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Flowering patterns of *Thymelaea velutina* at the extremes of an altitudinal gradient

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Abstract

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Environmental variability may cause changes in flowering phenology affecting plant reproductive success. Plasticity in phenological processes may guarantee species survival under new environmental conditions, such as those caused by global warming. Here we examined the flowering patterns of *Thymelaea velutina* (Thymelaeaceae), a dioecious shrub endemic to the Balearic Islands. We compared the two contrasting habitats where the species occurs: coastal dunes at sea level and mountain areas (c. 1200 m a.s.l.). We determined the relationship between three components of flowering phenology: initial date, flower duration, and synchrony, and assessed their association with traits describing plant size and fecundity. The increase in altitude results into a delayed flowering initiation and a shorter flowering period. In both habitats, male plants flowered earlier and for longer periods than females. At the mountain site, fruit set was associated to flower initiation, so that plants flowering earlier produced greater proportions of fruits. By contrast, fruit set at the dune site did not depend upon either flower initiation or flowering period; here, larger plants had longer flowering periods, though not necessarily produced more flowers and did not set more fruits than smaller plants. We attribute the differences in flowering patterns at different altitudes to phenotypic plasticity of the species; it is adapted to mountain conditions delaying the flowering period (probably adjusting it to the insect abundance at this altitude). Moreover, shortening of the flowering period may be also advantageous to reduce the stressful effects of higher temperature, radiation and drought that occur later in the summer.

Keywords: altitudinal variation, flowering phenology, reproductive success, Balearic Islands, Thymelaeaceae.

INTRODUCTION

Flowering time has been known for a long time to be a conservative trait, usually characteristic of a family or genus (Kochmer & Handel, 1986). Although it has a genetic component, environmental conditions can influence different flowering traits (Ollerton & Lack, 1998; Nikkanen, 2001; Ehrlén & Münzbergova, 2009) and many abiotic and biotic factors influence the optimal flowering phenology (Sola & Ehrlén, 2007 and references therein). In seasonal environments, such as the Mediterranean, flowering phenology must be such that climatic conditions are suitable for reproduction (Aizen, 2003; Bolmgren & Lönnberg, 2005). The most important climatic factors affecting phenological processes are temperature, precipitation and photoperiod (Arroyo, 1990a). Flowering patterns can be characterized by flowering start date (initiation), duration and synchrony, and climatic factors may influence flowering phenology in different ways. For example, rainfall variability has been shown to play an impor-

Resumen

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La variabilidad ambiental puede afectar a la fenología de la floración y al éxito reproductivo de la plantas, por tanto la plasticidad en los procesos fenológicos podría garantizar la supervivencia de las especies ante el cambio climático. En este estudio examinamos los patrones de floración de *Thymelaea velutina* (Thymelaeaceae), una especie dioica endémica de las Islas Baleares. Comparamos los dos ambientes en los que vive la especie: dunas costeras y áreas montañosas, aproximadamente a 1200 m de altitud. Estudiamos las relaciones entre el comienzo, la duración y la sincronía en la floración, con el tamaño y éxito reproductivo de las plantas. El incremento de altitud se tradujo en un retraso y disminución del periodo de floración. En ambas poblaciones, los individuos macho florecieron antes y durante más tiempo que las hembras. En las dunas, los individuos de mayor tamaño florecieron durante más tiempo, aunque ello no conllevó una mayor producción de flores o frutos. En la montaña, en cambio, la producción de frutos estuvo positivamente asociada al comienzo de la floración. Atribuimos las diferencias en los patrones de floración a distinta altitud a la plasticidad fenotípica de la especie; ésta se adapta a las condiciones de montaña retrasando el periodo de floración (probablemente ajustándolo a la abundancia de insectos a esta altitud) y también acortándolo, lo que probablemente reduce los efectos estresantes de mayor temperatura, radiación y sequía que tienen lugar más entrado el verano.

Palabras clave: variación altitudinal, fenología de la floración, éxito reproductivo, Islas Baleares, Thymelaeaceae.

tant role in the start and length of the flowering period in some species (Godoy & al., 2009). Climatic factors that vary over large temporal or spatial scales, as well as annual climate variability, can affect both plant phenology and growth. For example, in the Mediterranean basin, pronounced differences in olive flowering dates, for which long-term data are available, have been reported (Formaciari & al., 2000; Galán & al., 2005); such differences have been mainly attributed to differences in temperature, since a vernalization period is required prior to flowering (Hartmann & Whisler, 1975; Rallo & Martin, 1991). Orlandi & al. (2005) reported a delay of the flowering dates in Spanish olive groves compared to those found in Sicily attributing it to the more stable climatic conditions in the insular area. On the other hand, the decreasing temperature with altitude usually produces time delays from sowing to flowering and maturity (Silim & Omanga, 2001). In arctic-alpine plant species, phenology and growth appear to be related to snowmelt patterns (Walker & al., 1995). In some alpine and subalpine species, phenotypic plasticity allows the

