasonality modelling, Springer-Verlag, Berlin, 267.

[20] Ollerton J., Lack A.J., Flowering phenology: an example of relaxation of natural selection, TREE 7 (1992) 274–276.

[21] Orshan G., Approaches to the definition on Mediterranean growth forms, in: Kruger F.J., Mitchell D.T., Jarvis J.U.M. (Eds.), Mediterranean-type Ecosystems. The role of nutrients, Springer-Verlag, Berlin, 1983, pp. 86–100.

[22] Parrish J.A.D., Bazzaz F.A., Difference in pollination niche relationships on early successional plant communities, Ecology 60 (1979) 597–610.

[23] Picó F.X., Retana J., Temporal variation in the female components of reproductive success over the extended flowering season of a Mediterranean perennial herb, Oikos 89 (2000) 485–492.

[24] Rathcke B., Lacey E., Phenological patterns of terrestrial plants, Annual Review of Ecology and Systematics 16 (1985) 179–214.

[25] Reader R.J., Comparison of the annual flowering schedules for Scottish heathland and mediterranean-type shrublands, Oikos 43 (1984) 1–8.

[26] Tarasjev A., Ecography 20 (1997) 48–54.

[27] Widén B., Environmental and genetic influences on phenology and plant size in a perennial herb, *Senecio integrifolius*, Can. J. Bot. 69 (1991) 209–217.

[28] Zar J.H., Biostatistical analysis, Prentice & Hall, Upper Saddle River, 1996.