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Heterocarpy in *Calendula micrantha* (Asteraceae): The effects of competition and availability of water on the performance of offspring from different fruit morphs

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ABSTRACT

Heterocarpy is often associated with different flower morphs. However, in *Calendula micrantha*, a monoecious member of the Asteraceae, all six fruit morphs arise only from ray flowers. The maternal investment differs markedly among the fruit morphs, as does the growth, size and competitive ability of the resulting seedlings. The fruit morphs appear to be adapted to different conditions, as there were profound differences among the progeny of different morphs raised at different densities and in different watering treatments.

Keywords: Asteraceae, *Calendula micrantha*, heterocarpy, niche partitioning.

INTRODUCTION

Heterocarpy, the production of multiple fruit morphs by a single plant, is common among the Asteraceae (Koller and Roth, 1964; Flint and Palmblad, 1978; McEvoy, 1984; Venable, 1985; Venable and Levin, 1985; Tanowitz *et al.*, 1987; Venable *et al.*, 1987, 1998; De Clavijo, 1994). Heterocarpy is often associated with flower polymorphisms and influences both seed dispersal and seed germination (Silvertown, 1984; Maun and Payne, 1989; De Clavijo, 1994). Locally dispersed seeds usually exhibit delayed germination, while seeds dispersed over greater distances often lack dormancy (Venable, 1985; Venable and Levin, 1985; Venable *et al.*, 1987; De Clavijo, 1994). Within the Asteraceae, disc achenes are usually lighter and exhibit higher and faster germination rates (Tanowitz *et al.*, 1987).

Fruit polymorphisms are believed to evolve in response to environments that are spatially and temporally heterogeneous. A critical feature of that heterogeneity is population density (Geritz, 1995). As seed size is positively associated with the resulting adult plant size, competitive ability and the type of fruit the seed came from, individuals from heterocarpous

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species can alter the competitive profile of their offspring by altering the proportions of fruit types. Mechanistically, such alterations are apt to reflect both developmental time and nutritional status. Early developing seeds tend to have the greatest seed dormancy, whereas later developing seeds have the least (Silvertown, 1984). Within the Asteraceae, the ray flowers, which develop first, often have thicker pericarps and greater seed dormancy (McEvoy, 1984; Tanowitz *et al.*, 1987; Venable *et al.*, 1987). Plants in nutrient-rich areas are expected to have the greatest variation in fruit types, while those in nutrient-poor areas should have the least (De Clavijo, 1994; Geritz, 1995). Seeds which are dispersed in aggregate, or very locally, should also show the minimum variation in size, whereas those dispersed more broadly should be more variable (Geritz, 1995).

Although most heterocarpous species display two fruit types with two or three types of seeds (see Silvertown, 1984; De Clavijo, 1994), the genus *Calendula* is renowned for the wide diversity of fruit types produced by a single individual. Heyn and Joel (1983) document more than seven types of fruit produced by individuals of *C. arvensis* and *C. triptercarpa*, with even more types produced by their hybrids. *Calendula* is also unusual because the multiple fruit types *all originate from ray flowers*, and the larger fruits are less dense than the smaller fruits. Thus, small fruits (with smaller embryos) tend to drop under the parent, whereas larger fruits (with larger embryos) are dispersed more broadly (A. El-Keblawy, unpublished data).

Here, we examine the competitive ability and response to stress of individuals from different fruit morphs of *Calendula micrantha*. *C. micrantha* displays a wide variety of fruit types (Fig. 1), with many ornamented to favour animal or wind dispersal (morphs I, II and III), whereas others show no such ornamentation, and thus the morphs differ in dispersability. Like other heterocarpous species, *C. micrantha* (Philipupillai and Ungar, 1984; De Clavijo, 1994) is a desert annual.

We examined the proportion of fruit morphs produced by plants derived from different fruit morphs and reared in different irrigation treatments and at different densities. We also examined the masses of the pericarp and seed, seed germination, the number of leaves and the length of the longest leaf in each treatment. Finally, because *C. micrantha* is monoecious, producing both male and female flowers, we also report on the floral sex ratio.

Fig. 1. The six fruit morphs of *Calendula micrantha*. The fruits are arranged in ascending order from left to right (i.e. I–VI).

METHODS

Calendula micrantha is a desert annual primarily found inhabiting sandy soils in the Sinai desert. Fruits were collected in February 1995 near El-Arish, Egypt. To characterize the fruit morphs, we determined the total fruit, pericarp and embryo mass (± 0.001 mg) by weighing each separately. Total fruit weight is equal to the sum of the seed and pericarp weights. We also conducted germination studies using all six morphs. Plants in the first treatment were germinated at room temperature, whereas those in the second treatment were kept at room temperature for 12 h and then at 4°C for the remainder of the day. We refer to the latter as the 'cold treatment'. We used six replicates of 25–30 fruits for morphs II, III, IV and VI, and 45 fruits for morph I. Morph V is rarer than the other morphs and we only used 10 fruits per replicate of this morph. The number of germinated seeds was recorded daily and final germination percentages were compared among the morphs. The number of leaves, length of the longest leaf, root and stem were all measured (± 1 mm) 25 days post-emergence.

In a separate experiment, we assessed the response of individuals from fruit morphs I, II and III (Fig. 1) to different levels of density, irrigation and both intramorph and intermorph competition. Seeds were germinated on filter paper in petri dishes moistened with tap water in May 1997 in the greenhouse at Wayne State University, Detroit, MI. Seedlings were then transplanted into a sand : potting soil mix (9 : 1) in plastic pots (circumference of 48.7 cm and depth of 15 cm).

