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EVIDENCE FOR SELECTIVE EMBRYO ABORTION
IN *CRYPTANTHA FLAVA*

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Because plants usually initiate more fruits and ovules than they have resources to mature, selective abortion of these structures may occur following fertilization. Selective fruit abortion based on such criteria as seed number and pollen parentage is apparently common (Stephenson 1981; Stephenson and Bertin 1983). Stephenson and Winsor (1986) studied the consequences of selective fruit abortion in *Lotus corniculatus* (Leguminosae). They randomly hand-thinned young ovaries to a number they knew the plant could mature, thereby allowing the development of fruits that would normally abort. Fruits on hand-thinned inflorescences produced fewer seeds than those on inflorescences that were allowed to thin naturally, and the seeds were of lower quality. Fewer seeds germinated, and those that did gave rise to less productive individuals.

Theory predicts that selection should also operate at the level of the embryo (Charnov 1979; Westoby and Rice 1982; Stephenson and Bertin 1983; Willson and Burley 1983). In most species, however, it is not possible to hand-thin ovules in the same way as fruits; thus, demonstrating selective abortion of viable embryos based on pollen parentage or zygote quality is more difficult (but see Marshall and Ellstrand 1988).

I report the results of hand-thinning ovules in the herbaceous perennial *Cryptantha flava* as a means of testing the hypothesis that potentially viable but normally aborted ovules have less vigorous embryos than those that would normally develop. Typical of the Boraginaceae, the gynoecium consists of four single-ovulate subunits. In *C. flava*, normally only one of the subunits develops into a nutlet (seed), even though more than 60% of the flowers initiate embryos in three or four ovules (Casper 1983). The mature nutlet may occupy any one of the four positions in the ovary.

At least a portion of the normally aborted ovules are capable of developing (Casper 1984, unpubl. data). If two or three subunits within an ovary are destroyed soon after fertilization, a remaining subunit will mature more often than expected under the assumption that only one particular ovule is capable of developing. Here, I compare the performance of offspring under field conditions when I arbitrarily chose which of the four ovules was to develop with the

performance of offspring when the ovules were allowed to thin naturally. I monitored seedling emergence, survival, and plant size during the first two growing seasons.

MATERIALS AND METHODS

The Species

Cryptantha flava (A. Nels.) Payson is a distylous but self-compatible species (Casper 1985) that occupies sandy, semidesert habitats throughout the Colorado Plateau. Adults have woody, branched caudices supporting multiple rosettes of narrow, oblanceolate leaves, which appear in April and senesce in late July or early August. Dispersal occurs in late June and July, about a month after flowering. Nutlets are not individually deciduous but, together with aborted subunits, are retained within a highly pubescent, deciduous calyx. Long-term field experiments have shown that approximately 98% of the seeds that germinate do so during the first year after planting (Casper, unpubl. data). Most seedlings emerge during October rains and remain green through the winter, although a few emerge in early spring. Plants normally do not flower until they are at least 3 yr old.

Of the 126 plants that were used for experimental treatment, thus serving as seed sources in this experiment, 111 were located in Steinaker State Park (Uintah Co.), Utah, an area protected from disturbance by livestock. The remaining 15 were located in an unfenced (County Road) population 10 km away, which is accessible to livestock. Both populations are described elsewhere (Casper 1987).

Experimental Treatments

In 1985, a total of 1970 naturally pollinated flowers on which the corolla was faded but not yet wilted were selected for experimental treatment. At this stage in fruit development, the four subunits of the ovary are slightly enlarged but of equal size, and histological studies show that fertilization has occurred (Casper, pers. obs.). The corollas were removed, and with the aid of a magnifying lens, fine forceps were used to crush three arbitrarily selected subunits in each flower. On the same plants, another 1266 flowers on which the corolla was beginning to wither were selected to serve as controls. In these flowers, one of the subunits of the ovary was just larger than the other three, but no other differences were apparent. The three smallest subunits were crushed, leaving the largest to develop. Experimental and control flowers differed in age from anthesis by about 24 h. Sample sizes per plant depended on the number of flowers in the requisite stages of development at the time of the experiment. Manipulated flowers were identified by applying indelible ink to the calyx.

Inflorescences with manipulated flowers were later covered with bags of coarse nylon netting that permitted airflow but caught the mature calyces and enclosed nutlets as they abscised. Bags were collected after all manipulated flowers had matured, and the marked calyces sorted. A portion of each calyx was removed to determine if the remaining ovule had developed and if mature nutlets had been damaged by the forceps. Because many nutlets are damaged in the process of

separating them from the remainder of the ovary, the mass of nutlets was not measured.

