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Female performance in *Euphorbia characias*: effect of flower position on seed quantity and quality

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Abstract

Patterns of seed mass variation in the perennial spurge *Euphorbia characias* (L.) (*Euphorbiaceae*) in three populations from north-east Spain were examined. Mature inflorescences have a distinctive structure, with a distal umbrella of rays subtending dichotomously grown cyathia. Under the umbrella, cyathia are loosely arranged on rays growing from the bases of leaves. Seed characteristics were studied, especially in relation to position along the inflorescence. Maximum inflorescence height had no effect on seed set or seed mass. Seed set did not differ between populations. Flower position along the inflorescence had a marked effect on seed set and seed mass. Seed set was higher in the distal (upper) portion of the inflorescence. Seeds from the distal area had a greater mass than those from lower parts of the inflorescence. Seeds were planted in the field and observed under natural weather conditions. The bigger seeds from the higher position in the inflorescence produced seedlings with a greater percentage emergence, which, in addition, had an increased percentage establishment than seedlings originating from the smaller seeds from lower areas of the inflorescence. For the three populations considered together, seeds from the basal (lower) portion of the inflorescence were reduced in germination by 51% and establishment by 59%. No differences in seedling dry mass were observed. Seed dispersal-related structures (elaiosome and elaiosome/load ratio) did not vary in relation to position or population. Positional effects on female performance – seed quantity and quality – may be a very strong selective pressure for the peculiar flower disposition in the architecture of *E. characias*.

Keywords: *Euphorbia characias*, inflorescence architecture, positional effect, seed set, spurge

Introduction

Many plants have an extended shoot axis bearing flowers. Such elongated inflorescences confer a distinctive appearance during full blooming. This flowering pattern is usually interpreted as a consequence of apical dominance (the preferential growth of a plant from the apical meristem) associated with a suppression of lateral meristems (Aarssen, 1995). Tallness, *per se*, may confer distinct selective advantages, in terms of competition for light, pollinators, or the ability to disperse seeds (Aarssen, 1995). Maximum height of the inflorescence influences seed set and seed mass in several species (Pyke, 1981; Aker, 1982; Verbeek and Boasson, 1995).

Independent of the maximum height attained by an inflorescence, the physical location of a flower within an inflorescence may also influence fruit set (Wyatt, 1982; Klinkhamer and DeJong, 1987; Obeso, 1993a) and the number of seeds matured per fruit (Obeso, 1993b). Seedlings from larger seeds often have a size advantage over seedlings derived from smaller seeds (Fenner, 1985; but see Baskin and Baskin, 1998, table 8.10 for examples of the opposite effect). In summary, the architecture of the inflorescence (*sensu* Diggle, 1995) can be linked, directly or through fruit set, seed set, seedling emergence and establishment, to plant fitness.

Diaspore characteristics, such as elaiosome size and elaiosome/seed ratio, strongly influence the fate of myrmecochorous seeds (Gunther and Lanza, 1989; Oostermeijer, 1989; Hughes and Westoby, 1992; Gorb and Gorb, 1999). In this paper we focus on the inflorescence level and within-inflorescence variation and examine the relationships between flower position and seed traits. Furthermore, the effects of seed mass on seedling establishment were monitored. The following questions were addressed: (1) How do seed set, seed mass and seed investment in dispersal-related structures differ in upper versus lower flowers within a plant? (2) Do seeds from upper and lower fruits show similar emergence percentages? (3) Do seedlings originating from upper and lower seeds establish equally, and how well do they perform?

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The main focus of the work refers to within-individual variation in reproductive characteristics, i.e. to assess the influence of flower position in elongated inflorescences (upper versus lower) on female reproductive output. In three separate populations of *Euphorbia characias* (L.) (*Euphorbiaceae*), ecological implications of flower arrangement are documented and show strong and direct effects upon quantity and quality of the offspring. This is one of the very few examples in which seed set and seed mass (and the resulting offspring quality) are greater for seeds produced at higher positions on the inflorescence.

