

## Environmental Scales on the Reproduction of a Gypsophyte: A Hierarchical Approach

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- **Background and Aims** Environmental variability at several scales can determine plant reproductive success. The main goal of this work was to model the reproductive flexibility of a semi-arid specialist considering different scales of environmental variability.
- **Methods** A 2-year field study was performed on the determinants of the female reproductive success of *Helianthemum squamatum*, an Iberian gypsophyte, considering two scales of environmental variability: differences between two contrasting slope aspects; and, on individual scale, the neighbouring microenvironment. Generalized linear mixed models were used to evaluate simultaneously the potential effects of environmental variability at both scales, together with flowering phenology and plant size on the reproductive output of *H. squamatum*. The following reproductive response variables were considered: number of flowers, fruit-set, number of viable and aborted seeds per fruit, and number of seeds per plant.
- **Key Results** Contrary to expectations, environmental variability exerted a weak or even absent effect on the reproductive variables considered, while flowering phenology and plant size, which did not vary between slopes, played a major role. Surprisingly, the absolute reproductive variables were even higher in the extremely dry year of 2003, although only on the south-facing slope. The relatively milder conditions of the north-facing slope did not involve any advantage to this species in terms of reproductive output.
- **Conclusions** The species seemed to be considerably well adapted to the environmental unpredictability characteristic of Mediterranean systems, considering its ability to maintain reproduction across contrasting environments and contrasting climatic conditions. These findings make us face the question of what must be considered stressful conditions in the case of a stress-tolerant specialist.

**Key words:** *Helianthemum squamatum*, environmental variability, semi-arid, reproductive output, flowering phenology, gypsophyte.

### INTRODUCTION

Environmental heterogeneity has been successfully incorporated into ecological theory during the last two decades (Wiens, 2000). Environment-specific plant responses may involve not only phenological and vegetative characters but also reproductive one (Volis *et al.*, 2004). This implies that within the range of habitats occupied by a species some conditions will be more suitable for plant survival, growth and reproduction than others. Female reproductive success is determined by a wide variety of factors (Primack, 1987; e.g. plant size, onset of reproduction), which also vary among spatial scales. Consequently, environmental heterogeneity partially determines the female reproductive success of individual plants.

Most arid and semi-arid systems are highly variable at both spatial and temporal scales (Huenneke *et al.*, 2001). High levels of spatial heterogeneity are related to the existence of a patchy distribution of resources, whereas temporal heterogeneity is largely linked to high seasonality in the availability of resources (Goldberg and Novoplansky, 1997). Water is considered the most limiting factor for plant growth and reproduction in semi-arid environments, not only because of its scarcity but also because of its high variability in time and space (Sher *et al.*, 2004). This

feature is amplified under Mediterranean climates, where summer drought determines plant performance in multiple ways. Probably one of the most relevant sources of environmental variation in semi-arid Mediterranean systems is the slope aspect. North-facing slopes in the northern hemisphere receive lower solar radiation especially at the latitudes where Mediterranean systems occur. This effect results in lower evapotranspiration rates and lower daily maximal temperatures during summer water stress periods (Sternberg and Shoshany, 2001). These two contrasting scenarios (north versus south slopes) may affect the overall performance of plants developing in each of them. Specifically, they determine plant morphology and physiology which will be finally reflected in plant phenology, population dynamics and evolution (Linhart and Grant, 1996). Additionally, abiotic heterogeneity at smaller spatial scales may have a direct effect on female reproductive success, and control the direction and intensity of certain biotic interactions, such as plant–plant (Goldberg and Novoplansky, 1997; Armas and Pugnaire, 2005) or plant–animal interactions (Bronstein, 1994; Herrera, 1995, 1997; Zamora, 1999), which in turn may modulate the environmental control of reproduction. For instance, the presence of neighbouring plants may reduce thermal amplitude and decrease soil water evaporation (Domingo *et al.*, 1999; Armas and Pugnaire, 2005) and

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generate shade conditions which may protect understorey plants from photoinhibition (Moro *et al.*, 1997). The existence of neighbouring conspecifics may also represent an advantage as a source of pollen, in the case of xenogamous species, or by increasing pollinator visitation (Roll *et al.*, 1997). On the other hand, the negative effects of neighbours lie in inter- and intraspecific competition for resources.

The main objective of this work is to model the female reproductive success of a semi-arid soil specialist, considering different scales of environmental variability. Reproductive amplitude and adaptive potential are probably the most important mechanisms to face man-induced degradation of arid lands and pernicious consequences of rapid global warming. This is of special interest in the case of specialists, such as edaphic endemisms, for which the restriction to a specific substrate determines the species vulnerability to extreme climatic events, given that geographic migrations are not always feasible, especially when occurring in edaphic islands (Harrison *et al.*, 2006).