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high altitude populations to compensate the short growing season by reproducing more quickly than those of lower altitude (Starr & al., 2000; Stinson, 2004). Moreover, in regions influenced by Mediterranean climate, plant reproduction time is constrained by summer drought (Giménez-Benavides, 2007). In addition, García-Camacho (2009) found in *Armeria caespitosa* (a high mountain early-flowering species) that individuals with longer flowering periods showed significantly lower seed set and higher number of unviable seeds, which suggests that plants ripening their seeds into the summer drought have lower reproductive success.

In the case of dioecious species, differences in flowering patterns between males and females plants have also been found; the usual pattern is that male plants flower earlier, produce more flowers (Guitián, 1995) and have a longer period of flowering than females (Bullock & Bawa, 1981; Kidyoo & Mckey, 2012).

Finally, changes observed in plant phenology along the last decades have evidenced that ecosystems respond to human-caused environmental changes (Parmesan & Yohe, 2003; Root & al., 2005). An earlier flowering and an extended growth period in species from the northern hemisphere have been interpreted as responses to global warming; however, a number of species have displayed phenological delays (Cleveland & al., 2006; Sherry & al., 2007).

In this work we investigate the flowering phenology of the dioecious shrub *Thymelaea velutina* (Poiret ex Camb.) Endl. at the two extremes of the altitudinal gradient where this species lives. Currently, there are not populations at intermediate elevations, though they might have possibly exist in the past (Alomar & al., 1997), probably before human arrival to the islands more than 4000 y.a. *T. velutina* presents a single annual bout of flower production like most angiosperms (McClure, 1966; Frankie & al., 1974; Rathcke & Lacey, 1985), and its phenological plasticity allows its presence in two contrasting habitats: coastal dunes at sea level and mountain sites up to 1200 m (Tébar & Llorens, 1992). Our main aim is to assess the effects of the phenological components on its reproductive success. Specifically, we want: (1) to test for differences between populations, years and sexes in flowering initiation, duration and synchrony, and (2) to assess a possible relationship among these flowering phenology components and traits describing plant size and fecundity. In addition, we (3) determine whether populations differ in flower traits like size and weight which might also be related to reproductive success.

MATERIAL AND METHODS

Study species

Thymelaea velutina is a perennial shrub endemic to the Balearic Islands, specifically Mallorca and Menorca (Western Mediterranean). In Menorca, with a lower altitude (the highest mountain is 356 m tall), most populations are found in the coast. By contrast, most coastal Mallorcan populations have disappeared due to habitat alteration (mainly urbanization; Alomar & al., 1997), although there are a few populations located at mountain sites, up to nearly 1250 m of altitude. Shrubs can reach up to 1 m height, with the largest individuals being found in dune habitats. The plants are mostly

dioecious, although a few individuals may bear both male and female flowers, and it is ambophilous, i.e., is pollinated by both insects and wind (de la Bandera & Traveset, 2006a). Its most important pollinators are dipterans, specifically *Sarcophaga* flies in the dunes and the hoverfly *Eristalix tenax* in the mountain (de la Bandera & Traveset, 2006a). Inflorescences are axillary capitula bearing three to five flowers. Male flowers are yellow, with eight orange stamens in two series, and they present a rudimentary ovary. Female flowers are greenish and the ovary is uniovulate. Flowers of both sexes produce small amounts of nectar (pers. obs.). The lifetime of a flower is three to four days. A detailed description of the species can be found in Pedrol (1997). *T. velutina* is heterocarpic, the same individual producing two types of fruits: (1) dry fruits (achenes) that are covered by the hypanthium and are dispersed by barochory, most remaining under the mother plant; and (2) fleshy fruits, oval, yellow and translucent drupes, which break the hypanthium when ripening and fall to the ground. Such fleshy fruits are often consumed by beetles and ants once they are dropped. The seed produced in both types of fruit is dark brown and has a pyriform shape. More details on the reproductive ecology of the species can be found in de la Bandera & Traveset (2006a, b).