Materials and methods

The species

Euphorbia characias is a woody Mediterranean spurge that is found typically growing in full sun. Flowering shoots appear after plants are 3 years old or later. Mature inflorescences measure up to 1.3 m. Flowers are arranged in a distinctive structure, called a cyathium, that has a unique female flower with three single-ovuled carpels and a variable number of stamens, from 11 to 19 (mean ± SD = 16.3 ± 1.6; dissection of 142 cyathia from 10 plants; two populations). The cyathium acts functionally as a single flower (Strasburger, 1970). Cyathia appear to be protogynous (personal observation) as has been reported for other *Euphorbia* species (Ehrenfeld, 1976; Meeuse *et al.*, 1989). Pollen/ovule ratios for *E. characias* (mean ± SD = 7013 ± 2319; 44 cyathia of four plants from two populations) indicate that its breeding system may be xenogamous (Cruden, 1977), but this aspect remains to be tested experimentally.

The cyathia are found on shoots that have a long naked (leaves absent) basal part, a leafy medial zone, and a distal, elongated inflorescence (13.9 ± 6.6 cm height; n = 116 from one population) somewhat cylindrical in shape when mature (mean diameter ± SD = 6.4 ± 1.7 cm; n = 97). Cyathia are more numerous in the upper umbrella-like structure (Fig. 1) offering a somewhat curved, disc-shaped distal landing surface to flying pollinators. Under the umbrella, cyathia are more loosely distributed along the stem, growing from the base of the leaves.

Seeds are dispersed predominantly by ants. Seeds have a yellow, hard and durable elaiosome and are ballistically ejected when fruits mature. Some ants, upon finding the seeds, take them to the nest (Espadaler and Gómez, 1996). In one of the populations studied, virtually every seed was found and taken to the nest, due to a very high level of soil surface scanning by those ants (Espadaler and Gómez, 1997a). The presence of the elaiosome is critical for dispersal, since a seed with an elaiosome is seven times more likely to be taken to the nest if found by a non-granivorous ant than is a seed lacking an elaiosome (Espadaler and Gómez, 1997b). After eating the elaiosome, the seeds may remain inside the galleries or be discarded intact outside, in the refuse heap or at some further distance (Gómez and Espadaler, 1998a). Seed germination is enhanced by interaction with ants, as the presence of an elaiosome has a negative effect on germination (Gómez and Espadaler, 1998b). *E. characias* has epigeal germination.

Populations studied

Three populations in north-east Spain were studied to encompass a range of variation in climatological data and altitude, and to obtain a level of generalization for the species: (1) Collserola Park, Barcelona (UTM 31TDF28; elevation 315 m; 620 mm of annual rainfall; mean annual temperature 14.5°C; dry, subhumid climate); (2) Sant Llorenç del Munt Park, Barcelona (UTM 31TDG10; elevation 730 m; 675 mm annual precipitation; mean annual temperature 11.5°C; humid climate); (3) Montseny Park, Barcelona (UTM 31TDG42; elevation 522 m; 875 mm precipitation; mean annual temperature 12.5°C; humid climate). Populations were in protected zones, permitting continued observation and experimentation without unexpected disturbances.

Seed set, seed mass and elaiosome mass

Seed set (the number of seeds that develop per fruit) was assessed on 50 plants per population. The number of mature shoots, an indication of plant size, was noted, as was maximum inflorescence height at maturity. Five randomly chosen cyathia from the upper umbrella and five from the basal part of the inflorescence were examined to estimate seed set. Mature capsules may bear three, two, one or no seeds; this is easily seen on the capsule, without dissection, as three to none inflated swellings. Ten mature shoots of different plants from each population were collected in late May 1999. Upper and lower parts of the inflorescence were separated and allowed to dry and dehisce at room temperature inside separate cardboard boxes. Subsequently, seeds were collected and weighed with an electronic micro-balance. For every plant, 10 seeds from both upper and lower position classes were weighed individually to the nearest 10^{-4} g. The mean for the 10 seeds was used as an independent datum for each plant and position. Investment in elaiosome was measured by separately weighing the testa and its elaiosome. Due to the very small elaiosome mass, elaiosomes were weighed in groups of 10 and the pseudo-mean was used in the analyses. Ten seeds per position from 6–9 plants per