Seed Plantings

In late August 1985, experimental and control nutlets (entire ovaries) were planted at one site (site 1) in the County Road population and at four sites in Steinaker. Since adaptations to microsites might be important (Waser and Price 1985), locations were selected such that nutlets were usually planted within 10 m of their source plants, within the range of natural seed dispersal (Casper 1987). The top 5–7 cm of soil were screened to remove any nutlets of *C. flava* already present, and cylinders of stiff paper, 9 cm tall and 7–8 cm in diameter, were inserted into the soil protruding about 2 cm above the surface. These bottomless “cups” were placed approximately 0.5 m apart and organized in rows of various lengths, depending on the size and shape of the area of bare ground available. One nutlet was planted per cup, and nutlets from the two treatments were alternated. The cups helped stabilize the sandy soil and made it easy to determine losses caused by disturbance, usually trampling by deer. As much as possible, equal numbers of experimental and control nutlets were used from the same plants, and they were always planted alternately.

Cups were scored for the presence of surviving or dead seedlings in November 1985, June and July 1986, and late May 1987. In July 1986 and May 1987, plant height (measured from the point of attachment of the lowermost leaf) and the number of leaves were determined for each surviving seedling. The CATMOD procedure for multidimensional contingency-table analysis (SAS 1985) was used to compare between treatments and among sites (1) the total emergence by November 1985, (2) the survival of seedlings from November 1985 to July 1986, and (3) the proportions of seeds that yielded surviving seedlings at the July 1986 and May 1987 censuses. Size characteristics of seedlings were analyzed using SAS GLM for an unbalanced analysis of variance (ANOVA). Maternal plant was not included as a factor in the analysis since final sample sizes per plant were small. Any cups that had been disturbed were excluded from the calculation of percent emergence. Likewise, the death or disappearance of a seedling was not included in the survival data if the cup was severely disturbed.

RESULTS

Seed Maturation

Undamaged nutlets matured in 41.9% of the 1902 experimental flowers and 87.7% of the 1081 control flowers harvested. Among plants with 30 or more experimental flowers, the percentage of experimental flowers maturing a nutlet varied from 22.0% to 73.3% ($G_{\text{het}} = 41.6772$, $df = 12$, $P < 0.001$), indicating differences among plants either in the number of viable embryos per flower or in their ability to compensate for the loss of three ovules by maturing the fourth instead. Some undamaged nutlets in both groups were smaller than average or had thin, papery integuments. Since such nutlets occur in unmanipulated flowers and

TABLE 1
EFFECTS OF HAND-THINNING ON SEEDLING SURVIVAL

PARAMETER MEASURED	SITE					TOTAL
	1	2	3	4	5	
Total emergence						
Experimental	51.9 (52)	66.5 (176)	47.9 (267)	58.1 (136)	20.0 (150)	48.8 (781)
Control	61.5 (52)	60.8 (176)	52.6 (268)	60.3 (136)	38.0 (150)	58.6 (782)
Seedling survival (Nov. to July)						
Experimental	84.0 (25)	50.0 (114)	77.8 (126)	76.9 (78)	58.6 (29)	68.0 (372)
Control	70.0 (30)	76.7 (103)	70.2 (141)	86.1 (79)	64.9 (57)	74.1 (410)
Survival from planting to July 1986						
Experimental	44.9 (49)	36.3 (160)	40.4 (260)	48.5 (134)	12.5 (144)	35.9 (747)
Control	47.8 (46)	51.9 (160)	38.2 (262)	55.2 (134)	26.9 (145)	42.6 (747)
Survival from planting to May 1987						
Experimental	22.5 (49)	26.0 (158)	33.1 (260)	27.8 (133)	7.7 (143)	25.0 (743)
Control	32.6 (46)	32.1 (159)	31.3 (262)	39.4 (127)	14.7 (143)	29.7 (737)

NOTE.—The percentage of seeds emerging in November 1985, the percentage of seedlings surviving from November to July 1986, and the percentage of planted seeds yielding successful seedlings at the July 1986 and May 1987 censuses for each treatment. Sample sizes are in parentheses. Sites 2–5 are in Steinaker State Park; site 1 is 10 km away. Differences in sample sizes among censuses reflect loss of cups to disturbance.

are capable of germinating in the greenhouse (Casper, pers. obs.), they were included in the plantings. Another 7.8% of the experimental group and less than 1% of the control flowers produced nutlets that bore damage from the forceps. Only 5 experimental flowers and 7 controls matured two nutlets; some of these were also damaged. Damaged nutlets and those produced in pairs were not planted.