Study site

The study was carried out in two localities representing the two types of habitat where the species occurs. The coastal dune locality is within S'Albufera Natural Park, near the town of Ca'n Picafort (UTM: 31S EE10). This is currently the main population of the species, which has recently disappeared from all sites in southern Mallorca (Alomar & al., 1997). Here, the population of *T. velutina* consists of several hundreds individuals, living on fixed dunes and coexisting with *Cistus salvifolius* L., *Erica multiflora* L., *Halimium halimifolium* (L.) Willk., *Rosmarinus officinalis* L. and *Teucrium dunnense* Sennen. Mean annual temperature and precipitation at this locality are 17°C and 628 mm, respectively (mean for 20 years; Guijarro, 1986). Sex ratio is 1 female: 1.5 males (N = 429). The mountain population is located at Puig Major, the highest peak of Mallorca (1,450 m), at Sa Coma de N'Arbona (UTM: 31S DE08, 1250 m), within a military area and thus relatively free from human disturbances although presumably the military might create a bit of disturbance from time to time. The predominant vegetation here consists of *Ampelodesmos mauritanica* (Poiret) T. Durand and Schinz, *Hypericum balearicum* L., *Teucrium marum* L. and *Rosmarinus officinalis* L. The population of *T. velutina* consists of less than 150 individuals and the sex ratio is 1 female: 1.6 males (N = 120). Mean annual temperature and precipitation are 9 °C and 1121 mm, respectively (Guijarro, 1986).

According to data from the National Institute of Meteorology, mean minimum temperature during the two years of the study, 2000 and 2001, were 11.2 and 11.6 °C, at Ca'n Picafort and 8.0 and 8.6°C, respectively, at Puig Major.

Study design

In each population, we randomly marked ten female and five males in 2000 and 18 females and 18 males in 2001. Three

branches with similar size and number of flowering buds were selected on each individual. Flowers were monitored every three to four days, recording the number of buds, open, and withered flowers on each branch. At the dune locality, such monitoring took place within the periods March 4- April 30, 2000, and February 6- April 22, 2001, whereas at the mountain site it took place between May 6- June 19, 2000 and May 8- June 13, 2001. Once the flowering period was over, we bagged all marked branches in female plants with a gauze that allowed the passage of light and air but no fruits. This was done to avoid losing fruits potentially removed by ants or dropped by the plant. During the whole fruiting period, we monitored plants weekly, recording the number of fruits in each visit.

In 2001, for each individual plant at each site, we measured size (height, maximum crown diameter and trunk diameter) and standing flower crop. In order to estimate the flower crop we counted the number of flowers of ten branches in each plant and multiplied the mean by the total number of flowered branches. The plants size was recorded only once since the growth of the species is very slow. Fruit set was calculated as the mean ratio: number of total fruits / number of total flowers in the three branches. We assessed a possible association between these parameters and the following components of flowering phenology: (1) initiation, (2) duration, and (3) synchrony. The last variable was defined as the degree to which plant flowering period overlapped with that of the rest of individuals in the population, following Augspurger (1983). The index of synchrony for an individual was thus:

$$X_i = \left(\frac{1}{n-1} \right) \left(\frac{1}{f_i} \right) \sum_{j=1}^n e_{j \neq i}$$

where e_j is the number of weeks that the plant i and j overlapped in their flowering; f_i is the total number of weeks that individual i was in flower, and n is the number of plants in the sample. Two synchrony indexes were calculated for each individual, one that considered the synchrony with males and another that considered synchrony with female plants.

In order to determine if flower traits differ between the two populations, we collected a total of 50 flowers of both, males and females (five from each of ten individuals of each sex) from each population. Fresh flowers were individually weighed with a precision balance (Salter model HX-100) to the nearest mg. From each flower we also measured the length and width of the corolla, and the length of different flower elements: the two stamens series, anther, pistil, and ovule.

Statistical analysis

Differences between years in the three phenological variables were tested by mean of one-way ANOVAs whereas those between populations and sexes were tested with a two-way ANOVA, using population and sex as fixed factors. Another two-way ANOVA was also employed to test for differences in flower weight between populations and sexes. As flower size and fruiting duration could not be normalized with any transformation, we compared these variables between populations and sexes by means of the Mann Whitney

U-test. Finally, a Pearson correlation analysis tested for an association between the three phenological parameters and plant size, flower production and fruit set. All statistical analyses were performed with SYSTAT (v. 12).

RESULTS

Flowering and fruiting phenology

Flowering took place approximately three months later at the mountain than at the coast, and this was consistent in time ($F_{1,85} = 39.01$, $P < 0.001$; $F_{1,87} = 0.480$, $P = 0.49$; Figs. 1, 2). In both populations, males started flowering significantly earlier than females ($F_{1,85} = 5.35$, $P = 0.023$; Table 1), and flowering duration was about four weeks longer in dunes than in the mountain, and in males than in females ($F_{1,86} = 92.01$ and $F_{1,86} = 10.80$, respectively; $P < 0.001$) (Table 1). There was no interaction between population and sex ($F_{1,86} = 0.02$, $P = 0.9$), indicating that differences in flowering duration between sexes were consistent in the two populations. Flowering duration did not differ significantly between the two study years either ($F_{1,88} = 2.23$, $P = 0.14$).