For the density study, seeds of morphs I, II and III were sown singly as a control (0.53 $\text{plant} \cdot \text{dm}^{-2}$), two plants per pot (1.07 $\text{plants} \cdot \text{dm}^{-2}$), five plants per pot (2.65 $\text{plants} \cdot \text{dm}^{-2}$) and six plants per pot (3.18 $\text{plants} \cdot \text{dm}^{-2}$). Competition among morphs was examined using the following designs: morph II and morph I plants (5MII/1MI, 1MII/1MI), morph III and morph I plants (1MIII/1MI, 5MIII/1MI, 5MI/1MIII) and morph III and morph II plants (1MIII/1MII, 5MIII/1MII, 1MIII/5MII).

All pots were randomly numbered and assigned to a watering treatment – that is, wet, medium or dry. Dry pots were watered every third day, medium pots every second day and wet pots every day. At each watering, plants received 150 ml of tap water. Plants were grown from May to August 1997. There were five replicates per treatment.

From 16 June until 30 July 1997, the number of inflorescences was counted and the number of male and female flowers determined. The various fruit morphs were harvested and counted as they developed. At week 7, the experiment was terminated. The plants were then harvested and dried at 80°C for 2 weeks. After drying, the total weight of individual plants and the total weight of inflorescences were determined.

Data analyses

Diversity of fruit morphs produced by each plant was computed using the information index (H'; Ludwig and Reynolds, 1988). All data were analysed using SPSS. Means were compared using an analysis of variance (ANOVA) and *post-hoc* Student Newman-Keuls multiple range tests. Categorical data were analysed using a chi-square analysis. The lengths of the roots and stems, number of leaves, length of the longest leaf and seedling mass were all log-transformed to meet the assumptions of ANOVA. We present the untransformed data, but the statistics are from the transformed data.

RESULTS

Germination

We assessed germination of all six fruit morphs at room temperature (Table 1). The percentage of seeds that germinated was dependent upon fruit morph. Seeds from morph I had significantly lower germination (standardized residual = 5.10, $P < 0.01$) and seeds from morphs III and IV had significantly higher germination (standardized residuals = 3.3 and 2.1 respectively) than one would expect by chance. The results of the cold germination trials at 4°C did not differ from those at room temperature for all morphs combined ($\chi^2 = 0.04$, $P > 0.8$) or for any fruit morph (Table 1).

Fruit, embryo and pericarp weights

Total embryo weight, fruit and pericarp weights differed significantly among the morphs ($F_{5,89} = 9.74$, $P < 0.001$; $F_{5,107} = 49.59$, $P < 0.001$; $F_{5,89} = 37.59$, $P < 0.001$, respectively) (Fig. 2). Fruits from morphs I and II were significantly smaller than those from morphs V and VI, which, in turn, were significantly smaller than fruits from morphs III and IV. Pericarps from morphs I and II weighed less than those from morphs V and VI, which

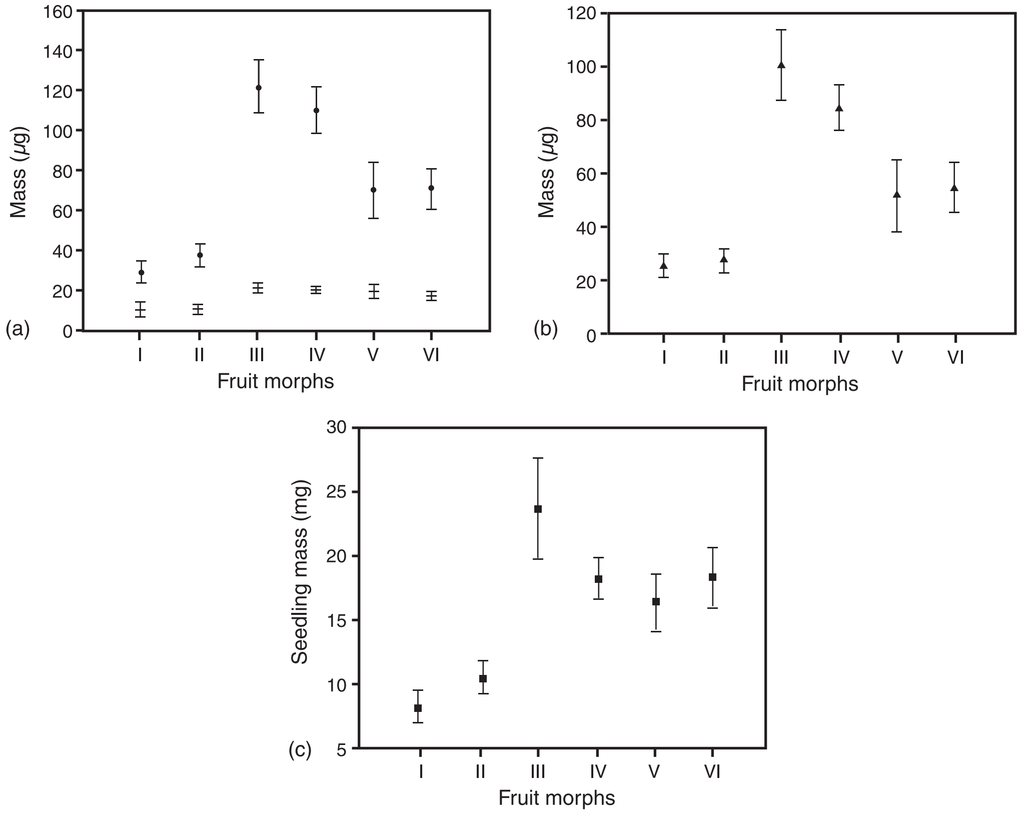

Fig. 2. The mean and 95% confidence intervals for (a) total fruit mass (●) and embryo mass (—), (b) pericarp mass and (c) seedling mass of the various morphs.

weighed less than those of morph III. Pericarps from morph IV weighed significantly less than those from morphs III–VI, while the embryos from morph III weighed significantly more than those of morph VI. There was no significant difference among the embryo weights of morphs III and V.