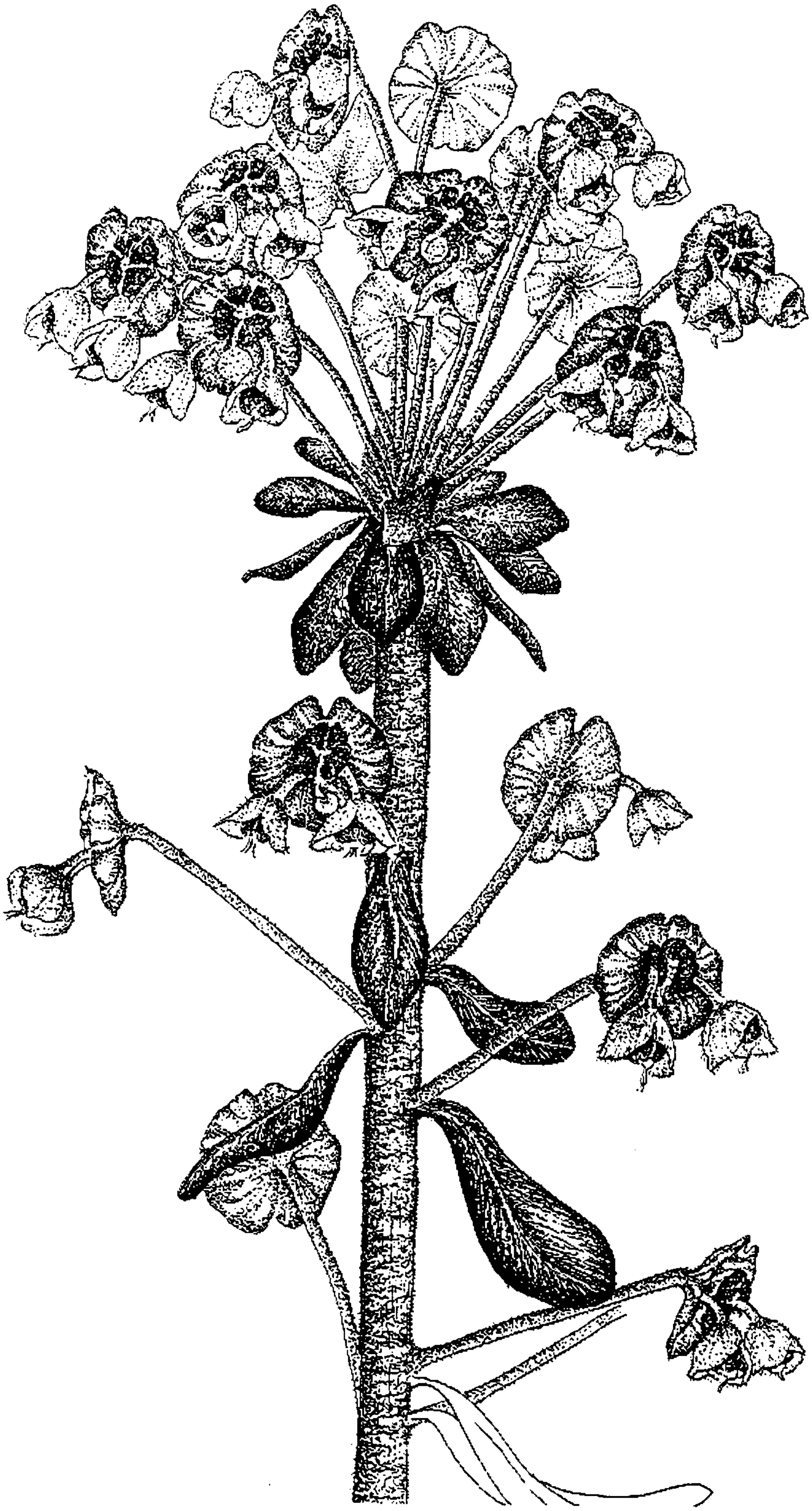

Figure 1. Distal part of the inflorescence of *Euphorbia characias* (L.). Dichotomously growing cyathia are grouped in an upper umbrella with radially disposed rays. Under the umbrella, cyathia are subtended by single rays. Drawing by Joaquim Conca.

population were studied. In this last analysis, the smaller sample size reduced the statistical power of the test and results should be considered indicative. Seed viability was determined with 2,3,5-triphenyl tetrazolium chloride (TTZ) (Scharpf, 1970) on 100 (50 distal + 50 basal, mixed) seeds from each population, and compared with a test of difference between pairs of percentages. Seeds with a red-stained embryo were considered viable.

Analyses of population variation have been conducted considering plants as replicates representative of within-population variation. Simple linear regression was used to determine the relationship of maximum inflorescence height, seed set and seed mass. Seed set was analysed assigning population as a fixed effect, and position as a within-plant repeated measures effect in the analysis of variance. As plant size is known to influence seed size (Aker, 1982; Nakamura, 1988), the number of shoots of each plant was introduced as a covariate. Seed set was arcsin square-root transformed to meet the assumptions of the ANCOVA. Seed mass was log-transformed and analysed using the same model. Elaiosome mass was analysed without transformation and the elaiosome/seed ratio was arcsin square-root transformed. Tukey HSD *post hoc* comparisons were used to detect significant differences among populations. Means did not differ significantly when $P > 0.05$.