Emergence and Seedling Survival

By the November 1985 census, 96% of all emergence had occurred; the remainder had taken place by June 1986. Emergence by November was significantly higher in the controls than in the experimentals ($P < 0.03$), but there were large differences among sites ($P < 0.0001$) and a significant treatment-by-site interaction ($P < 0.03$; tables 1, 2). The interaction term probably reflects more emergence in the experimental group at site 2. No seedlings were dead at the November 1985 census.

The proportion of seedlings present in November 1985 that survived until July

TABLE 2
EFFECTS OF HAND-THINNING ON SEEDLING SURVIVAL ANALYZED USING A
THREE-WAY CONTINGENCY TABLE

EXPERIMENTAL FACTOR	EMERGENCE (Nov. 1985)		SEEDLING SURVIVAL (Nov. 1985– JULY 1986)		SURVIVAL (PLANTING– JULY 1986)		SURVIVAL (PLANTING– MAY 1987)	
	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
Treatment (df = 1)	4.74	0.0294	0.74	0.3898	8.57	0.0034	7.27	0.0070
Site (df = 4)	85.18	0.0001	18.00	0.0012	65.27	0.0001	43.96	0.0001
Treatment by site (df = 4)	11.40	0.0224	18.21	0.0011	11.46	0.0219	6.00	0.1993

1986 did not differ between treatments. The proportion of seeds yielding an established seedling in July 1986, which included emergence after the November 1985 census, was greater in the controls ($P < 0.004$). For both measures of seedling survival through July 1986, there were highly significant differences among sites and significant treatment-by-site interactions. The interaction was less pronounced for survival from planting ($P < 0.03$), however, than for the survival of seedlings from November until July ($P < 0.002$). Because seedling mortality offset the higher emergence in the experimentals at site 2, survival from planting at site 2 was 36.3% in the experimentals and 51.9% in the controls by July 1986. The survival of seedlings from November to July was greater for the experimentals at sites 1 and 3. Survival from planting until July 1986 was greater for the experimentals only at site 3.

Although a significant treatment-by-site interaction term may make evaluation of the treatment effect problematic, the interaction was not significant for survival from planting until May 1987, the date of the last census ($P < 0.1993$; tables 1, 2). The control group still yielded significantly more seedlings ($P < 0.007$), and differences among sites were still highly significant ($P < 0.0001$). Overall, survival from planting had declined from 39% in July 1986 to 27% in May 1987.

Seedling Size

Treatments did not differ in the number of leaves per seedling or in plant height in either 1986 or 1987 (tables 3, 4). In each analysis, the site effect was highly significant ($P < 0.0001$), but there was no treatment-by-site interaction.

DISCUSSION

This study provides the first evidence that higher-quality plant embryos selectively mature. The experimental treatment caused many fertilized ovules that normally would have aborted to develop into seeds. These seeds were less successful in establishing seedlings than were naturally maturing seeds. The results are consistent with the predictions of Westoby and Rice (1982) that plants make ovule-abortion decisions based on the vigor of the developing offspring.

TABLE 3
 MEAN NUMBER OF LEAVES AND MEAN HEIGHT FOR SEEDLINGS ALIVE AT THE
 JULY 1986 AND MAY 1987 CENSUSES

PARAMETER MEASURED	SITE					TOTAL
	1	2	3	4	5	
1986						
No. of leaves						
Experimental	5.9 (21)	6.1 (56)	7.7 (101)	5.1 (60)	4.9 (18)	6.4 (256)
Control	5.8 (22)	6.3 (83)	7.1 (98)	5.2 (70)	4.4 (37)	6.0 (310)
Plant height (mm)						
Experimental	18.4 (21)	25.9 (56)	30.3 (101)	20.6 (60)	21.0 (18)	25.4 (256)
Control	17.7 (22)	25.2 (83)	29.0 (98)	19.7 (70)	20.9 (37)	24.0 (310)
1987						
No. of leaves						
Experimental	12.9 (11)	25.6 (40)	18.6 (83)	12.5 (37)	10.3 (11)	18.0 (182)
Control	12.3 (14)	28.0 (52)	18.9 (81)	12.9 (48)	9.0 (21)	18.4 (216)
Plant height (mm)						
Experimental	31.6 (11)	39.2 (40)	38.9 (83)	30.2 (37)	18.3 (11)	35.5 (182)
Control	32.9 (14)	38.0 (52)	37.6 (81)	27.2 (48)	22.9 (21)	33.6 (216)

NOTE.—Sample sizes are in parentheses; sites are as in table 1.