Fruit morph and seedling sizes

In the germination experiments, the lengths of the root and stems and the seedling weight all differed significantly among the six fruit morphs ($F_{5,130} = 6.00$, $P < 0.001$; $F_{5,116} = 3.34$, $P < 0.007$; $F_{5,130} = 34.74$, $P < 0.001$, respectively). Seedlings from morph VI had significantly longer roots than did those of the other morphs; however, there was no difference among the other morphs (Table 2). Morph VI also had longer stems and roots than morph I. The *post-hoc* analyses divided the seedlings into four weight groups in ascending order of weight: morph I; morph II; morphs V, VI and IV; morphs VI, IV and III (Fig. 2). This pattern is similar to that observed for embryo mass, except that morphs VI, IV and III differ from morph V in seedling mass, but not embryo mass.

Number of leaves

The watering treatment, density and size of fruit all significantly affected the number of leaves. The number of leaves per plant increased significantly as the amount of water increased during watering (Table 3; $F_{2,393} = 24.94$, $P < 0.001$). Plants in the dry treatment produced significantly fewer leaves than those in the other two watering treatments. The number of leaves per plant varied with density in the following order: 2 plants/pot > 6 plants/pot > 5 plants/pot > 1 plant/pot (Table 4; $F_{2,393} = 3.30$, $P < 0.03$). Plants in the two-plants-per-pot treatment produced significantly more leaves than plants in the one- and six-plants-per-pot treatments, but not more than the five-plants-per-pot-treatment, which did not differ significantly from the other treatments. The number of leaves differed among the three fruit size categories and increased with increasing fruit size ($F_{2,393} = 13.35$, $P < 0.001$). The density × fruit size interaction was also significant for the number of leaves (Table 5; $F_{6,393} = 7.01$, $P < 0.001$). Plants from the largest fruits had more leaves per plant in all treatments. However, the number of leaves per plant was less for plants from morph II fruits at low density than for plants from morph I fruits. At high density, this pattern was reversed.

Length of longest leaf

The length of the longest leaf also varied with the watering treatment, density and size of fruit. The length of the longest leaf increased in response to an increase in watering treatment (Table 3; $F_{2,773} = 35.62$, $P < 0.001$) and fruit size ($F_{2,773} = 31.231$, $P < 0.001$, data not shown). The length of the longest leaf varied with density in the following order: 2 plants/pot > 5 plants/pot > 1 plant/pot > 6 plants/pot (Table 4; $F_{3,773} = 19.672$, $P < 0.001$). The watering treatment × density and the density × size interactions were both significant at $P < 0.001$ ($F_{6,773} = 2.37$ and $F_{6,773} = 13.95$, respectively). All density treatments (1–6 plants/pot) demonstrated an increase in the length of the longest leaf corresponding to the watering treatment ($F_{4,393} = 2.21$, $P < 0.05$). Plants from the highest density treatment (6 plants/pot) did not exhibit as much of a difference between the dry and wet treatments as the less dense treatments ($F_{4,393} = 13.62$, $P < 0.001$).

Table 1. The influence of germination temperature on the types of fruit produced (expected values are shown in parentheses)

Germination of seeds at:	Morph I	Morph II	Morph III	Morph IV	Morph V	Morph VI
Room temperature	30.88 (59.04)**	52.56 (59.10)**	82.67 (59.07)**	74.32 (59.07)**	66.67 (59.00)**	75.00 (59.08)**
4°C	31.37 (59.71)**	57.33 (30.20)**	80.00 (59.73)**	65.33 (59.73)**	73.33 (59.67)**	69.33 (59.73)**
$\chi^2 = 79.14$, $P < 0.001$						

* $P < 0.05$, ** $P < 0.01$.

Table 2. The effect of fruit type on plant root length (means with standard deviations in parentheses)

	Morph I	Morph II	Morph III	Morph IV	Morph V	Morph VI	$F_{5,130}$
Root length	16.17 (1.23)	15.38 (1.32)	17.79 (1.30)	17.17 (1.19)	16.77 (1.14)	21.25 (1.37)	6.00***

*** $P < 0.001$.

Table 3. The effects of watering frequency on aspects of plant reproduction (means with standard deviations in parentheses)

	Wet	Intermediate	Dry	d.f.	F
Leaves per plant	6.39 (1.36)	7.55 (1.57)	7.69 (1.75)	2,393	24.94***
Length of longest leaf (cm)	1.97 (0.57)	2.25 (0.60)	2.44 (0.78)	2,773	35.618***
Total flowers	18.35 (0.38)	15.54 (0.44)	12.49 (0.63)	2,1039	12.85***
Total inflorescences mass (mg)	2.51 (2.14)	1.28 (1.09)	0.58 (0.51)	2,254	22.8***
Inflorescences per plant	3.79 (4.38)	19.45 (2.60)	0.42 (0.93)	2,640	62.8***
Male	7.74 (0.27)	6.09 (0.31)	7.96 (0.307)	2,1039	14.96***
Female	10.61 (0.19)	9.46 (0.21)	4.53 (0.45)	2,1039	6.72***
Sex ratio	0.75 (0.03)	0.64 (0.0035)	0.58 (0.05)	2,1039	19.34***

*** $P < 0.001$.

Table 4. The effects of density on aspects of leaf development and plant reproduction (means with standard deviations in parentheses)