This paper reports the results of a 2-year field study on the determinants of the female reproductive success of *Helianthemum squamatum*, an Iberian semi-arid specialist restricted to gypsum soils. Hierarchical generalized linear mixed models (GLMMs) were used to analyse the potential effects of environmental variability, together with other predictors such as phenological traits and plant size, which are known to control reproductive success, and are also partially affected by the environment. The approach used leads to a rational separation of all these effects. Different scales of environmental variability were considered: (a) a landscape scale, that included the extremes of a spatial gradient of environmental conditions determined by two contrasting slope aspects (north- versus south-facing slopes) which control the local climate; and (b) a smaller scale, consisting of the characteristics of the local neighbourhood of individual plants, which may mitigate adverse conditions or exacerbate restrictions. The consideration of these microhabitat variables also allows the statistical assessment of the potential density-dependent processes. It was expected that slope aspect would exert a high control on reproduction, given the relatively milder conditions of north slopes in semi-arid central Spain, and that reproductive output would be modulated in a hierarchical process by smaller-scale spatial factors. The specific questions of this study are: (a) what are the main factors controlling the reproductive output of *H. squamatum*; (b) what is the relative importance of different scales of environmental variability? (c) do these factors and their relative importance vary between years?

## MATERIALS AND METHODS

### *Plant species and study area*

*Helianthemum squamatum* (L.) Dum. Cours (Cistaceae) is a small perennial sub-shrub (10–40 cm) that grows exclusively on gypsum soils in the semi-arid Mediterranean climate of the Iberian Peninsula. It is one of the most abundant gypsophytes in Spain and constitutes a

diagnostic species of Iberian gypsum vegetation (Rivas-Martínez and Costa, 1970). Flowers are hermaphroditic, yellow-coloured, and are arranged in dense inflorescences at the tip of new branches. Fruits are small multi-seeded capsules (3 mm in diameter) (López-González, 1993). Preliminary results reveal a certain ability of this species to self-fertilize, although it is found to be predominantly xenogamous (*pers. obs.*).

The study was carried out in a gypsum landscape located close to Chinchón (40°08'N 3°26'W, 673 m a.s.l.) 45 km south of Madrid, in Central Spain. The area has a Mediterranean semi-arid climate, with an annual average rainfall of 396 mm, with a severe summer drought, and a mean annual temperature of 14.1 °C (29-year climatic data record from the thermopluviometric station of Arganda, 40°19'N 3°26'W). The study period comprises two years, 2002 and 2003, which were noticeably different in terms of mean temperature and rainfall (Fig. 1). While 2002 conditions were similar to the long-term average climatic data (hereafter normal year), 2003 was characterized by a severe drought from April to July (dry year).

The study was performed at two sites with contrasting slope aspects (north and south) located within a distance of 250 m from each other, in order to minimize climatic and geological differences. Two plots in each site were established and 120 reproductive plants per plot were randomly selected. Plot dimensions varied in order to get the same number of plants per plot: 16 m<sup>2</sup> and 55 m<sup>2</sup> on the south-facing slope (170° and 175°, respectively), with a minimum distance of 6.30 m between them, and 55 m<sup>2</sup> and 108 m<sup>2</sup> on the north-facing slope (330° and 310°, respectively), with a minimum distance of 15.30 m. The south-facing slope was covered by a sparse patchy perennial shrubland where patches of genuine gypsophytes were interspersed in a bare matrix covered by a very rich biological gypsum crust (Martínez *et al.*, 2006). The north-facing slope was covered by a richer and denser shrub community, where together with some strict gypsophytes, calcicole plants or gypsovags were dominant. This site did not show a typical gypsum soil crust but a lichen layer dominated by *Cladonia convoluta*.

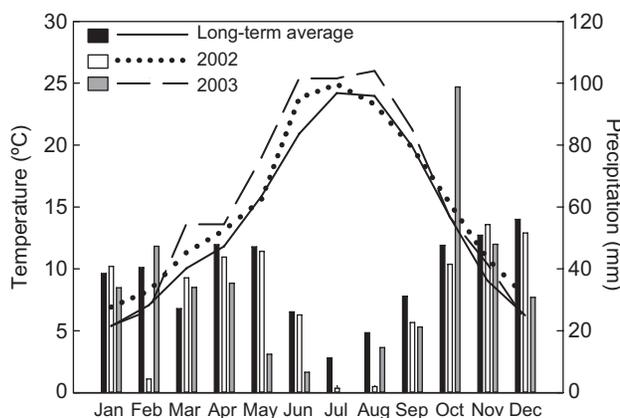


FIG. 1. Climatic conditions at the study site. Columns and lines represent monthly mean precipitation and mean temperature, respectively, during the period 1972–2001 and in the two years studied, 2002 and 2003.

### Census scheme

Selected plants were tagged in March 2002, before the flowering period. Maximum height and maximum diameter were measured in 2002 and 2003. Plant size was estimated as a function of these two measurements [ $h\pi(d/2)^2$ ].