Regarding flowering synchrony, this was similar between populations ($F_{1,45} = 0.32$, $P = 0.58$) and years ($F_{1,45} = 1.12$, $P = 0.30$). The overlapping of (1) males with females, (2) females with males, and (3) males with males, was significantly higher in 2000 at the mountain site and in 2001 at the dune (Table 1). This result is reflected in the significant interaction population \times year in the three cases ($F_{1,37} = 6.45$, $P = 0.015$; $F_{1,45} = 14.83$ and $F_{1,37} = 16.96$, $P < 0.001$).

A significant association between crown diameter and flowering initiation was found ($r = -0.47$, $P = 0.03$), but only at the dune site in 2001. Moreover, at this site and year, larger plants also flowered for a longer period, although the correlation was not very high ($r = 0.57$, $P = 0.004$). By contrast, at the mountain site, plants that flowered early were not necessarily the larger ones but they tended to have a higher fruit set ($r = 0.67$, $P = 0.047$); flowering duration was also positively associated to flower crop in this population ($r = 0.54$, $P = 0.028$).

Fruit set was not correlated with flowering duration in either population or year (all $P \gg 0.05$), indicating that plants producing flowers for longer do not necessarily set more fruits per flower. Likewise, fruit set was not associated with flowering synchrony of female plants with males at either site ($r = 0.29$, $P = 0.12$; $r = 0.14$, $P = 1.00$, respectively), in spite of the latter being negatively associated with flower crop; at least at the mountain site, plants with low flower crops were found to be more synchronized than those with larger crops ($r = -0.51$, $P = 0.02$ and $r = -0.69$, $P < 0.001$, for males and females, respectively). However fruit set was not associated to any of variables variable describing either plant size or flower crop in either population.

Fruiting took place from April 30 to May 21 (2000) and April 1 to June 6 (2001) at the dune site, and from July 1 to July 13 (2000) and June 20 to July 6 (2001) at the mountain site. Although fruiting duration was longer in the former, differences were only significant in 2001 ($U = 240.00$, $P < 0.001$; Table 1). Female plants that flowered earlier also began their fruiting period earlier, but this was only observed at the dune site in 2001 ($r = 0.88$, $P < 0.001$).

