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## POSTDISPERSAL SIBLING COMPETITION AND THE EVOLUTION OF SINGLE-SEEDEDNESS IN *CRYPTANTHA FLAVA*

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The evolution of indehiscent (unopening) single-seeded fruits dehiscent, multiseeded fruits has apparently occurred many times among flowering plants (Stebbins 1967; Cronquist 1968; Casper and Wiens 1981; Uma Shaanker et al. 1988). In some taxa, single-seededness is achieved through a reduction in ovule number, whereas in others more than one ovule is present, but only one matures into a seed. The repeated evolution of single-seededness together with indehiscence suggests strong selection pressure for single-seeded dispersal units (Cronquist 1968; Casper et al. 1992).

Single-seeded dispersal units could have several advantages. For wind-dispersed species in which the entire fruit serves as the diaspore, a reduction in seed number can increase dispersal distance (Augsburger and Hogan 1983; Augsburger 1986), which is important when the probability of postdispersal seed predation and/or seedling mortality increases with local seed densities or proximity to the parent plant (Janzen 1970; Connell 1971; Howe and Smallwood 1982). However, because the association of single-seededness and indehiscence also occurs among species dispersed by animals (Casper et al. 1992), additional, more-general fitness advantages are likely. Packaging only one seed per fruit could minimize predispersal seed predation (Herrera 1984) or compensate for increases in the number of fruits or seed size (Adams 1967; Marshall et al. 1985). Uma Shaanker et al. (1988) suggest that the abortion of all but one ovule results from competition among the developing offspring and may not be in the best interest of the maternal plant. This study tests another possibility—that sibling competition arising when more than one seed germinates in the same location is an important factor selecting for single-seeded dispersal units (Casper and Wiens 1981; Casper et al. 1992).

Sibling competition is used here to mean a density-dependent reduction in performance among interacting siblings relative to the performance of siblings when they are not interacting, the definition favored by Cheplick (1992). Sibling competition has also been applied to the relative intensity of competition among genetically similar individuals compared with competition among individuals less closely related (Williams and Mitton 1973; Williams 1975; Maynard Smith 1978). Although both forms of sibling competition may be relevant to some evolutionary problems, the first usage more often is considered important in the evolution of some dispersal and seed dormancy traits (Hamilton and May 1977; Venable and Lawlor 1980; Schoen and Lloyd 1984; Ellner 1986; Quinn and Engel 1986), whereas the latter form is more often hypothesized to be a factor in the evolution of sexual breeding systems and outcrossing (Williams and Mitton 1973; Williams 1975; Maynard Smith 1978; Taylor 1979; Bulmer 1980). Empirical studies, which have addressed mostly the second hypothesis (e.g., Ellstrand and Antonovics 1985; Schmitt and Antonovics 1986; Willson et al. 1987; Kelley et al. 1988; McCall et al. 1989; Tonsor 1989), differ widely in their findings (Cheplick 1992).

In this study, competition among seedlings from the same dispersal unit is examined in the semidesert, herbaceous perennial *Cryptantha flava*. Like most members of the Boraginaceae, *C. flava* has four ovules; although all four ovules often initiate embryos, usually only one (sometimes two) develops into a mature nutlet (seed). At least eight congeneric species exhibit this fixed reduction in seed number, and in all cases, the nutlet is persistent within a highly pubescent calyx, which serves as the dispersal unit and is functionally analogous to an indehiscent fruit. The unit is dispersed by wind, but one- and two-

seeded dispersal units do not travel different distances (Casper and Grant 1988). In species that mature one to four ovules, the nutlets separately abscise.

The fitness consequences of postdispersal sibling competition in *C. flava* were examined over a 9-yr study. The maturation of all four ovules per dispersal unit was simulated by planting four nutlets, collected from the same maternal parent, together in clusters. Survival and inflorescence production are compared for individuals arising from these four-seeded "dispersal units" and those generated by planting nutlets individually.

#### MATERIALS AND METHODS

The study species grows in sandy soils throughout the semiarid Colorado Plateau of eastern Utah and adjoining states. The woody, often branched caudex—a shortened, mostly underground stem—bears densely packed rosettes of nearly vertical, narrow oblanceolate leaves, such that the aboveground morphology resembles a clump of grass. Leaves initiate in early spring and are largely senescent by late summer. A rosette dies after producing a single inflorescence which, on average, bears 25–40 flowers. Flowering begins in early to late May, depending on the location and year and continues for about a month. Nutlets ripen approximately a month later. Most seedlings emerge with October rains and remain green throughout the first winter, although a few new seedlings may emerge in early spring (Casper pers. obs.). Herbivory is confined mostly to inflorescences (Casper pers. obs.).

The two field sites are located about 12 km apart in Uintah County in northeastern Utah. Both are dominated by *Juniperus osteosperma* and various species of shrubs, especially *Artemisia tridentata*. Site 1 is located on rangeland managed by the United States Bureau of Land Management; site 2 is protected from grazing within the boundaries of Steinaker State Park. Cattle rarely damage plants by trampling, and they do not usually forage on them. The natural population of *Cryptantha flava* is more extensive, and mean plant size is larger at site 1 (Casper unpubl. data).