The microhabitat characteristics were determined in 2002 by taking digital photographs of each tagged plant situated in the middle of a square frame of 50 cm × 50 cm. The criterion to select these dimensions was based on previous studies, describing demographic patterns of this species, its radical system, and the intensity and spatial scale of plant–plant interactions (Romão, 2003; Escudero *et al.*, 2005). Cover percentages of neighbour conspecifics and of other perennial plant species, and the distance to the nearest *H. squamatum* plant on the digital image were measured by using Corel Draw (version 10.4102000; Corel Corporation). Distance to the nearest *H. squamatum* plant was measured in the field when it was situated outside the frame.

The flowering phenology was monitored every 3–5 d throughout the flowering period (from the end of May until the beginning of July) during two consecutive years, 2002 and 2003. The number of inflorescences with at least one open flower at each census was counted.

The following phenological variables for each individual were calculated from flowering data: (a) flowering onset, as the number of days elapsed since the first of May to the appearance of the first flower in the plant; (b) flowering peak, as the number of days elapsed since the first of May to the day on which the maximum number of inflorescences with open flowers was reached; (c) flowering duration, as the number of days the plant remained in bloom; and (d) flowering synchrony, flowering overlap among individuals within each of the contrasting sites, calculated as follows (Albert *et al.*, 2001):

$$S_i = \frac{1}{n-1} \sum_{j=1}^n \frac{a_{ij}}{b_{ij}}$$

where  $n$  is the total number of plants studied,  $a_{ij}$  is the number of days on which both individuals  $i$  and  $j$  flower synchronously and  $b_{ij}$  is the number of days on which at least one of them ( $i$  and/or  $j$ ) is flowering. This index ranges from 0, no synchrony, to 1, complete flowering overlap.

The female reproductive success was estimated by considering absolute and relative reproductive variables. The former set included total number of flowers and total number of seeds per plant. Relative reproductive variables were fruit-set and mean number of seeds (viable and aborted) per fruit. The total number of inflorescences per plant was counted at the end of the fruiting period. Five inflorescences were harvested per plant and the number of fruits and withered flowers were counted in order to calculate the mean number of flowers and the mean number of fruits produced per inflorescence and per plant. This sample of inflorescences represented 17% of the

inflorescences produced in 2002 (in both slopes) and 8% and 12% in 2003, for the south and the north slopes, respectively (see Results), which is high enough to obtain accurate estimates. Total number of flowers and total number of fruits were estimated by multiplying these mean values by the total number of inflorescences. Fruit-set was the percentage of flowers setting fruits. The mean number of seeds per fruit was determined by taking a random sample of ten fruits per plant and counting the number of viable and aborted seeds. The total number of seeds per plant was calculated by multiplying the mean number of seeds per fruit by the total number of fruits per plant.

### Data analysis

The potential effect of the environmental variability at both scales (slope aspect and microhabitat characteristics), flowering phenology and plant size on the reproductive output of *H. squamatum* were evaluated by fitting generalized linear mixed models (GLMMs) via restricted maximum likelihood (REML). GLMMs provides a flexible way to model traits which do not satisfy the assumptions of a standard linear model, allowing the distinction between fixed and random factors in the model. Their use in this case is justified by the non-normal distribution of dependent variables under consideration and for the inclusion of random sources of variation (for further details of GLMMs, see Littell *et al.*, 1996). The models were performed with the SAS GLIMMIX macro (SAS Institute, Cary, NC, USA).

The data were analysed following a hierarchical approach, considering plants nested within plots and plots nested within slope aspects, as variance components (random factors), and slope aspect, nearest-neighbour distance, cover percentage of conspecifics, cover percentage of other perennials, flowering onset, flowering peak, flowering duration, flowering synchrony and plant size, as explanatory variables (fixed factors). Satterthwaite's method was used to approximate the degrees of freedom of the denominator.

Due to the low number of plants surviving up to the second year (see Results), the GLMMs were performed for each year separately. The following response variables were considered: total number of flowers per plant, assuming a gamma error distribution with a log link function, fruit-set, assuming a binomial error distribution with a logit link function, and number of viable seeds per fruit, number of aborted seeds per fruit, and number of seeds per plant assuming a Poisson error distribution with a log link function. The canonical link functions for the presumed error distribution of the data were selected in each analysis according to McCullagh and Nelder (1989). To test the differences between years a simpler GLMM was performed for each of the response variables, considering exclusively the variables year, slope aspect, the interaction between them and plant size as fixed factors, and the random factor plot as in previous analysis. The variable plant size was included in this case, in order to avoid bias due to differences in plant performance among individuals. In these models only the plants that survived and

flowered both years were taken into account. Also the same reduced models were built to explore the variability of the predictors considered in the previous analysis (microhabitat variables, phenological parameters and plant size) between the two contrasting slope aspects and between years. A Poisson error distribution with a log link function was assumed in all cases, except for flowering synchrony, which follows a binomial distribution. The DIFF option in the LSMEANS statement of the GLIMMIX procedure was used to identify specifically the levels of the factors where significant effects appeared.