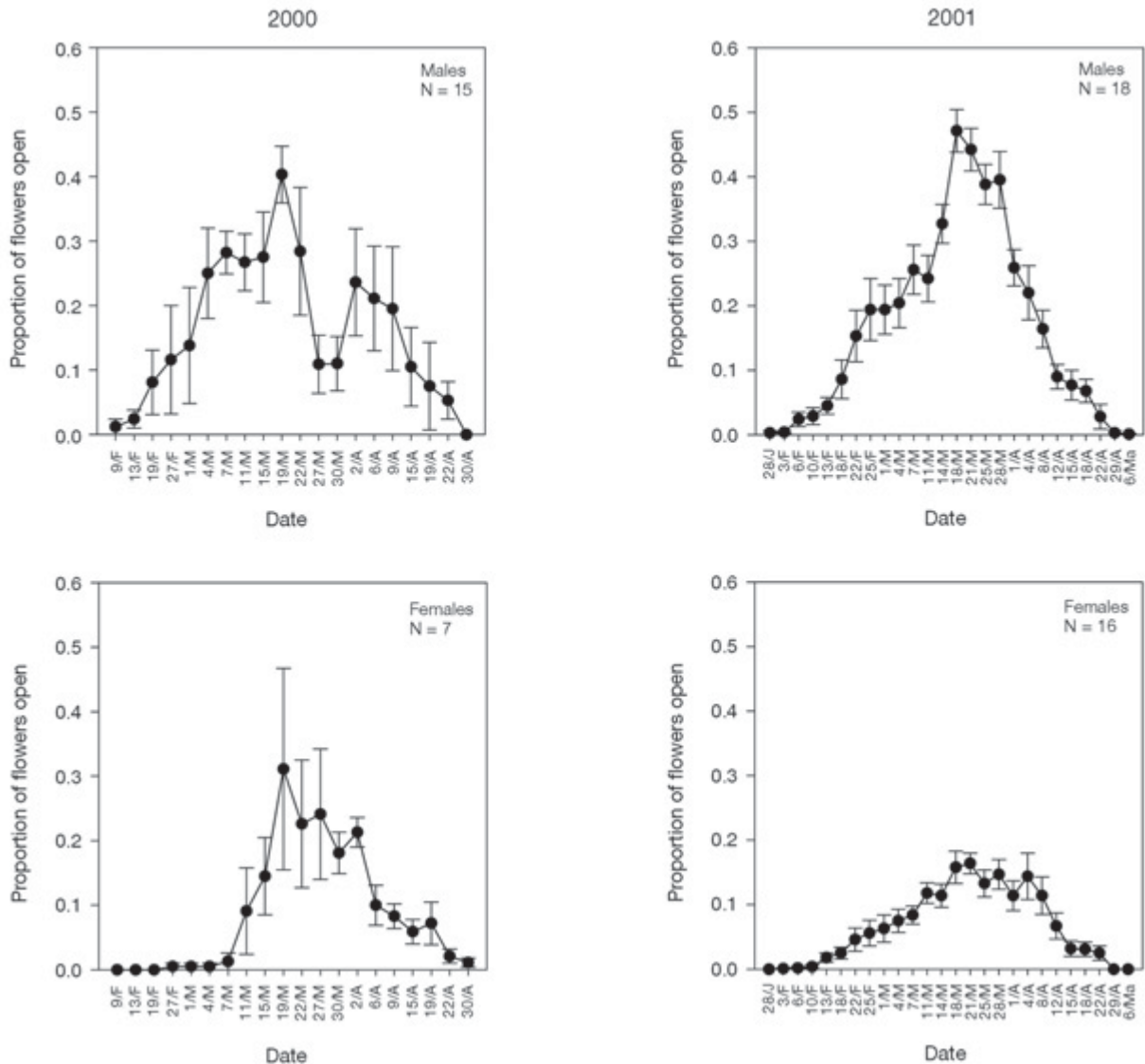


Fig. 1. Flowering phenology curve for males and females of *Thymelaea velutina* in dunes during 2000 and 2001. Proportion of flowers open was calculated for each plant and day, with respect to the total flowers produced by each individual during the flowering period. Abbreviations: J = January; F = February; M = March; A = April; Ma = May.

Floral traits

The corollas of male flowers were longer and wider than those of females in both populations ($U = 12.00$ and $U = 321.00$, respectively, $P < 0.001$). Overall, flower size was similar in the two populations, but male flowers from the dune were somewhat wider than those from the mountain (Table 2). However, stamens were significantly longer at the mountain site (Table 2). Female flowers had a similar size at both localities, but ovules were somewhat longer at the dune than at the mountain ($U = 1760.50$, $P < 0.001$; Table 2).

Flowers also had a similar fresh weight at both sites ($F_{1,196} = 0.001$, $P = 0.97$) but male flowers were heavier than females ($F_{1,196} = 200.70$, $P < 0.001$). Interestingly, a significant interaction population \times sex was found ($F_{1,196} = 10.54$, $P = 0.001$). Male flowers at the dune were heavier than at the mountain (5.57 ± 0.23 mg, $N = 50$ vs 4.97 ± 0.15 mg, $N = 50$, respectively), but the opposite occurred with females (3.20 ± 0.10 mg, $N = 50$ vs 3.50 ± 0.09 mg, $N = 50$, respectively).

DISCUSSION

Temperature differences between the two sites are the most likely cause for the later flowering period of *T. velutina* at the mountain site, which began about three months later than at sea level. A delay in flowering time with the increase in elevation seems to be frequent in species that can grow along altitudinal or latitudinal gradients (Silim & Omanga, 2001), and has been previously documented in Mediterranean shrublands (Arroyo, 1990 a,b,c; Giménez-Benavides & al., 2007). The delayed flowering in *T. velutina* in the mountain increases its reproductive success although it is lower than in the coastal dune, as flowering coincides with a greater abundance of insects at that altitude (de la Bandera & Traveset, 2006a). Moreover, the flowering delay in the mountain may also allow fruits to develop under optimal conditions to ripen (Bishop & Schemske, 1998 and references therein). Interestingly, the earliest flowering plants at the mountain site tended to show greater fruit set. This might be attributable, to a low-