	Plants per pot					
	1	2	5	6	d.f.	*F*
Leaves per plant	6.667 (1.348)	7.761 (1.493)	7.089 (1.773)	7.220 (1.671)	2,393	3.3*
Length of longest leaf (cm)	2.164 (0.541)	2.539 (0.603)	2.261 (0.693)	2.151 (0.694)	3,773	19.672***
Total flowers	20.857 (8.413)	19.562 (6.456)	17.510 (6.467)	15.701 (5.755)	3,1039	1.978*
Inflorescences per plant	2.705 (3.232)	3.440 (4.831)	2.323 (3.529)	1.586 (2.605)	3,640	10.5***
Total inflorescence mass (mg)	2.100 (1.611)	3.021 (2.775)	1.868 (1.749)	1.414 (1.326)	3,254	5.4***
Male	9.661 (5.404)	8.695 (4.505)	7.803 (4.682)	6.529 (4.039)	3,1039	1.821*
Female	11.196 (3.646)	10.867 (3.140)	9.707 (3.116)	9.173 (2.602)	3,1039	3.43*
Sex ratio	0.872 (0.493)	0.816 (0.413)	0.841 (0.548)	0.714 (0.428)	3,1039	1.423*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 5. The effects of water treatment, seed size and density on aspects of leaf and plant development and plant reproduction (means with standard deviations in parentheses)

	Plants per pot					
	1	2	5	6	d.f.	*F*
Leaves per plant						
Morph I	6.733 (1.335)	7.724 (1.251)	6.065 (1.218)	5.888 (1.482)	6,393	7.01***
Morph II	5.800 (1.320)	7.172 (1.490)	7.347 (2.063)	7.030 (1.407)		
Morph III	7.467 (0.834)	8.367 (1.520)	7.486 (1.482)	8.210 (1.359)		
Plant mass						
Morph I	0.166 (0.192)	0.176 (0.257)	0.129 (0.214)	0.103 (0.126)	6,640	3.4***
Morph II	0.292 (0.260)	0.221 (0.245)	0.165 (0.183)	0.101 (0.148)		
Morph III	0.251 (0.320)	0.329 (0.383)	0.100 (0.117)	0.120 (0.132)		
Inflorescences per plant						
Wet	4.133 (3.681)	6.821 (5.963)	4.537 (4.500)	2.764 (3.591)	4,640	2.6*
Intermediate	3.286 (3.384)	2.433 (3.803)	1.855 (2.703)	1.729 (2.030)		
Dry	0.733 (1.100)	0.962 (1.371)	0.438 (1.147)	0.273 (0.611)		
Total inflorescence mass (mg)						
Wet	2.640 (1.581)	4.510 (2.988)	2.477 (2.042)	1.946 (1.592)	6,254	2.9**
Intermediate	2.275 (1.547)	2.121 (1.808)	1.067 (0.736)	1.048 (0.752)		
Dry	0.400 (0.408)	0.688 (0.360)	1.167 (1.079)	0.472 (0.424)		

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Adult plant size

Plant mass varied significantly among the density treatments (Tables 5 and 6), watering treatments and fruit size. Plants from the lower density treatments (1 and 2 plants/pot) exhibited a greater dry weight than those from the higher density treatments (5 and 6 plants/pot) ($F_{3,640} = 27.1$, $P < 0.001$). Plant dry weight decreased significantly as the frequency of watering decreased ($F_{2,640} = 170.0$, $P < 0.001$).

Plants from morph I fruits were significantly smaller than those from morph II and morph III fruits when watering frequency was decreased ($F_{2,640} = 5.2$, $P < 0.001$). The density × seed size (Table 5; $F_{6,640} = 3.4$, $P < 0.003$), density × watering treatment ($F_{6,640} = 10.7$, $P < 0.001$, data not shown) and seed size × watering treatment (Table 6; $F_{4,640} = 2.6$, $P < 0.03$) interactions were all significant, as was the three-way interaction ($F_{12,640} = 3.3$, $P < 0.001$). Plants in the highest two density treatments differed significantly from those in the one- and two-plants-per-pot treatments. Plants from morph I fruit were smaller than those from morph II and morph III fruits, although a *post-hoc* test did not indicate that they were significantly smaller, even though the ANOVA indicated a significant seed size effect. Plant mass increased significantly with increasing water.

Frequency of flowering

The proportion of plants that flowered differed significantly among the watering treatments ($\chi^2 = 99.9$, $P < 0.001$) (Table 7). Plants in the wet treatment were significantly more likely to flower than plants in the medium and dry treatments. This was true even when the data were analysed separately for each class of fruits ($\chi^2 = 31.7$, $\chi^2 = 32.7$ and $\chi^2 = 25.9$ for morphs I, II and III fruits respectively; all $P < 0.001$). The proportion of plants that flowered was greater than expected at the lowest density and less than expected at the highest density; however, this difference was not quite significant (Table 7; $\chi^2 = 6.38$, $P < 0.094$). When the data were analysed separately by fruit morph, density was found to have a significant effect on the likelihood of plants from morph II fruits flowering ($\chi^2 = 8.3$, $P < 0.05$). Plants in the lowest density treatment were significantly more likely to flower. This one treatment contributed 80% of the chi-square value. The same trend was observed in the morph I seed, although it was not significant. Nevertheless, two-thirds of plants from morph I fruits at the lowest

Table 6. The effects of water treatment and seed size on aspects of plant development and plant reproduction (means with standard deviations in parentheses)

	Morph I	Morph II	Morph III	$F_{6,640}$
Plant mass				
Wet	0.264 (0.240)	0.269 (0.242)	0.298 (0.269)	2.6*
Intermediate	0.079 (0.076)	0.110 (0.104)	0.092 (0.080)	
Dry	0.028 (0.021)	0.037 (0.066)	0.057 (0.092)	
Inflorescences per plant				
Wet	4.914 (5.273)	3.325 (4.200)	3.465 (3.747)	N.S.
Intermediate	1.492 (2.037)	2.650 (3.420)	1.635 (1.931)	
Dry	0.429 (1.021)	0.400 (0.969)	0.439 (0.850)	

* $P < 0.05$.

density flowered, whereas only 45% of those in the highest density treatment flowered. Whether or not a plant flowered was independent of the size of fruit a plant came from ($\chi^2 = 0.52$, N.S.).