## RESULTS

The plants that died in 2002 before flowering were discarded, so 465 plants were monitored in the first year. Survival rate in 2003 was around 50% (45% on the south

slope, 51% on the north one). Consequently, the data set for the second year comprised 220 plants, a number high enough for our modelling purpose. Mortality was not size-dependent, although this result is not shown here (unpubl. res.).

Percentages of plants that flowered in 2002 and 2003 were, respectively, 90.91% (south, 95.3%; north, 86.52%) and 98.7% (south, 100%; north, 97.4%), with a mean fruit-set of 64.4% (Fig. 2D). The average number of fruits per plant ( $\pm$  s.e.) for 2002 and 2003 were, respectively,  $238.7 \pm 32.5$  and  $205.0 \pm 25.8$  on the south slope, and  $221.1 \pm 30.4$  and  $326.4 \pm 75.7$  on the north slope. Nearly all of the dissected fruits also yielded at least one potentially viable seed (percentages for 2002 and 2003, 99.1% and 98.6%, respectively).

Flowering of *H. squamatum* during the study period extended from the end of May until the beginning of July,

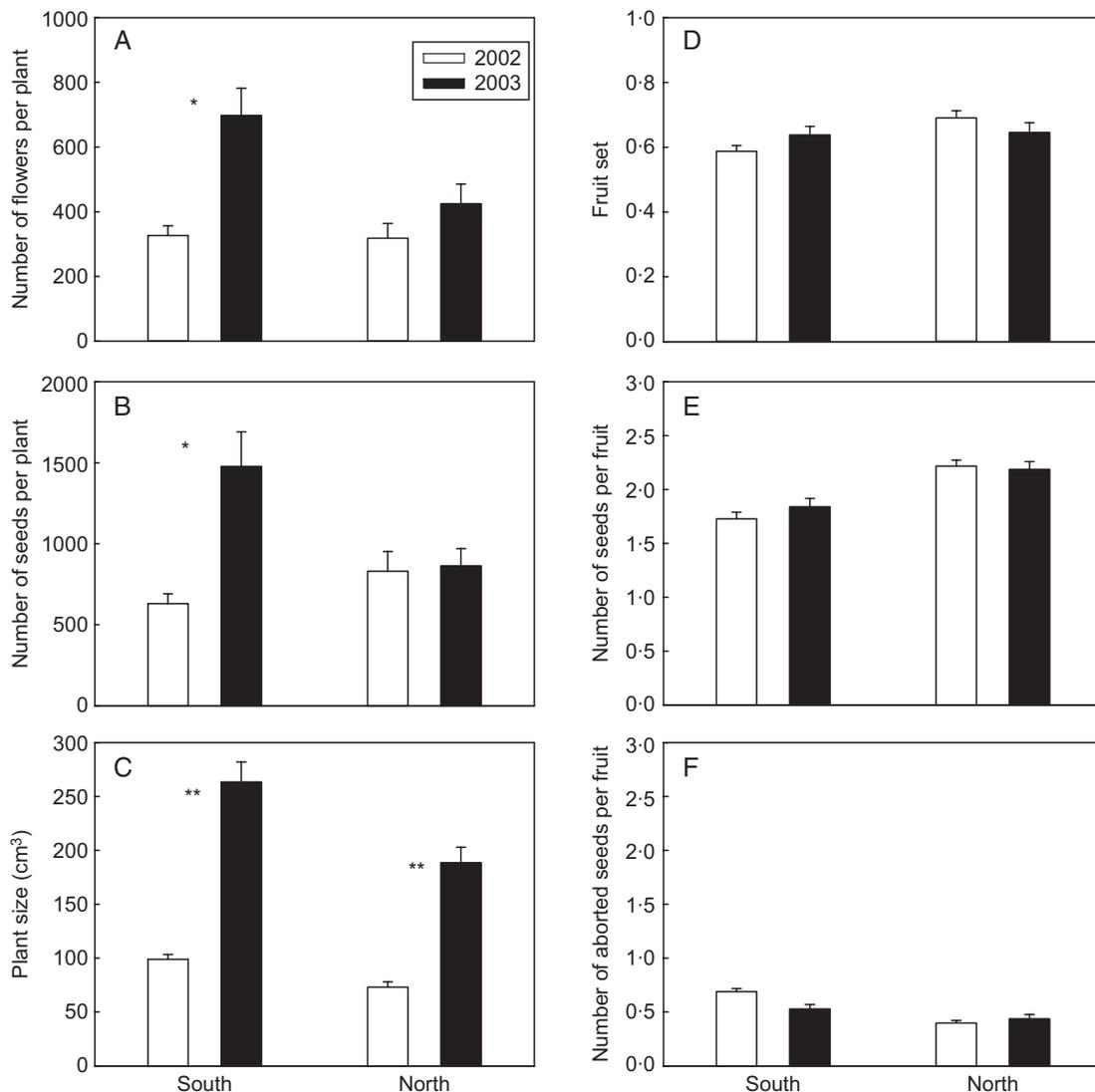


FIG. 2. Annual variation in (A) total number of flowers per plant, (B) total number of seeds per plant, (C) plant size, (D) fruit-set, (E) number of viable seeds and (F) aborted seeds per fruit, for the south- and north-facing slopes. Columns represent mean values and vertical lines the s.e. Asterisks indicate significant differences between years (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ).

reaching the peak of flower production around mid-June (Fig. 3). There were almost no significant differences in the phenological traits studied between the two contrasting slope aspects, although plants on the south-facing slope bloomed earlier ( $F = 48.46$ ,  $P = 0.0023$ ) and were more synchronous ( $F = 9.36$ ,  $P = 0.0379$ ) compared with those of the north-facing slope, but only in 2002.

Average cover percentages of *H. squamatum* plants and of other surrounding perennials were, respectively,  $6.74 \pm 0.38$  and  $7.13 \pm 0.60$  on the south-facing slope and  $3.56 \pm 0.25$  and  $12.15 \pm 0.68$  on the north-facing slope. No significant differences were detected for microhabitat characteristics between the contrasting slopes or for plant size (Fig. 2C).

Results of the GLMMs for every response variable are summarized in Table 1. No significant effect of the slope aspect was found on the reproductive variables studied, whereas some effect of the microhabitat variables occurred. Cover percentage of neighbouring conspecifics had a positive effect on the total number of seeds per plant in both years, while the cover percentage of other neighbouring perennials negatively affected flower production and total seeds per plant in 2003.