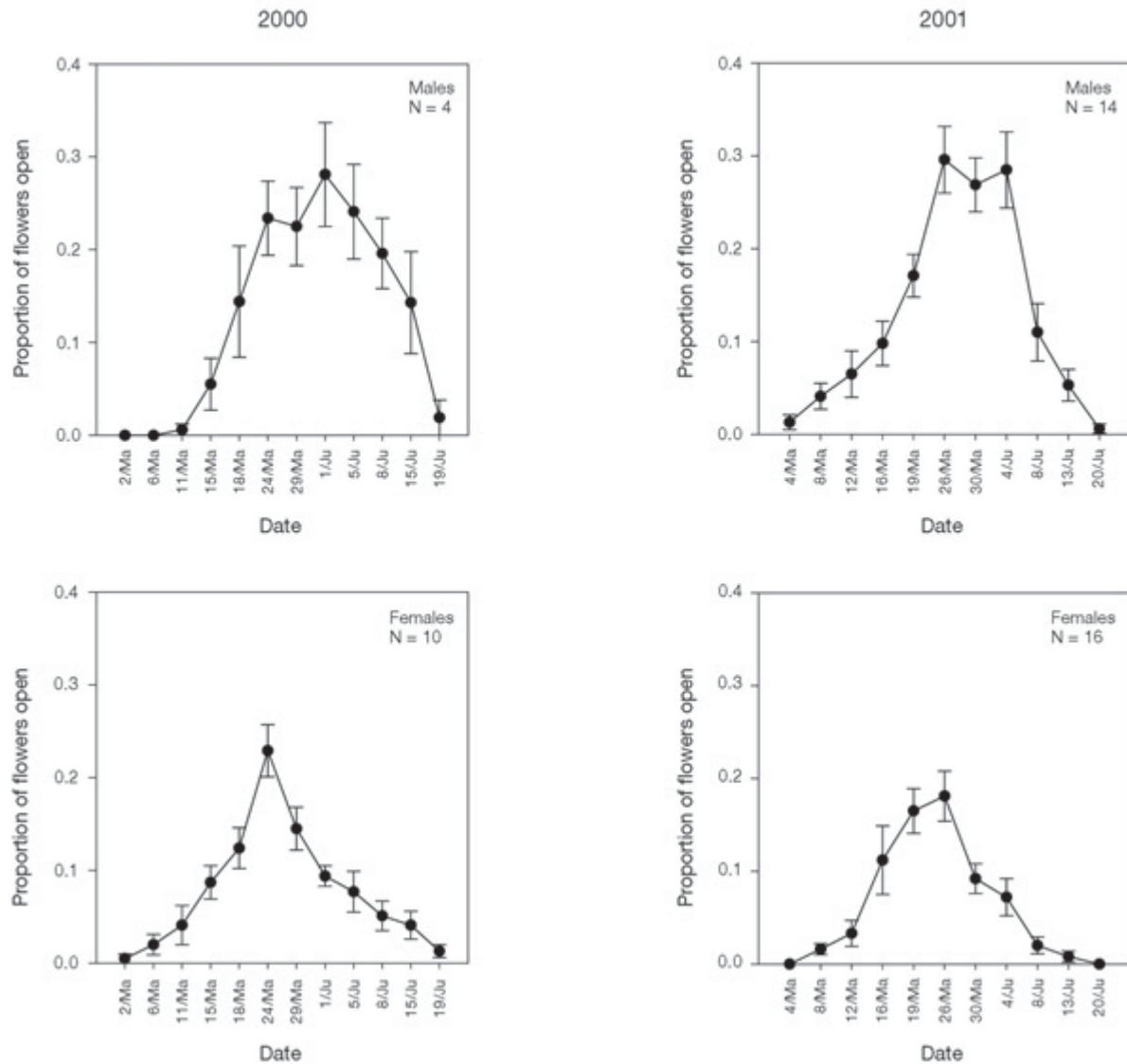


Fig. 2. Flowering phenology curve for males and females of *Thymelaea velutina* at the mountain site during 2000 and 2001. Proportion of flowers open was calculated for each plant and day, with respect to the total flowers produced by each individual during the flowering period. Abbreviations: Ma = May; Ju = June.

er intraspecific competition for insect pollinators due to the lower amount of plants flowering early in the season at those altitudes. One possible reason why such a correlation was not observed at the dune may be that the earliest plants at this site flowered in February-March, when insects are still rather scarce.

Plants at the mountain site showed a shorter flowering period than those at the dune site. This may be because the period of favourable conditions is also shorter in the former. However, a shorter flowering with altitude has not been observed in other species, and an extended flowering period at high altitudes has even been reported in some cases (Arroyo & al., 1981; Giménez-Benavides & al. 2007). Although overall fruit set was lower at the mountain site in a two-year study (de la Bandera & Traveset, 2006a), this does not seem to be due to the shorter flowering period, since we found no relationship between these two variables. Such lower fruit set in the mountain was not caused by a lower frequency of insect

visits to flowers either (de la Bandera & Traveset, 2006a). By contrast, it was most likely due to the low winter temperatures, with strong winds that promote stomata closure, and to the shallow, stony soil at this site which may cause a lower photosynthetic rate and, ultimately, a lower fruit set compared to plants at sea level, where the winter is milder (de la Bandera & al., 2008).