Number of inflorescences

The number of inflorescences differed among the density treatments (Table 4; $F_{3,640} = 10.5$, $P < 0.001$), fruit size or morph classes (Table 8; $F_{2,640} = 2.9$, $P = 0.058$) and water treatments (Table 3; $F_{2,640} = 62.8$, $P < 0.001$). There were significant density × water treatment ($F_{6,640} = 4.5$, $P < 0.001$) and water treatment × fruit size ($F_{4,640} = 2.6$, $P < 0.037$) interactions (Tables 5 and 6). The density × fruit size class interaction and the three-way interaction were not significant. Plants in the one- and two-plants-per-pot treatments produced significantly more inflorescences than plants in the six-plants-per-pot treatment. There were no differences between the number of inflorescences produced by the five- and six-plants-per-pot treatments, or the two- and five-plants-per-pot treatments. Inflorescence number increased with increasing fruit size and increasing amounts of water.

Mass of combined inflorescences

The mass of combined inflorescences varied significantly for the watering treatments ($F_{2,254} = 22.8$, $P < 0.001$) and density treatments ($F_{3,254} = 5.4$, $P < 0.001$), but not fruit size

Table 7. The influence of watering frequency and density on flowering, and the proportion of plants that fruited (expected values are shown in parentheses)

	Flowers	No flowers	Fruit	No fruit
Watering frequency				
Wet	156 (117.3)	68 (106.7)	33 (43.1)	191 (180.9)
Intermediate	144 (123.1)	91 (111.9)	70 (45.2)	165 (189.8)
Dry	54 (113.6)	163 (103.4)	27 (41.7)	190 (175.3)
	$\chi^2 = 99.99$, $P < 0.001$		$\chi^2 = 26.2$, $P < 0.001$	
Density				
1 plant/pot	29 (23.0)	15 (21.0)	12 (8.5)	32 (35.5)
2 plants/pot	47 (44.0)	37 (40.0)	7 (16.2)	77 (67.8)
5 plants/pot	91 (85.9)	73 (78.1)	46 (31.5)	118 (132.5)
6 plants/pot	187 (201.1)	197 (182.9)	65 (73.80)	319 (310.2)
	$\chi^2 = 6.38$, $P < 0.094$		$\chi^2 = 17.8$, $P < 0.001$	

Table 8. The effect of seed size on plant reproduction (means with standard deviations in parentheses)

	Morph I	Morph II	Morph III	d.f.	F
Inflorescences per plant	2.373 (3.878)	2.200 (3.451)	1.779 (2.704)	2,640	2.9

$P = 0.058$.

($F_{2,254} = 0.6$, N.S.) (Tables 3 and 4). Only the density × watering treatment interaction (Table 5) was significant ($F_{6,254} = 2.9$, $P < 0.01$). Plants in the two-plants-per-pot treatment produced a greater biomass of inflorescences than in the other treatments; no other differences were significant. The total biomass of inflorescences increased significantly with increasing water, being highest in the wet treatment.

Mass of individual inflorescences

The mass of individual inflorescences varied only among the watering treatments ($F_{2,254} = 3.9$, $P < 0.001$). Plants in the dry treatment produced significantly lighter inflorescences than the other two treatments, while those in the intermediate watering treatment produced lighter inflorescences than plants in the wet treatment.

Numbers of flowers

Date. The total number of flowers differed significantly among the six dates ($F_{5,1039} = 7.97$, $P < 0.001$) (Fig. 3). Similarly, the number of female and male flowers also differed among the dates ($F_{5,1039} = 2.25$, $P < 0.048$; $F_{5,1039} = 11.64$, $P < 0.001$, respectively) (Fig. 3). The ratio

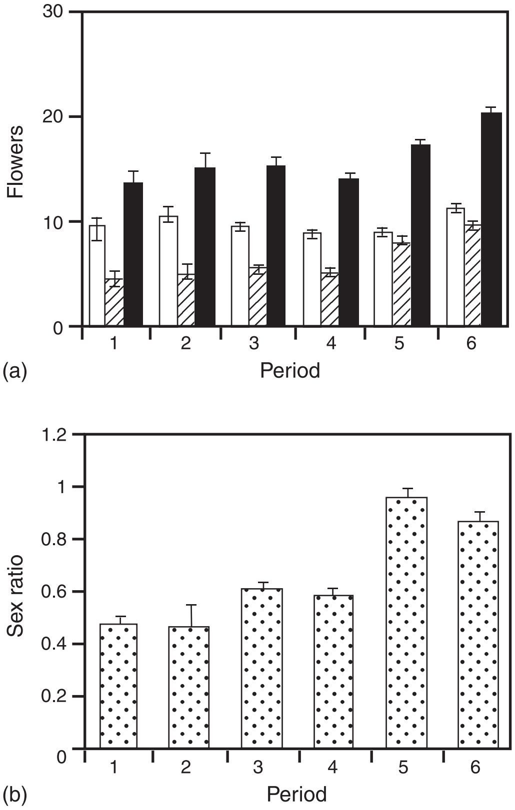

Fig. 3. The numbers of female (□), male (▨) and total (■) flowers (a) and the floral sex ratio (b) as a function of time. Note the increase in the floral sex ratio with time.

of male to female flowers also differed among the dates ($F_{5,1039} = 10.49$, $P < 0.001$). In general, the number of flowers and the proportion of male flowers increased throughout the season.