That many normally aborted ovules developed is indicated by the high percentage of experimental flowers in which a seed matured. If only one particular ovule were capable of developing in each ovary, a seed would have matured in 25% of the experimental flowers. In fact, a seed developed in 41.9%. This difference would be even greater if calculation of the expected took into account the 10%–26% of all naturally pollinated flowers that usually do not produce seeds and the 4%–10% that produce two (Casper 1983).

The difference in quality between embryos that would normally be aborted and those that would mature may be underestimated. When I destroyed three ovules in the experimental flowers, I had no way of identifying and thus always eliminating the one ovule that would have matured naturally. At least 25% of the seeds in the experimental group would have been among those maturing in the absence of my experimental treatment.

The ability to establish, which includes both emergence and seedling survival, may be the only component of plant fitness through which between-treatment differences in seed quality are expressed in this experiment. The lack of a treatment effect for both measures of plant size may mean that the remaining individuals will not differ in ultimate reproductive output. The high variation among sites for all measures of performance may be due either to maternal effects, since seeds were planted only in their native sites, or more likely, to local soil types, which

TABLE 4
ANALYSES OF VARIANCE OF SIZE DATA IN TABLE 3

Source	Sum of Squares	df	F	P
1986				
ln plant height*				
Treatment	0.08	1	1.58	0.2771
Site	17.92	4	47.17	0.0001
Treatment by site	0.19	4	0.50	0.7352
Error	52.79	556		
Number of leaves				
Treatment	3.05	1	0.85	0.4094
Site	530.96	4	45.91	0.0001
Treatment by site	14.41	4	1.25	0.2901
Error	1607.46	556		
1987				
Plant height				
Treatment	0.25	1	0.00	0.9599
Site	12296.91	4	20.31	0.0001
Treatment by site	351.84	4	0.58	0.6766
Error	71693.48	388		
Number of leaves				
Treatment	3.55	1	0.13	0.7390
Site	12168.18	4	28.22	0.0001
Treatment by site	111.30	4	0.26	0.9047
Error	41830.73	388		

NOTE.—Treatment was considered a fixed effect and site a random effect.

* Plant height in 1986 was ln-transformed to equalize the variances.

differ noticeably in color and amount of clay. A large between-treatment difference in survival from planting occurred at site 5, where overall establishment was lowest. Selection against offspring arising from normally aborted seeds may be more pronounced in unfavorable habitats.

Before a possible adaptive significance can be assigned to embryo abortion, it is important to determine whether the first ovule fertilized is the one that usually matures. If it is, what could be interpreted as selective ovule abortion might really be an expression of pollen-tube competition (Mulcahy and Mulcahy 1975; Lee 1984; Lee and Bazzaz 1986). The production of extra ovules and the abortion of some viable embryos would then have little function in improving the quality of offspring.

Even if the first ovule fertilized is the one that usually matures in *C. flava*, the extra ovules might still be important as backups if the first ovule should fail. Although they may be of lower quality on the average, many of the normally aborted ovules are capable of developing into productive seeds.

The difference in seed quality observed in this study may have been caused by different physiological responses of the ovaries and not by the genotypes of the embryos. The control flowers were about 24 h older than the experimentals, and the time in development when the ovules are destroyed might be important. Prematurely removing some reproductive structures might upset initial source-sink relationships (Lovett Doust and Eaton 1982; Watson and Casper 1984) and

thus plant-resource levels, adversely affecting seed quality. In addition, forcing a flower to distribute resources to an ovule that it normally would not mature might itself result in an inferior seed. These cautions apply to fruit-thinning experiments as well.

SUMMARY

In each ovary of *Cryptantha flava*, three of the four ovules usually fail to develop, even though all of them may be fertilized. I tested the hypothesis that ovules with more-vigorous embryos selectively mature. Following fertilization but before ovule abortion, three arbitrarily selected ovules were destroyed in each of 1970 (experimental) flowers. The performance of offspring produced by these flowers was compared with the performance of offspring from control flowers in which any one of the four ovules could develop. In the control flowers, when one ovule was just larger than the others, the other three ovules were destroyed. The seeds resulting from both treatments were planted near their source plants at several locations in the field. Emergence, seedling survival, and seedling size were monitored through two growing seasons. Less emergence occurred in seeds produced by the experimental treatment than in control seeds, but seedling survival during the first year did not differ significantly. Overall survival from planting was greater for the controls in both years. Plant height and the number of leaves per plant did not differ between treatments for either year. For all measures of success, there were significant differences among sites and, for some, significant treatment-by-site interactions. The results are consistent with the selective maturation of higher-quality embryos, but alternative explanations are also given.

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