As predicted by the sexual selection hypothesis for the evolution of dioecy (Bawa, 1980; Willson, 1983), our results showed a longer flowering period in male plants of *T. velutina*. Thus, pollen availability during the entire flowering period of the females was guaranteed, and although male plants initiated flowering earlier, the high synchrony between sexes, also recorded in other dioecious plants (e.g., Guitián, 1995), probably increases species fitness as attraction of pollinators is enhanced (Gómez, 1993; Michalski & Durka, 2007). Contrary to the expected, we found no relationship between flowering duration and fruit set in *T. velutina* in either population. Like-

Table 1. Mean and standard error of flowering and fruiting parameters (in 2000 and 2001), plant size, and fecundity (in 2001) of *Thymelaea velutina* in the two populations. Numbers in parentheses indicate sample size.

| | | Dune | | Mountain | |
|------------------------|---|------------------|-------------------------|-------------------|------------------------|
| | | 2000 | 2001 | 2000 | 2001 |
| Flowering duration | + | 47.20 ± 8.31 (5) | 60.33 ± 2.56 (18) | 33.00 ± 1.15 (4) | 30.00 ± 1.93 (14) |
| | + | 36.71 ± 4.28 (7) | 51.63 ± 3.64 (16) | 29.00 ± 3.22 (10) | 23.75 ± 1.48 (16) |
| Male synchrony index | + | 0.77 ± 0.06 (5) | 0.87 ± 0.02 (18) | 0.94 ± 0.03 (4) | 0.78 ± 0.02 (14) |
| | + | 0.66 ± 0.12 (5) | 0.79 ± 0.02 (18) | 0.82 ± 0.01 (4) | 0.71 ± 0.03 (14) |
| Female synchrony index | + | 0.77 ± 0.02 (7) | 0.91 ± 0.01 (16) | 0.90 ± 0.04 (10) | 0.85 ± 0.02 (16) |
| | + | 0.76 ± 0.05 (7) | 0.83 ± 0.02 (16) | 0.80 ± 0.04 (10) | 0.81 ± 0.02 (16) |
| Fruiting duration | + | — | — | — | — |
| Height (cm) | + | 9.0 ± 2.0 (7) | 19.50 ± 2.53 (16) | 12.0 ± 0.0 (10) | 6.33 ± 1.51 (14) |
| | + | | 65.89 ± 3.28 (18) | | 27.14 ± 2.06 (14) |
| Crown Diameter (cm) | + | | 107.22 ± 8.19 (18) | | 73.29 ± 6.72 (14) |
| | + | | 72.50 ± 6.23 (16) | | 65.00 ± 5.90 (16) |
| Trunk Diameter (mm) | + | | 18.33 ± 1.27 (18) | | 14.00 ± 1.15 (14) |
| | + | | 18.50 ± 1.70 (16) | | 12.81 ± 1.66 (16) |
| Flower crop | + | | 6947.72 ± 1040.76 (18) | | 4787.86 ± 1040.09 (14) |
| | + | | 11651.44 ± 2873.63 (16) | | 3733.00 ± 558.09 (16) |
| Fruit set proportion | + | | — | | — |
| | + | | 0.47 ± 0.05 (16) | | 0.31 ± 0.22 (16) |

wise, there was no consistent association between phenological parameters and plant size or fecundity. A lack of correlation between flowering duration or flowering synchrony and reproductive success has also been reported in other species, e.g., *Hormatophylla spinosa*, *Lupinus lepidus* var. *lobbii*, and *Silene acutifolia* (Gómez, 1993; Bishop & Schemske, 1998; Buide & al., 2002). Plant size has been reported to affect flowering duration in some species: in *Ochrademus baccatus* large individuals can flower all year long whereas smaller individuals only do so in the most favourable season (Wolfe & Burns, 2001); in *Lotus corniculatus*, larger plants flowered earlier and also had a longer flowering period (Ollerton & Lack, 1998). However, the opposite, small plants flowering earlier than large ones, has also been reported in *Senecio integrifolius* (Widén, 1991). It is therefore not possible to generalize, especially since the corre-

lation between size and flowering time can also vary among years and populations (Ollerton & Lack, 1998).

The relevance of individual plant size-dependent phenology on female reproductive success and the relationship between flowering synchrony and fitness has been recently reported in *Erodium paularense* (Albert & al., 2008). However, in *T. velutina*, the relationship of flowering phenology components with plant size and reproductive success was inconsistent, what suggests that differences between populations in flowering patterns are probably due to phenotypic plasticity (Lande & Arnold, 1983; Mitchell-Olds & Shaw, 1987; Jump & Peñuelas, 2005).