The experiment was begun in late August 1983 by planting nutlets collected from 50 maternal parents at site 1 in July. At each planting location, the soil was screened to remove any nutlets dispersed naturally, and bottomless paper cups, 7.0 cm to 8.0 cm in diameter, were inserted into

the soil such that about 2.0 cm protruded above the surface. The cups stabilized the sandy soil and defined the exact planting locations. Cups were placed in association with shrubs, arbitrarily selected without regard to species. At each shrub, four cups were placed under the edge of the canopy, and four were placed in the open, at least 0.5 m from the shrub. *Cryptantha flava* occurs naturally in both microhabitats (Casper pers. obs.). Cups were spaced at least 0.4 m apart and were alternately planted with one or a cluster of four nutlets. All four nutlets within a cluster, and in most cases all nutlets planted in association with a particular shrub, were from the same maternal plant. Thus, seeds planted in clusters were at least half-sibs as they would be if they had matured within the same dispersal unit. The plantings were replicated at 190 shrubs at site 1 and 144 at site 2 for a total of 6680 planted nutlets.

Censuses were conducted in November 1983, three times during the growing seasons of 1984 and 1985, and once annually, usually in late May, thereafter. Dead plants often remained until the next census, and missing plants were scored as dead unless there was evidence of disturbance. Plants were individually tagged in 1985 with color-coded wires. Several plant size parameters were measured once in 1984 and 1985 and at each subsequent census, but only survival and numbers of inflorescences, both important fitness components, are reported here. Mean lifetime numbers of inflorescences per plant were calculated by including all plants that flowered at least once, regardless of whether they were still alive at the end of the 9 yr of observations.

In 1992, whole, mature fruiting stalks were collected from plants currently growing alone and with at least one other individual to determine if density affects the number of flowers or the number of nutlets per inflorescence. For each plant, up to four inflorescences were examined, and values were expressed as the mean number of flowers (or nutlets) per inflorescence. Sampled plants were selected arbitrarily and were equally distributed between the two microhabitats.

Because most measures of plant performance differed greatly between the two sites, data for each site were analyzed separately. The SAS CATMOD procedure (SAS 1985) was used to analyze survival as a function of density and microhabitat. Randomization techniques (Manly 1991) were used to determine probability levels in ANOVA examining lifetime inflorescence

TABLE 1. Percentage of survival during the first growing season, in all subsequent years, and for all years combined for each microhabitat/density combination. Microhabitats are either under or away from shrubs. Density category is status at the beginning of each time period.

	November 1983–August 1984		August 1984–May 1992		November 1983–May 1992	
	One	Clump	One	Clump	One	Clump
<b>Site 1</b>						
Under	39.4	36.5	37.6	24.4	14.5	13.0
Away	32.4	34.4	22.0	21.3	7.7	7.4
<b>Site 2</b>						
Under	54.9	48.4	29.3	26.6	15.4	11.2
Away	58.0	53.8	17.0	12.1	9.3	6.9

production and year of first flowering when transformation failed to normalize data.

## RESULTS

### Survival

Long-term survival was not density dependent at either site. A total of 1769 seedlings emerged at site 1 and 1274 at site 2 representing 44.7% and 48.6%, respectively, of the planted seeds. The highest annual mortality occurred between the first census in November 1983 and the last census of 1984, the end of the first growing season. During that time, 63.3% of all seedlings died at site 1, and 45.2% died at site 2, but mortality was independent of density category (based on one versus more than one seedling emerging) and microhabitat at both sites. Mortality leveled off to between 8.0% and 22.0% in most subsequent years but jumped to 30.4% at site 1 and 38.3% at site 2 between 1988 and 1989, a year of apparently severe drought (Casper pers. obs.). When mortality from August 1984 to May 1992 was analyzed as a function of density status in August 1984 and microhabitat, the effect of density approached significance only for site 1 ( $\chi^2 = 3.47$ ,  $P = 0.06$ ) and was insignificant at site 2 (table 1). From 1984 to 1992 percentage mortality was greater in the open at both sites ( $\chi^2 = 6.92$ ;  $P < 0.01$  for site 1;  $\chi^2 = 15.93$ ;  $P < 0.001$  for site 2). Similarly, when mortality over the entire course of the experiment was analyzed as a function of whether one or more than one seedling emerged, mortality was found to be greater in the open microhabitat ( $\chi^2 = 14.05$ ,  $P < 0.001$  for site 1;  $\chi^2 = 6.98$ ,  $P < 0.01$  for site 2) but not different between emergence densities. The density-by-

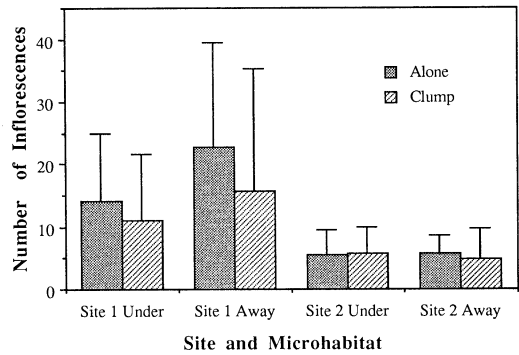


FIG. 1. Lifetime number of inflorescences (mean  $\pm$  SD) produced by all plants that flowered at least once, for each planting density and microhabitat combination.

microhabitat interaction term was not significant in any analysis.