Seedling emergence and establishment and dry mass

From each of 10 plants at the three study sites, 15 seeds were collected from each position-class within an inflorescence (distal, basal) (total 900 seeds). Seed elaiosomes were removed by hand. The 15 seeds for each position were sown in a circular design (15 cm diameter) in small field plots at Collserola Park in July 1999. Each group was separated from its adjacent group by a 15 cm buffer zone. Distal and basal seeds from a given plant were planted next to each other, but otherwise the arrangement of plots in the field was assigned randomly in a grid of 12 columns and 5 rows, as permitted by the available surface. Seeds were planted at a soil depth of 2–3 cm. Seedling emergence after the first autumn rains (late September) was recorded weekly for 10 weeks, then once per month for the following 3 months. A seedling was considered fully established when two leaves appeared in addition to the green cotyledons. The cumulative number of emerged seedlings and the number of established seedlings after 10 weeks was used in an ANCOVA (same model as above) after log x+1 transformation.

Before the initiation of the growing season (late winter), seedlings were excavated, washed, dried to constant weight at 100°C for 2 days and weighed individually. As the number of surviving seedlings was variable at all levels (population, position), causing many missing cells, a full ANOVA could not be performed; in addition, cells (position × population) had a different number of replicates. Only those plants from which data for seeds were available from distal and basal position classes were used. The analysis was a repeated measures (within plant) ANOVA, with the number of shoots as a covariate. All statistical analyses were performed using the Statistica 5.5 system (StatSoft; Tulsa, OK, USA).

Results

Height of inflorescence and number of shoots

The maximum height of inflorescences was not different among populations (Collserola, 86.9 ± 12.3 cm; Sant Llorenç, 83.7 ± 20.7 cm; Montseny, 83.3 ± 17.0 cm; $n = 50$; $F_{2,147} = 0.64$; $P = 0.52$). The maximum height attained by inflorescences did not show any relationship with seed set ($r^2 = 0.003$) or seed mass ($r^2 = 0.01$). Thus, plants with taller inflorescences produced no more seeds, nor larger seeds, than plants with shorter inflorescences. The number of shoots per plant in Collserola (10.3 ± 4.9) was significantly higher than in Montseny (4.9 ± 3.4) and Sant Llorenç (2.3 ± 1.3) (ANOVA, $F_{2,147} = 65.7$; $P < 0.0001$).

Pattern of seed set, seed mass and investment in elaiosomes

Position along the inflorescence had a marked effect on seed set ($F_1 = 40.8$; $P < 0.001$), but seed set did not differ significantly among populations ($F_2 = 1.3$; $P = 0.27$) (Fig. 2A). Cyathia from the distal position-class had significantly higher seed set than cyathia from the basal position-class (Table 1). Seed mass from distal fruit was significantly larger ($F_1 = 24.3$; $P = 0.002$) (Fig. 2B) than the seed mass of basal fruits, and was also different among populations ($F_2 = 4.4$; $P = 0.02$) (Table 1). A Tukey's *post hoc* test indicated that significance was due only to differences between the Collserola and Sant Llorenç populations. In the three populations seed mass from basal capsules was more variable (see SD, Table 1) than was seed mass from distal capsules. Neither the absolute elaiosome mass nor the elaiosome/seed ratio differed significantly among populations nor among fruit-position classes (Table 1). Seed viability was 89% from Collserola, 79% from Sant Llorenç and 88% from Montseny populations, and was not different among the three populations.