Reproduction was strongly affected by flowering phenology. Flowering peak had a significant effect on fruit-set and seed production (both per fruit and per plant) in 2002. Plants that reached the peak of flowering earlier achieved higher rates of fruit-set and produced more seeds per plant and more viable seeds per fruit, while plants that delayed the flowering peak experienced relatively higher levels of intrafruit seed abortion (Fig. 4; 2002). Flowering duration was positively related to number of flowers and total seeds per plant. Finally, flowering synchrony was positively related to the amount of flowers produced, and also

favoured fruit-set, total seed production per plant and viable seeds per fruit.

Plant size positively affected absolute reproductive variables, number of flowers and number of seeds per plant, in both years, and additionally viable seeds per fruit in 2002.

No significant effect of the random factor 'plot' on the reproductive variables was found, while the 'plant' factor always had a significant effect.

Most phenological variables and plant size varied significantly from one year to the next. Flowering peak shifted significantly towards earlier dates in both slopes in the dry year of 2003 compared with the previous year (south,  $F = 70.49$ ,  $P = 0.0011$ ; north,  $F = 83.52$ ,  $P = 0.0008$ ), while flowering onset happened significantly earlier only on the northern slope ( $F = 37.10$ ,  $P = 0.0037$ ). Moreover, the flowering period got significantly shorter in 2003, but only on the southern slope ( $F = 30.42$ ,  $P = 0.0054$ ; Fig. 3). Flowering synchrony within-sites was also significantly higher in 2003 on both slopes (mean  $\pm$  s.e.; south,  $0.62 \pm 0.01$  and  $0.70 \pm 0.01$ , for 2002 and 2003, respectively,  $F = 26.51$ ,  $P = 0.0068$ ; north,  $0.46 \pm 0.01$  and  $0.59 \pm 0.01$ , for 2002 and 2003, respectively,  $F = 50.32$ ,  $P = 0.0021$ ). In addition, average plant size significantly increased from 2002 to 2003 on both slopes (south,  $F = 81.39$ ,  $P = 0.0009$ ; north,  $F = 100.37$ ,  $P = 0.0006$ ; Fig. 2C).

Absolute reproductive variables differed significantly between years, but only on the south-facing slope. Total flower production and total seed production per plant in 2003 doubled those of 2002 (see Fig. 2A, B).