Flowering duration determines the resource allocation to growth vs. reproductive output (Reekie & Bazzaz, 1987; Kozłowski, 1992; Molau, 1993). The costs of producing larger

Table 2. Mean and standard error of flower size in *Thymelaea velutina* in the two populations. Abbreviations: L = flower length (mm); W = flower width (mm); FSSL = first stamen serie length (mm); SSSL = second stamen serie length (mm); AL = anthera length (mm); GL = pistil length (mm) and OL = ovule length (mm). Numbers in parentheses indicate sample size. *** $P < 0.001$; ** $P < 0.01$.

| Sex | | Dune | Mountain | Mann Whitney U-test |
|------|---|------------------|------------------|---------------------|
| L | + | 2.84 ± 0.03 (50) | 2.93 ± 0.04 (45) | 885.00 ns |
| | + | 2.02 ± 0.03 (50) | 2.02 ± 0.03 (50) | 1212.50 ns |
| W | + | 2.01 ± 0.06 (50) | 1.83 ± 0.04 (45) | 1459.00 ** |
| | + | 1.44 ± 0.04 (50) | 1.49 ± 0.03 (50) | 1172.50 ns |
| FSSL | + | 2.04 ± 0.03 (50) | 2.18 ± 0.03 (45) | 592.00 *** |
| | + | — | — | — |
| SSSL | + | 1.57 ± 0.03 (50) | 1.72 ± 0.03 (45) | 659.50 *** |
| | + | — | — | — |
| AL | + | 0.44 ± 0.01 (50) | 0.43 ± 0.01 (45) | 1204.50 ns |
| | + | — | — | — |
| GL | + | — | — | — |
| | + | 1.10 ± 0.02 (50) | 1.06 ± 0.02 (50) | 1496.50 ns |
| OL | + | — | — | — |
| | + | 0.54 ± 0.01 (50) | 0.49 ± 0.01 (50) | 1760.50 *** |

and heavier flowers of male plants and for a longer period might be similar to the costs imposed by fruit production by females (Ehrlen, 1991). This might be the reason for the lack of differences in either size or growth rate between sexes (de la Bandera & Traveset, 2006a; de la Bandera & al., 2008). On the other hand, differences in flower size and weight have been reported in species living along an altitudinal gradient. Herrera (2005) reported an increase in the size of the flowers of *Rosmarinus officinalis* with altitude. In *Rhamnus lycioides*, however, Gulías & Traveset (2012) found the opposite pattern. In the case of *T. velutina*, wider and heavier flowers were found at the sea level locality but this occurred only in male flowers.

Towards the end of this century, the temperature of the planet is expected to increase between 2.5 and 5°C in the northern hemisphere, and reductions in water availability in many places are predicted (Jump & Peñuelas, 2005; Hobbs & al., 2006; Williams & Jackson, 2007). Plants from high latitudes and altitudes are especially sensitive to this global warming (Aerts & al., 2006). Different plant species have shown a tendency towards advanced phenophases (Arft & al., 1999; Dunne & al., 2003; Aerts & al., 2006). Moreover, insect phenology has shown a steeper advance than plant phenology in the last decades, especially in spring and summer (Gordo & Sanz, 2005). However, it is still hard to make generalizations, as the effect of global warming for one species at one location may be different from that elsewhere (Primack & al., 2009).

The increase in temperature might be expected to advance the flowering period of *T. velutina* at high altitude and result in a decoupling with its pollinators. Although it is an ambophilous species, the role of insects is very important for its pollination success, especially at the mountain site where fruit set is lower (de la Bandera & Traveset, 2006a). Thus, an earlier flowering might well affect plant reproductive success, as has been found in a number of studies (e.g., Dunne & al., 2003; Nickens, 2007). This could be especially important for the small-size populations (Bishop & Schemske, 1998). Additionally, the decrease in water availability that usually accompanies the temperature increase in the Mediterranean area suggests that plant growth could be limited by this resource (Peñuelas & al., 2004). Both parallel effects have therefore the potential to further limit the distribution of this endemic plant in the Balearic Islands.

In conclusion, the increase in altitude and the associated differences in temperature between populations result in a delayed flowering initiation and in a shorter flowering period of *Thymelaea velutina* at the mountain site. Such delay, in turn, increases its reproductive success, since flowering coincides with a greater abundance of insects in that altitude which results into a higher frequency of insect visitation to flowers. The higher probability of fruit set of early flowering female plants on the mountain is attributable to a lower competition for pollinators. Moreover, the relationship between flowering phenology components, plant size and reproductive success in *T. velutina* was inconsistent between populations and years, what suggests that differences between populations in flowering patterns are probably due to phenotypic plasticity, and that the environmental conditions are unlikely to exert any selective pressure on them.

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