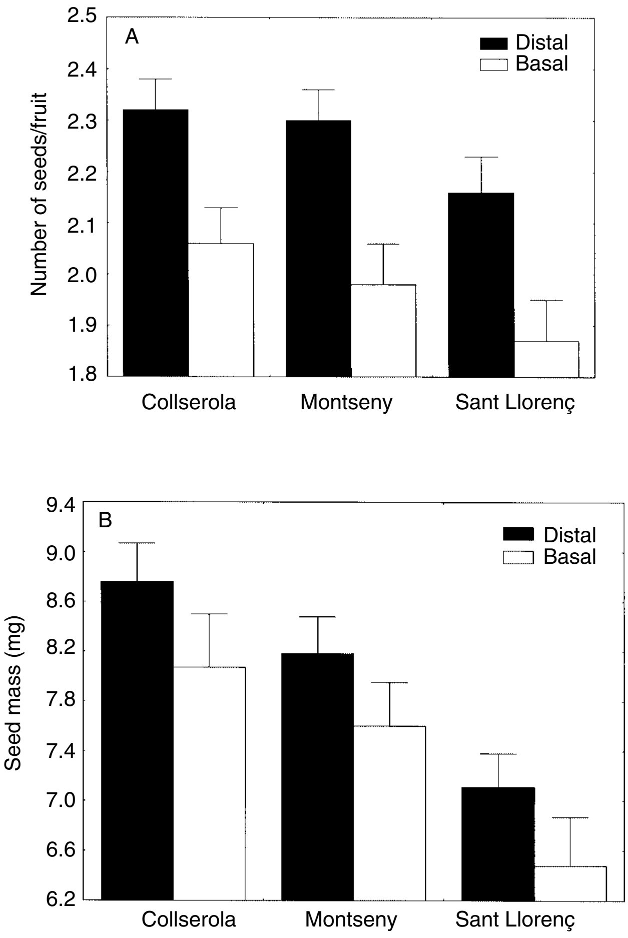

Figure 2. The effects of floral-position classes (distal, topmost umbrella of cyathia; basal, below the umbrella) on (A) number of seeds/fruit ± SE and (B) mean seed mass (mg) ± SE, for three populations of *Euphorbia characias*.

Pattern of seedling emergence and establishment and dry mass of seedlings

Cumulative seedling emergence did not differ significantly among populations (F_2 = 2.5; P = 0.09) (Table 1), while flower position had a significant effect on seedling emergence (F_1 = 5.4; P = 0.02) (Fig. 3A). If plant size was not introduced as a covariate, populations appeared as different (P < 0.001). Establishment shows the same pattern (Fig. 3B), with a significantly greater number of seedlings arising from distal seeds surviving at the end of the experiment than seedlings arising from basal seeds (F_2 = 4.6; P = 0.04) (Table 2). For the three populations considered together, being lower in the inflorescence reduced the germination of seeds by 51% and the establishment by 59%. Seedling dry mass did not differ significantly among populations (F_2 = 0.7; P = 0.5) or fruit-position classes (F_1 = 0.2; P = 0.6) when the number of shoots was used as a covariate (Table 1).

Discussion

In the three populations studied, no effect of maximum plant height was observed on any of the variables measured. *E. characias* is a shrub growing in open fields, borders of tracks or woods, without much surrounding vegetation. The crowding of vegetation is loose, and this habitat possibly does not impose a strong selective pressure for absolute plant height in *E. characias* at the time of flowering (March–April).

Among-population variation

Population differences in seed quality for a given species are widely known (Schimpf, 1977; Cideciyan and Malloch, 1982; Melzack and Watts, 1982; Susko and Lovett-Doust, 2000). At the level of the whole plant, causes may be extremely varied, extrinsic and/or intrinsic: the germination response may vary when mother plants produce seeds under different day length, different levels of mineral nutrients or temperatures (Baskin and Baskin, 1998), and seed size may be affected as a consequence of the environment where plants grow (Baskin and Baskin, 1998, table 8.7). In our system, the differences detected between populations in seedling emergence, when plant size (number of shoots) is not considered, could be due to a distinct dormancy level. Seeds of some *Euphorbia* species are known to have physiological dormancy (*E. corollata, E. dracunculoides, E. esula, E. maculata, E. marginata, E. nutans* and *E. polycarpa*), although the seeds of *E. geniculata* (Kigel *et al.*, 1992) and *E. hirta* (van Rooden *et al.*, 1970) may have no dormancy. Seeds of *E. characias* from the three populations in this study germinated readily after 7–10 d of watering under lab conditions, independent of sowing date, from 2–16 weeks after release from parent plants (data not shown). Under natural conditions in the field, seeds germinate only after 3 months following dispersal, with the onset of autumn rains. For one of the populations studied, no seed bank was detected previously (Espadaler and Gómez, 1996). The lower seedling emergence from the Sant Llorenç population was probably due to smaller mean seed mass than in other populations. Seed size can have a strong effect on seed germination (Simons and Johnston, 2000) or seedling emergence (Stanton, 1984; Yanful and Maun, 1996).