## DISCUSSION

Contrary to our expectations, *H. squamatum*'s reproduction was not controlled by the landscape scale of environmental variability. Following a well-established criterion related to the availability of water in Mediterranean habitats during the limiting summer drought (Kutiel, 1992; Sternberg and Shoshany, 2001; Bellot *et al.*, 2004), the south-facing slope was expected to be the more stressful habitat in the present study. As a part of another study, significant differences were found in soil water content between the two slopes, at least during the 2004 reproductive season, a relatively wet year (unpubl. res.). Therefore, a better plant performance was expected and consequently a higher reproductive output in north-facing slope plants. However, slope aspect was not a significant predictor for any reproductive variable. Furthermore, neither flowering phenology nor plant size were affected by the slope aspect. This suggests that the individual variability in reproduction cannot be explained by phenological or plant size-related processes mediated by environmental differences. Furthermore, individual variability in reproduction was the most important source of variation in all the models (plant factor; Table 1). This great individual variability, under a wide range of selection pressures due to the heterogeneity of the environment, could determine the high reproductive amplitude of this species and help to explain the existence of a similar reproductive output throughout the contrasting scenarios considered. Such

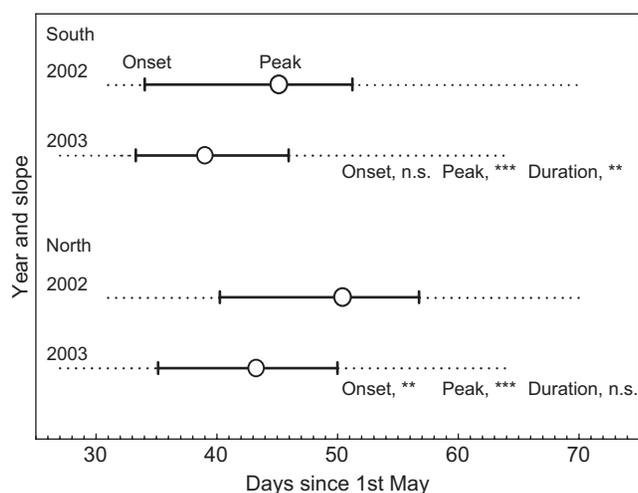


FIG. 3. Flowering period of *H. squamatum* on the south- and north-facing slopes in 2002 and 2003. Dotted lines represent the absolute flowering duration (first and last time at which at least one open flower was observed), while bold lines represent the average duration in each slope. Average flowering onset and flowering peak (circles) are represented on the bold lines. Significant differences between years (within each slope) in the average values of flowering onset, peak and duration are given from right to left (\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ ).

TABLE 1. Generalized linear mixed models for the reproductive response variables in each study year (2002 and 2003): total flower production, fruit-set, number of viable and aborted seeds per fruit, and total seeds per plant

	Flowers		Fruit-set		Viable seeds per fruit		Aborted seeds per fruit		Total seeds per plant	
	2002	2003	2002	2003	2002	2003	2002	2003	2002	2003
<i>Fixed factors</i>										
Slope aspect	-8.08 <sub>1,1-19</sub>	+0.07 <sub>1,1-32</sub>	-5.14 <sub>1,1-93</sub>	-0.53 <sub>1,1-95</sub>	-27.64 <sub>1,1-48</sub>	-1.10 <sub>1,1-92</sub>	+16.42 <sub>1,1-98</sub>	+0.49 <sub>1,1-87</sub>	-4.05 <sub>1,2-08</sub>	+1.05 <sub>1,1-28</sub>
Nearest H.s	+0.20 <sub>1,413</sub>	+2.48 <sub>1,210</sub>	+0.00 <sub>1,411</sub>	-2.18 <sub>1,209</sub>	-3.44 <sub>1,386</sub>	+0.72 <sub>1,197</sub>	+1.03 <sub>1,385</sub>	-0.01 <sub>1,198</sub>	+2.40 <sub>1,389</sub>	+0.38 <sub>1,197</sub>
Cover H.s	+0.56 <sub>1,369</sub>	+1.43 <sub>1,65-7</sub>	+2.99 <sub>1,405</sub>	-0.00 <sub>1,197</sub>	-1.38 <sub>1,236</sub>	+0.81 <sub>1,195</sub>	+0.00 <sub>1,266</sub>	-0.20 <sub>1,178</sub>	+41.18 <sub>1,388</sub> ***	+5.07 <sub>1,20-4</sub> *
Cover perennials	-2.49 <sub>1,392</sub>	-6.51 <sub>1,198</sub> *	+1.30 <sub>1,409</sub>	-0.65 <sub>1,210</sub>	-0.00 <sub>1,329</sub>	-0.34 <sub>1,195</sub>	-1.16 <sub>1,291</sub>	+1.39 <sub>1,199</sub>	-0.00 <sub>1,388</sub>	-5.08 <sub>1,197</sub> *
Flowering onset	-0.15 <sub>1,412</sub>	-3.39 <sub>1,210</sub>	-2.65 <sub>1,411</sub>	-0.02 <sub>1,209</sub>	-3.54 <sub>1,387</sub>	-1.24 <sub>1,198</sub>	+2.42 <sub>1,387</sub>	+0.53 <sub>1,199</sub>	-3.51 <sub>1,388</sub>	+0.02 <sub>1,190</sub>
Flowering peak	-3.75 <sub>1,413</sub>	-1.32 <sub>1,210</sub>	-14.91 <sub>1,411</sub> ***	-0.14 <sub>1,209</sub>	-20.99 <sub>1,381</sub> ***	-1.45 <sub>1,197</sub>	+4.25 <sub>1,383</sub> *	+2.33 <sub>1,198</sub>	-7.20 <sub>1,388</sub> **	+0.85 <sub>1,190</sub>
Flowering duration	+25.54 <sub>1,402</sub> ***	+31.06 <sub>1,182</sub> ***	+2.31 <sub>1,412</sub>	+0.81 <sub>1,210</sub>	+0.75 <sub>1,305</sub>	-0.25 <sub>1,199</sub>	+0.07 <sub>1,364</sub>	-0.12 <sub>1,198</sub>	+19.40 <sub>1,389</sub> ***	+19.43 <sub>1,51-7</sub> ***
Synchrony	+89.49 <sub>1,343</sub> ***	+9.82 <sub>1,210</sub> *	+14.49 <sub>1,400</sub> ***	+12.44 <sub>1,209</sub> ***	+6.28 <sub>1,156</sub> *	+2.75 <sub>1,197</sub>	-0.17 <sub>1,216</sub>	-0.01 <sub>1,197</sub>	+18.75 <sub>1,381</sub> ***	+14.10 <sub>1,190</sub> ***
Plant size	+200.57 <sub>1,412</sub> ***	+122.91 <sub>1,210</sub> ***	+1.29 <sub>1,410</sub>	+2.57 <sub>1,208</sub>	+6.48 <sub>1,387</sub> *	+0.14 <sub>1,197</sub>	+3.64 <sub>1,386</sub>	+0.49 <sub>1,198</sub>	+44.48 <sub>1,389</sub> ***	+132.94 <sub>1,190</sub> ***
<i>Random factors</i>										
Plot	0.81	0.56	0.91	0.90	0.57	0.93	0.69	0.85	0.92	0.05
Residual (plant)	14.33***	10.18***	14.32***	10.20***	13.86***	9.92***	13.88***	9.92***	13.91***	9.94***
Number of cases	423	220	422	220	397	209	397	209	397	209