Density. Fewer female flowers were produced at higher densities ($F_{3,1039} = 3.43$, $P < 0.05$) (Table 4). The same trend was seen with male flowers, although the data were not significant ($F_{3,1039} = 1.82$, $P < 0.05$). The sex ratio and the total number of flowers did not differ among the density treatments.

Fruit size. The size of the fruit did not influence the number of flowers produced, either in total or for either sex, nor did it influence the floral sex ratio.

Watering treatment. The watering treatment significantly influenced the total number of flowers (Table 3) ($F_{2,1039} = 12.85$, $P < 0.001$), the number of female flowers ($F_{2,1039} = 6.72$, $P < 0.001$) and the number of male flowers ($F_{2,1039} = 14.96$). The floral sex ratio decreased significantly as the frequency of watering increased ($F_{2,1039} = 19.34$, $P < 0.001$).

The frequency of fruiting

Whether or not a plant produced fruit depended on the density of plants in the pots ($\chi^2 = 17.78$, $P < 0.001$) (Table 7), the watering treatment ($\chi^2 = 26.2$, $P < 0.001$) (Table 7) and the size of fruit the plant came from ($\chi^2 = 33.4$, $P < 0.001$). Plants from the morph III fruit size category produced fruits significantly more often than plants from other two size categories. Only 15.4% of plants from morph I fruits produced fruits, while 20.8% of morph II fruits produced fruits and 63.8% of plants from morph III fruits produced fruits. Plants from the one- and five-plants-per-pot treatments were significantly more likely to produce fruits than plants in the two- and six-plants-per-pot treatments. Surprisingly, plants in the five-plants-per-pot treatment are largely responsible for the significance of this result. Most of these plants that produced fruits were from morph III fruits (29 of the 46 plants that fruited were from morph III fruits, only 3 were from morph I fruits). Plants in the intermediate water treatment produced fruit significantly more often than plants in the other two watering treatments. Of the 61 plants that produced fruit in this treatment, 46 were from morph III fruits.

Number of fruit produced

The number of fruits produced was independent of density ($F_{3,111} = 2.60$, $P > 0.10$), watering treatment ($F_{2,111} = 0.29$, $P > 0.75$) and the size of the parental fruit ($F_{2,111} = 2.12$, $P > 0.10$).

Proportions of fruit types

The proportions of fruit types depended upon density ($\chi^2 = 73.32$, $P < 0.0001$) (Table 9). For example, 21.9% and 31.3% of the fruits produced by plants in the one- and two-plants-per-pot treatments respectively were morph II fruits, while only 11.4% and 13.9% respectively of the fruits produced in the five- and six-plants-per-pot treatments were morph II fruits. In contrast, the proportion of other fruit types was fairly uniform among the density treatments. Roughly one-third of the fruits produced by plants in each treatment were morph I fruits (a low of 30% in the two-plants-per-pot treatment and a high of 34.4% in the five-plants-per-pot treatment).

Table 9. The influence of density, watering treatment and seed size on the types of fruit produced (expected values are shown in parentheses)

	Morph I	Morph II	Morph III	Morph IV	Morph V	Morph VI	Morph VII
Density							
1 plant/pot	69 (73.3)	49 (33.0)	32 (17.2)	30 (44.8)	29 (25.9)	7 (18.1)	8 (11.8)
2 plants/pot	24 (26.2)	25 (11.8)	4 (6.2)	15 (16.0)	10 (9.3)	0 (6.5)	2 (4.2)
5 plants/pot	238 (226.6)	79 (101.7)	52 (53.2)	142 (138.0)	69 (79.9)	67 (55.8)	44 (36.3)
6 plants/pot	260 (265.6)	113 (119.5)	51 (62.5)	174 (162.2)	101 (93.9)	72 (65.5)	41 (42.7)
$\chi^2 = 73.32$, $P < 0.001$							
Watering frequency							
Wet	156 (156.3)	87 (70.4)	29 (36.8)	95 (95.5)	38 (55.3)	45 (38.6)	28 (25.1)
Intermediate	375 (364.7)	146 (164.1)	87 (85.8)	211 (222.8)	153 (129.0)	88 (90.1)	55 (58.6)
Dry	60 (70)	33 (31.5)	23 (16.5)	55 (42.8)	18 (24.8)	13 (17.3)	12 (11.3)
$\chi^2 = 30.61$, $P < 0.0023$							
Seed size							
Morph I	95 (94.8)	44 (42.7)	23 (22.3)	39 (57.9)	45 (33.5)	20 (23.4)	24 (15.2)
Morph II	162 (145.9)	43 (65.7)	43 (34.3)	71 (89.1)	41 (51.6)	57 (36.0)	29 (23.4)
Morph III	334 (350.3)	179 (157.7)	73 (82.4)	251 (214.0)	123 (123.9)	69 (86.5)	42 (56.3)
$\chi^2 = 65.18$, $P < 0.001$							

The type of fruit produced also depended on the watering treatment ($\chi^2 = 30.61$, $P < 0.0023$) (Table 9). Only 3.3% of the fruits produced by plants in the dry treatment were morph I fruits, whereas 20.8% of the fruits produced by plants in the intermediate watering treatment were morph I fruits. In contrast, morph VI fruits were produced in about the same proportions (9.4%, 7.9% and 6.1%) by plants in the wet, intermediate and dry treatments. Finally, the types of fruit produced by a plant depended upon the type of fruit that the plant came from ($\chi^2 = 65.18$, $P < 0.001$) (Table 9). For example, only 13.4% of the fruits produced by plants from morph I fruits were of morph IV, while 23.4% of fruits produced by morph III fruits were of morph IV.