Among-inflorescence variation

Seed characteristics

Flowers that mature at different times during the flowering season produce seeds that vary in their ability to germinate, or time of germination (Weis, 1982; Gross and Werner, 1983; Cavers and Steel, 1984; Wolfe, 1992; Baskin and Baskin, 1998, chapter 8.VI). In

Table 1. Seed set (number of seeds/fruit), seed mass, investment in elaiosome, seedling emergence and establishment in three populations of *Euphorbia characias* from north-east Spain. Position-class (distal or basal) indicates the location of mature capsules along the inflorescence. Elaiosome mass and elaiosome/seed ratio are based on a variable number of plants per population (indicated by values in parentheses), 10 seeds per position and plant. Elaiosomes were weighed *en masse* and the mean used. Seedling dry mass is the mean per plant, based on a variable number of seedlings and plants, indicated by values in parentheses, i.e. 43 seedlings from 9 plants. Values are mean ± SD

	Collserola		Sant Llorenç del Munt		Montseny	
	Distal	Basal	Distal	Basal	Distal	Basal
Seeds/fruit	2.32 ± 0.06	2.06 ± 0.07	2.16 ± 0.07	1.87 ± 0.08	2.30 ± 0.06	1.98 ± 0.08
Seed mass (mg)	8.76 ± 0.99	8.07 ± 1.37	7.11 ± 0.86	6.48 ± 1.24	8.18 ± 0.95	7.60 ± 1.11
Elaiosome mass (mg)	0.57 ± 0.09 (9)	0.56 ± 0.10 (9)	0.61 ± 0.14 (6)	0.57 ± 0.15 (6)	0.58 ± 0.07 (7)	0.57 ± 0.15 (7)
Elaiosome/ seed ratio	6.68 ± 0.80	6.79 ± 0.95	7.98 ± 1.44	7.97 ± 1.60	7.32 ± 0.73	7.48 ± 0.71
Emergence (from 15)	7.9 ± 4.4	5.8 ± 4.1	1.6 ± 2.3	0.5 ± 0.9	5.6 ± 4.6	2.4 ± 2.0
Establishment (from 15)	4.9 ± 3.1	3.8 ± 3.5	0.9 ± 1.2	0.1 ± 0.3	2.2 ± 2.8	0.8 ± 0.9
Seedling dry mass (mg)	98.5 ± 34.6 (43, 9)	90.9 ± 34.2 (31, 7)	41.6 ± 14.9 (10, 4)	28.0 ± 8.0 (5, 3)	43.8 ± 17.6 (32, 7)	43.3 ± 17.8 (4, 4)

E. characias the first cyathia to mature are those from under the topmost umbrella that grows from the base of leaves; floral buds of the most basal cyathia usually do not develop to maturity. The flowering season of *E. characias* extends over a period of 7–8 weeks. During that time up to three cohorts of cyathia develop and mature fruit, so there is the potential for differences in reproductive output generated by the time of flowering.

One major finding of this study is that flowers situated near the apex of the inflorescence set more and larger seeds than basal flowers. The physical location of a flower within an inflorescence can alter the number of seeds that mature in many species (Gutterman, 1992). Fruits lower in the inflorescence in *Parkinsonia aculeata* produced more seeds than those toward the top of the raceme (Wyatt, 1982), and a similar effect was detected by Obeso (1993a) in *Asphodelus albus*. In addition, Klinkhamer and DeJong (1987) showed that flowers closest to the main stem produced heavier seeds in *Cynoglossum officinale*; Obeso (1993b) showed that seeds of *Asphodelus albus* at the bottom of the inflorescence were heavier than seed from upper flowers. We found the reverse trend: distal fruits set more and heavier seeds than basal fruits. Differences in seed mass may influence seedling traits (Baskin and Baskin, 1998, table 8.11). As a result, more seedlings originating from distal fruits emerged and survived during the experiment.

Coefficients of variation for seed properties, seedling emergence and establishment are shown in Table 2. Seed set and seed mass were less variable on distal cyathia; seedling establishment was also less variable on seeds from distal cyathia. Emergence was less variable although not significantly different.