Data represent the Wald-type  $F$ -statistic (Wald  $Z$ -statistic for random factors) with the degrees of freedom given in subscript, and the sign (+ or -) indicating the direction of the effects.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

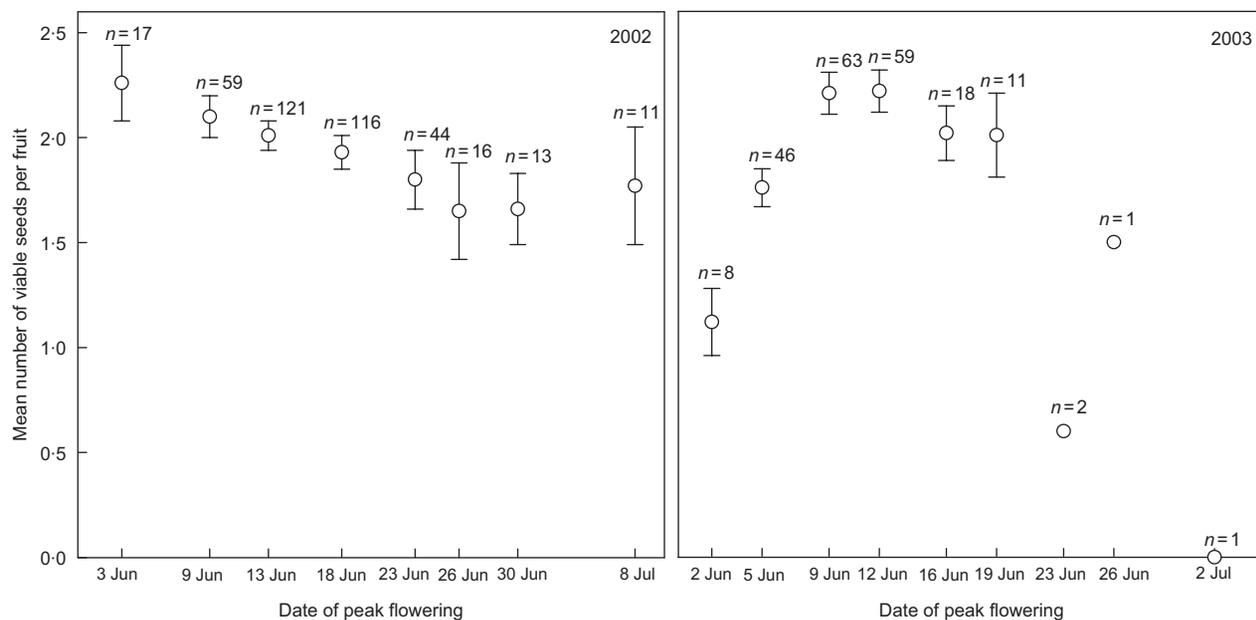


FIG. 4. Number of viable seeds per fruit produced by the plants in relation to the timing of their flowering peak in 2002 and 2003. Data points represent the mean  $\pm$  s.e., considering all the plants ( $n$ ) that reach the peak of flowering on a given date.

extremely variable responses at the individual level must be especially important in Mediterranean habitats, where environmental factors are inherently variable (Blondel and Aronson, 1999).