Diversity of fruit types produced

The diversity of fruit types was independent of fruit size, watering treatments and density.

DISCUSSION

Evolutionarily we might expect that the different fruit morphs produce offspring that have different life-history properties because they are adapted to different environments (see Venable, 1985; Venable and Levin, 1985; Venable *et al.*, 1987, 1998; Venable and Burquez, 1989). We found that maternal investment in pericarp and embryo mass differed among the fruit morphs. Morph I fruits had significantly thinner pericarps and smaller embryos, although the differences in embryo weights were less than those of fruit weights (embryo weight varied by two-fold, whereas fruit weight varied by three-fold). Germination rate was highest for those morphs where the maternal parent had made the greatest investment (i.e. the large fruits had not only more massive pericarps but also larger embryos). Fruit morph profoundly impacted several early life-history features: seed germination, root and stem length and leaf number.

Fruit morph also influenced many later life-history parameters, including plant size, the number of inflorescences, the mass of the inflorescences, the frequency of fruiting and the proportion of fruit morphs produced. However, fruit morph did not influence the number of flowers or the floral sex ratio. In general, resource-intensive parameters (producing inflorescences or fruits) were enhanced by increasing fruit size, while parameters related to male fitness (the production of male flowers, floral sex ratio, frequency of flowering) were independent of fruit size.

To ascertain if the different morphs are adapted to different environments, we computed two composite fitness measures for the different morphs in each environment. The first is based upon the number of inflorescences (and thus flowers) and the second is based upon fruits. The first gives a measure of male reproduction and the second examines more directly female reproduction. In the first (Fig. 4) we computed the product of (1) the probability of a seed germinating, (2) the probability of survival, (3) the probability of flowering and (4) the number of inflorescences. For the second measure (Fig. 5) we multiplied the first composite measure by the average number of fruits per inflorescence. We then normalized the data to the most fit fruit morph.

In terms of inflorescences (flowers), plants from morph I fruits had their highest fitness at low density in the dry treatment (Fig. 4). In that environment, they were more fit than any of the other morphs; however, as density or water increased, the relative fitness of plants from morph I fruits declined. Plants from morph II fruits had higher fitness than morph III

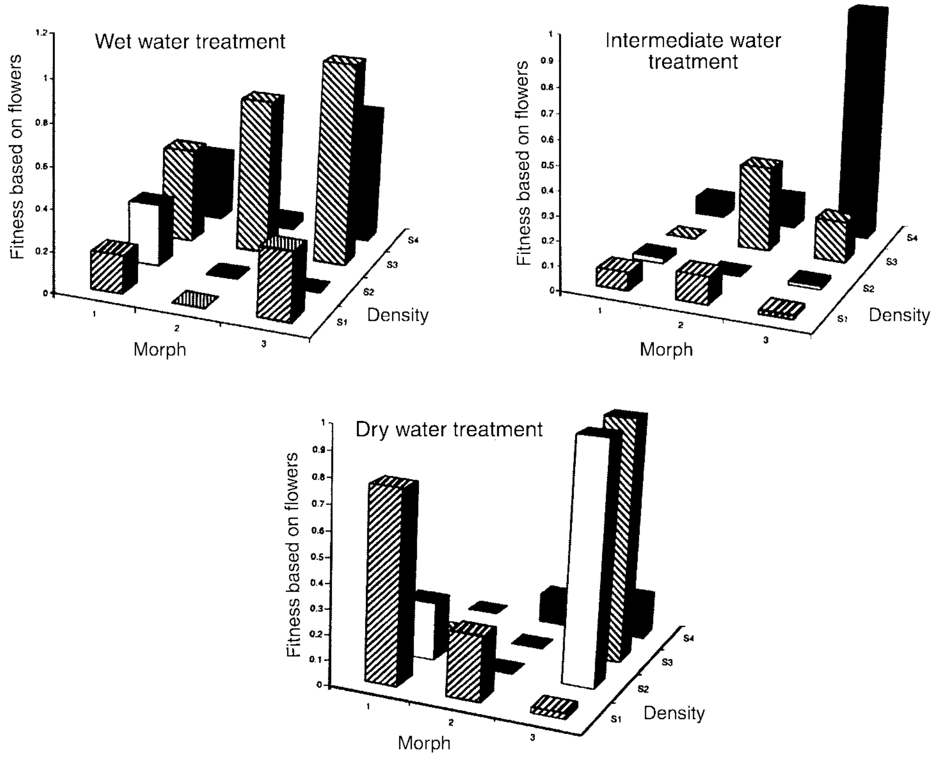

Fig. 4. Fitness based upon flower production should give an indication of reproductive potential via pollen. We computed this estimate as the product of the probability of a seed germinating, the probability of survival to flowering, the probability of flowering and the number of inflorescences. Here we show this measure differed among fruit morph, density and watering treatments.

in the dry treatment at a density of one plant per pot. However, as density increased, their fitness also declined. Plants from morph II fruits had their highest relative fitness at the five-plants-per-pot treatment in both the wet and intermediate watering treatments. In the intermediate water treatment, these plants were the most fit morph at a density of five plants per pot. Plants from morph III fruits were most fit at the two- and five-plants-per-pot densities in the dry treatment and were overwhelmingly more fit at higher densities in the wet treatment.

In terms of fruit production, plants from morph I fruits were overwhelmingly the most fit fruit morph in the dry treatment at a density of one plant per pot (Fig. 5). At higher densities, plants from the morph III fruits were considerably more fit in all watering treatments. Morph II only produced appreciable numbers of fruits at a density of five plants per pot in the intermediate watering environment. Thus, the different fruit morphs do appear to be adapted to different conditions. How this adaptive phenotypic plasticity evolved is not clear, but that it did evolve suggests that there are fine-scale persistent habitat differences in the Egyptian deserts.