A selective pressure seems to be acting, within each inflorescence, with top flowers being favoured. This shows that descendants from a single plant differ in terms of seed quality and that there is potential for selection acting on the architecture of the inflorescence that produces such different seeds. Proximate mechanisms may be multiple: under the ‘effective pollination hypothesis’ (Aarssen, 1995), taller plants may have an advantage by being more visible to pollinators (Peakall and Handel, 1993; Verbeek and Boasson, 1995), thus receiving more pollen. In addition to absolute plant height, differences also exist as a positional effect (top versus bottom) in inflorescences within plants (Lortie and Aarssen, 1999). Pollen load, then, may affect seed quality via gametophytic and zygotic competition and mate choice by females (Marshall and Folsom, 1991; Mitchell, 1997). Plant height in *E. characias*, specifically inflorescence height, may act as a cue for pollinator attraction. Insect visitors (mainly flies and wasps) reach the plant from above; they land preferentially on the upper umbrella and depart from there after probing several nectaries from different cyathia. Such behaviour may favour the particular type of inflorescence in *E. characias*. Also, as shown for *Croton capitatus*, an increase in projection height results in greater dispersal distances attained (Garrison *et al.*, 2000) and this, according to the ‘effective dispersal hypothesis’ (Aarssen, 1995), may affect colonization in ruderal habitats or minimize density-dependent seed predation.

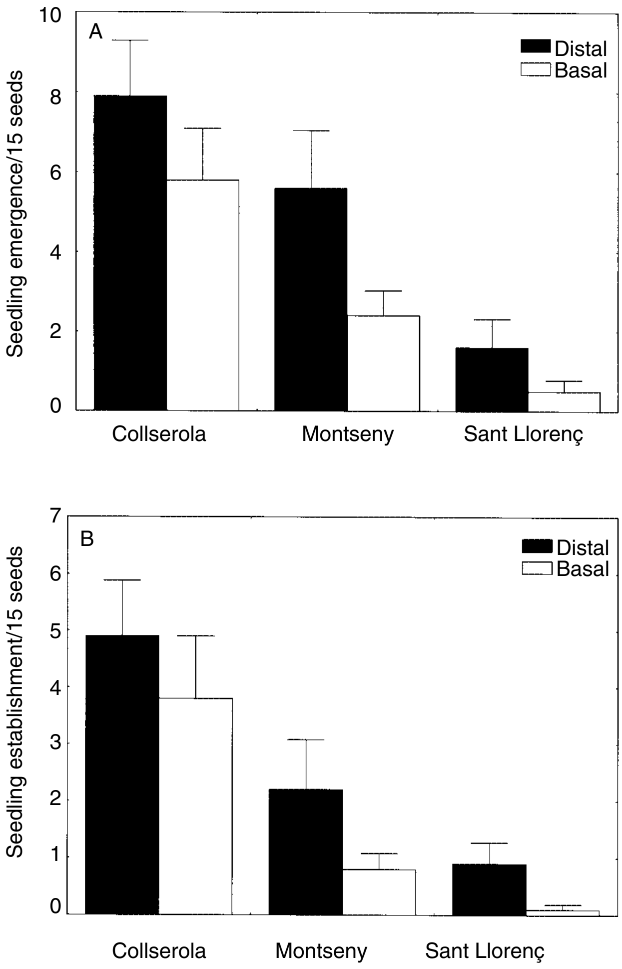

Figure 3. The effects of floral-position classes (distal, topmost umbrella of cyathia; basal, below the umbrella) on (A) seedling emergence ± SE, and (B) establishment ± SE, for three populations of *Euphorbia characias*. Seedling emergence is the cumulative number of seedlings from 15 planted seeds, appearing during 10 weeks, before winter. Establishment is a subset of those emerged seedlings, which were considered established when a pair of leaves appeared in addition to the cotyledons.

Alternatively, a purely architectural effect (Diggle, 1995) could be acting, alone or in conjunction with any of the above mentioned effects. Seed traits could differ because the cyathia along the inflorescence have variable gynoecial characters (i.e. basal female flowers are smaller than distal female flowers). It must be stressed that these multiple possibilities are not mutually exclusive.

For myrmecochorous plants, it is assumed that both elaiosome size and elaiosome/load ratio affect the behaviour of ants (Hughes and Westoby, 1992) which, in turn, may have been an important selective force in the evolution of myrmecochory. In our system we could not detect any difference in absolute or relative elaiosome mass. An explanation may be that any *E. characias* seed that reaches the soil is retrieved so rapidly (Espadaler and Gómez, 1996, 1997a) that there is no selective force acting on elaiosome characteristics. This specific phase of the dispersal process, the first seed–ant contact, does not seem to bear on the evolution of the elaiosome mass in *E. characias*. It is also possible that, due to our grouping of elaiosomes in order to estimate their mass, the mean value used in the analysis is less variable than if individual masses had been used.