Small-scale environmental variation, such as soil properties immediately beneath individuals or plant cover, can determine substantially the dynamics of plant interactions in semi-arid environments (Schenk *et al.*, 2003; Armas and Puignaire, 2005), where facilitative and competitive interactions are thought to be of great importance (Whitford, 2002). In this study, the individual scale of environmental variability had only a weak effect on the reproduction of *H. squamatum*. For instance, the presence of other non-conspecific neighbouring perennials appeared to negatively affect flower and seed production per plant in the dry year of 2003. This may be interpreted as a shift towards stronger interspecific competition in response to the harsher climatic conditions of this extremely dry year, when the greatest heat wave registered in the last 150 years took place in Europe (Schär and Jendritzky, 2004). On the other hand, the positive effect of conspecific neighbouring plants on the production of seeds per plant suggests the relevance of allogamous pollen to successfully reproduce, which has been previously reported for other *Helianthemum* species (Herrera, 1987; Tébar, 1997; Rodríguez-Pérez, 2005).

Individual plant phenology was found to be of great importance to the reproductive output of *H. squamatum*. Flower and seed production per plant were strongly related to flowering duration and synchrony. This was an expected result as plants producing more flowers are able to reach longer blooming periods (Schmitt, 1983; Widén, 1991; Ollerton and Lack, 1998). On the other hand, a high degree of flowering synchrony among plants resulted in greater values of fruit-set, viable seeds per fruit and/or

seeds per plant, which is consistent with an allogamous breeding system of *H. squamatum*. The higher level of flowering synchrony detected in 2003 may be a consequence of a shorter blooming period, likely caused by the drier conditions of this year. Moreover, the relationship between earlier flowering peaks and relative reproductive success observed in 2002 has already been reported in other studies (Bishop and Schemske, 1998; Torres *et al.*, 2002). Early flowering has been considered as a drought avoidance strategy (Farris and Lechowicz, 1990; Stanton *et al.*, 2000; Volis *et al.*, 2004), and might be especially important in the case of a relatively late-flowering plant such as *H. squamatum*. However, under the extreme water shortage that occurred during spring 2003, the advantages of an earlier flowering were not so evident, and resulted in less viable seed production (Fig. 4). These results also suggest certain decoupling between flowering season and pollinator activity in the dry 2003 (Rathcke and Lacey, 1985; Herrera, 1988; McCarthy, 2001), and agree with the reported shifts to earlier flowering dates with warmer conditions (Peñuelas *et al.*, 2002).

Together with plant phenology, individual plant size was an accurate predictor of absolute reproductive components, as is expected for an indicator of plant maternal resources (Samson and Werk, 1986; Herrera, 1991; Mitchell, 1994; Ollerton and Lack, 1998; Albert *et al.*, 2001; McIntosh, 2002). It is noteworthy that the increase in average plant size from one year to the next was not due to mortality of small-sized plants, but exclusively to plant growth.

Absolute reproductive variables were significantly higher during the drier year, but only on the south-facing slope. This suggests that the north-facing slope represent a more stable habitat for reproduction whereas the south-facing slope may provide an advantage during certain

extremely hot and dry years. These results are worth noting, since north-facing slopes have been widely recognized as more favourable locations for plant performance (Escós *et al.*, 2000; Bellot *et al.*, 2004).

In conclusion, reproduction of *H. squamatum* is flexible enough to counteract very different environmental conditions at several scales and climates. Even more, absolute reproductive variables reached a maximum in the south-facing slope plots during the heat wave of 2003. This result brings us to the question recently posed by Körner (2003) about what must be considered a stressful environment in the case of stress-tolerant plants. Contrary to our expectations, what we considered the more favourable habitat in our study system was not so for this species, at least in reproductive terms. Since stress is an individual-based concept and stressful environments hardly exist (see Körner, 2003, 2004), it can be concluded that the environmental conditions on the south-facing slope during an extreme heat-wave did not necessarily represent a stressful scenario for this species. Furthermore, reproductive costs for surviving plants have not been detected since (unpubl. res.). We think that there must be some other factors actually limiting reproduction in what we initially considered more benign conditions. Obviously, understanding the physiological mechanisms by which these plants are able to reproduce under such environmental conditions and the extent of this reproductive flexibility in the plant community need further study.

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