In testing the various hypotheses proposed to explain heterocarpy, it is important that we have significant treatment effects. For example, plants in the wet and lowest density

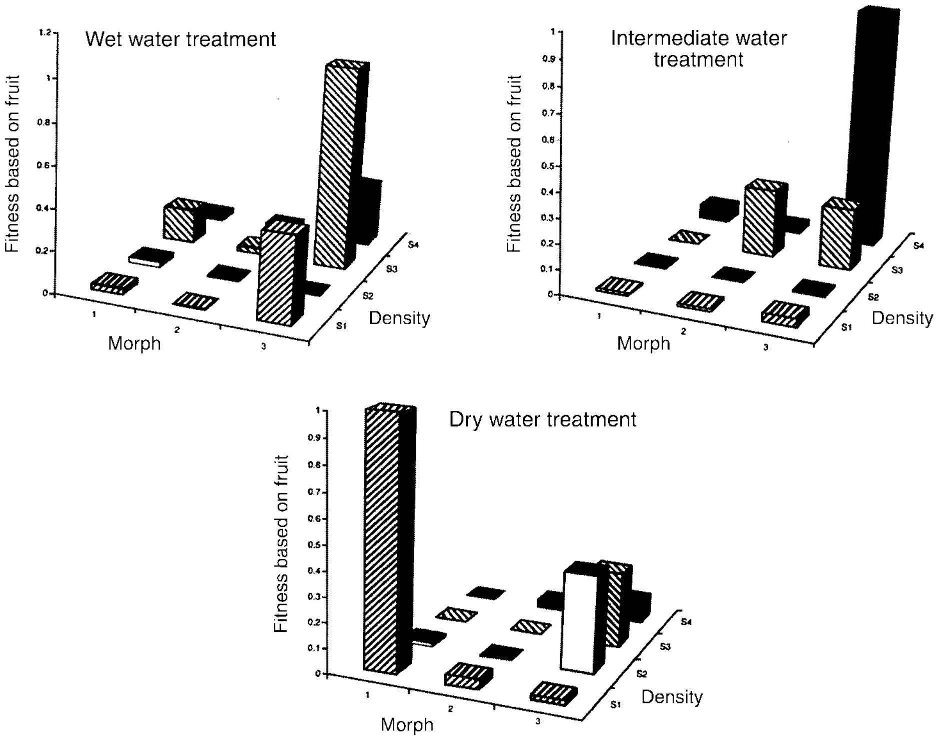

Fig. 5. Fitness based upon fruit production is an estimate of the reproductive potential via the female sexual function and was computed as the product of the fitness based on flower production and the average number of fruits per inflorescence. Here we show how this estimate of fitness is influenced by fruit morph, density and watering treatments.

treatments are expected to have the highest amount of resources and, according to theory, to produce the greatest diversity of fruit type. Thus, it is important to establish that our treatments influenced the plants. Our watering treatments significantly influenced plant size, the frequency of flowering, the number and mass of inflorescences, the frequency of fruiting and the proportion of fruit types. Similarly, our density treatments significantly impacted plant size, mass of inflorescences, the number of flowers, the frequency of fruiting and the proportion of fruit types. Thus, the plants were responsive to the gradients we imposed. Given this, we can now examine the specific predictions made regarding heterocarpy.

The hypotheses regarding fruit size are contrary to those regarding dispersal mechanisms (Venable, 1985; Venable and Levin, 1985; Venable *et al.*, 1987; De Clavijo, 1994). Locally dispersed fruits should have the greatest dormancy; that is, in our case, the small non-ornamented fruits are expected to show the greatest dormancy. We clearly found seeds from these fruits to have the lowest germination rate, even when vernalized. On the other hand, dispersed fruits (i.e. our ornamented fruits) should not display dormancy; these fruits clearly had the highest germination rates. Thus, our data match the expectations of the dispersal hypotheses. However, early developing fruits were predicted to have the greatest dormancy (i.e. our biggest ornamented fruits that developed most slowly and are expected to exhibit dormancy). Contrary to these expectations, seeds from these large fruits had the highest germination rates at both temperatures. While late developing fruits were expected to have the least dormancy (i.e. our small non-ornamented fruits should not be dormant), these seeds had the lowest germination rate. There were two hypotheses that dealt with diversity. Plants in nutrient-rich environments (our wet environment) were predicted to have the greatest variation in the types of fruits produced, and locally dispersed fruits were predicted to produce the lowest diversity of fruit types (McEvoy, 1984; Tanowitz *et al.*, 1987; Venable *et al.*, 1987). The diversity of fruit types was largely independent of watering treatment, density and the size of fruit the parent plant came from. These factors should profoundly impact available resources. Thus, our results do not support either prediction.

CONCLUSION

Calendula micrantha is unique in the Asteraceae in that it produces six types of fruits exclusively from ray flowers, and the largest fruits are adapted to be most broadly dispersed, have the largest embryos and are best able to accommodate highly competitive situations. Each fruit type does appear to be adapted to different environmental conditions. As a general rule, parameters associated with male fitness, flower number, frequency of flowering and floral sex ratio were unaffected by the size of fruit a plant came from. However, resource-intensive parameters (e.g. fruit number and fruit mass) were strongly influenced by the size of fruit a plant came from. Coupled with our results on density, this suggests that, as fruit population density increases, plants modify their own resource investments (into the various different morphs) and that this, in turn, has profound implications for sex allocation strategies of their progeny.

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