Seedling emergence, establishment and dry mass

Higher emergence and establishment levels were observed from distal seeds than from basal seeds of *E. characias*. It is to be expected that natural selection favours a pattern of resource allocation to seeds that would maximize plant fitness. Here, myrmecochory matters. In effect, seeds of myrmecochorous plants, as a result of ant gathering, may end up in clusters inside the nest or in the midden (Beattie, 1985; Bennett and Krebs, 1987). It is known for many species that, for a given depth of burial, the larger the seed, the earlier the seedling emerges (Harper, 1977) and captures a disproportionate share of environmental resources. Under dense conditions, a crowd of seedlings may compete for light or soil resources, reducing an individual's chance to establish (Howe, 1989). Therefore, under the stress from neighbours at high densities, even a small advantage in seedling size can be critical. A test of this hypothesis for variation in seed size within inflorescences for myrmecochorous plants would be to compare seed characteristics of *E. characias* to non-myrmecochorous *Euphorbia* species with elongated inflorescences; under this hypothesis, we suggest there should be much less variation in seed size than that detected in *E. characias* in the present study. The experimental design used for seedling evaluations did not allow a determination of a possible interaction between seed mass and depth of burial.

Measurable effects of position or seed size on seedling dry mass were not detected in *E. characias*. Gross (1984) showed a significant seed-size effect for six perennial plants grown in competitive conditions but not in a non-competitive cover. Taking into account the low power of analysis due to reduced number of replicates, it is also possible that seedling differences due to seed size were not fully expressed in our particular growing conditions (isolated seedlings) but only when seedlings are in tight clumps that emerge from ant nests. Alternatively, the absence of differences could be due to the delayed sampling date. Soon after emergence, associations of plant characteristics with seed size have been shown for *Rhaphanus raphanistrum*, but plant size in

Table 2. Means ± SD (n) and coefficients of variation ± SE (Sokal and Rohlf, 1995) for measures of seed and seedling size and performance according to floral position-class. Data from the three populations were pooled together. Emergence and establishment are based on 15 sown seeds per plant

	Seed position			Seedling position	
	Distal	Basal		Distal	Basal
Seed set (%) (150 plants)	75.5 ± 16.5	65.7 ± 18.9	Emergence (30 plants)	5.0 ± 4.6	2.9 ± 3.4
C.V.	21.8 ± 1.3***	28.7 ± 1.7	C.V.	92.0 ± 19.5 ns	119.3 ± 30.2
Mass/seed (mg) (30 plants)	8.0 ± 1.1	7.3 ± 1.3	Establishment (30 plants)	2.6 ± 2.9	1.5 ± 2.5
C.V.	13.7 ± 1.8**	17.8 ± 2.3	C.V.	112.9 ± 27.4*	167.3 ± 55.4

Statistical differences between coefficients (distal versus basal) are indicated as: ns, non-significance; * , $P < 0.05$; **, $P < 0.01$; ***, $P < 0.005$, according to the test in Dawkins and Dawkins (1973).

greenhouse studies became entirely independent of seed size within 40 d (Stanton, 1984). The positive relation between seed size and seedling size can be reduced after a few days because of the inverse correlation of seed size and relative growth rate (Westoby *et al.*, 1992).

The relationships between flowers, fruits and seeds and, ultimately, plant fitness, may be extremely complex (Primack, 1987). It is now widely accepted that hermaphroditic plants enhance fitness through both female and male fertilities (Morgan and Schoen, 1997). We have not analysed an eventual relation between flower position and any correlate of male function (number of stamens, pollen content), and the possibility remains that male contributions via pollen donation show differences according to flower position. This was proposed by Sutherland (1987) for *Agave mckelveyana*, in which the flowers of lower branches contribute mainly to male fitness, not to female fitness; data concerning this point are lacking for *E. characias*.

Our observations suggest that plant architecture can greatly influence recruitment probabilities of individual seeds, although it is not easy to distinguish between alternative hypotheses (resources, phenology, pollination, architecture) to account for differences in female performance (Lubbers and Christensen, 1986; Wolfe, 1992; Campbell and Halama, 1993; Brunet, 1996). On a broader scale, this shows that it is important to consider the within-plant level, as seeds from a parent plant differ in quality, showing strong variation in establishment success. Whether the variation detected in seed size is due to variation in the pollination level, to differences in resource availability during the growing season or to an architectural (positional) effect is currently being addressed through hand pollination and experimental manipulation of fruit set and seed set.

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