### Reproduction

Plant density did affect reproduction but only at one site. The mean lifetime number of inflorescences produced per flowering individual differed with planting density at site 1, where flowering individuals arising from single nutlets produced, on average, 1.35 times more inflorescences than did individuals arising from a cluster of nutlets (fig. 1;  $F = 4.64$ ,  $P < 0.05$ ). The mean lifetime number of inflorescences was also higher for plants growing in the open at site 1 ( $F = 8.16$ ,  $P < 0.01$ ) but did not differ between microhabitats at site 2. On average, plants arising from one nutlet at site 1 flowered sooner than those planted in clusters (fig. 2,  $F = 13.88$ ,  $P < 0.002$ ), and those growing in the open flowered before

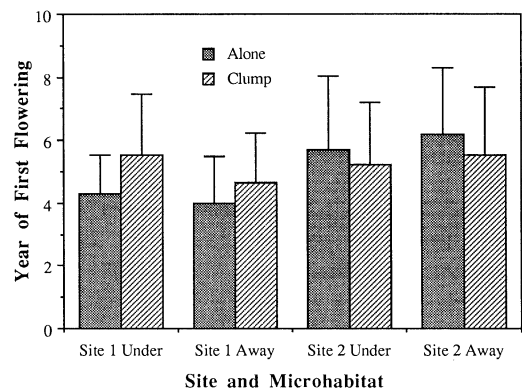


FIG. 2. Year of first reproduction (mean  $\pm$  SD) for each planting density and microhabitat combination.

those under shrubs ( $F = 15.80$ ;  $P < 0.02$ ). Nutlets planted in all combinations of density and microhabitat were equally likely to produce a plant that lived to flower at least once.

For the fruiting stalks collected in 1992, the mean number of flowers per inflorescence varied greatly among individuals (range 11.0–90.0, site 1; 7.0–51.3, site 2) as did the mean number of nutlets per inflorescence (range 1.3–61.5, site 1; 6.0–50.0, site 2). Neither quantity differed between current density categories at either site (Mann-Whitney  $U$ -Test,  $P > 0.11$ ).

#### DISCUSSION

Sibling competition does not appear to be a strong selective force in the evolution of single-seeded dispersal units in *Cryptantha flava*. Post-dispersal sibling competition arising from simulated four-seeded dispersal units reduced lifetime reproductive output and delayed the age of first reproduction at only one of the two study sites. No density-dependent effect on long-term survival existed. Apparently the fitness gained by eliminating postdispersal sibling competition does not equal the lost fitness potential of the three abortive seeds. The evolution of single-seededness was likely accompanied by increases in some other component(s) of seed yield such as flower (fruit) number or nutlet size.

At the site where density-dependent responses were observed, a mean of 0.59 flowering stalks was generated per nutlet for nutlets planted singly under the canopy of shrubs and 0.39 for nutlets planted in the same microhabitat but in clusters of four, yielding a selection coefficient of about 0.34. Planting density affected fitness less in the open microhabitat, resulting in a selection coefficient of 0.21. Thus, four nutlets produced in four separate flowers should yield, on average, only 1.39 times more flowering stalks than four nondeciduous nutlets produced in the same flower. The above calculations of fitness do not take into account (1) differences in the age of first reproduction, which gives single nutlets a slightly greater fitness advantage, (2) differences among sites in the strength of density-dependent effects, or (3) fitness increases resulting from selective abortion of genetically inferior embryos (Casper 1988). Dispersing seeds in clusters might also reduce fitness further by increasing inbreeding among the offspring.

Few experimental studies have evaluated the importance of sibling competition in the evolution of single-seededness. Like *C. flava*, the

tropical tree *Platypodium elegans* and *Quercus macrocarpa*, bur oak, have ovaries with multiple ovules but mature one or, less often, two seeds. Glasshouse experiments examining seedling emergence and performance found one- and two-seeded fruits of *P. elegans* equally likely to generate only one surviving seedling (Augspurger 1986); twin seedlings of bur oak were smaller but survived as well as single seedlings (Garrison and Augspurger 1983). In both species, the smaller biomass of seeds from two-seeded fruits accounted largely for the differences in performance. Similarly, seed-size differences probably also explain the results of a field experiment comparing seedling establishment from naturally produced one-seeded and two-seeded dispersal units of *C. flava* (Casper 1990); the nutlets of single-seeded dispersal units were more likely to produce successful seedlings than were the smaller nutlets of two-seeded dispersal units, but two-seeded dispersal units were more likely to generate at least one seedling.

Quinn (1987) examined the possibility that postdispersal sibling competition played a role in the evolution of differential seed germinability in *Buchloe dactyloides*, which produces burs containing one to five seeds with often staggered germination. Competition affected seedling size but not survival, and Quinn concluded that the benefits of packaging seeds in burs outweigh costs of any multiple germinations from the same dispersal unit.

This study is based on the assumption that the perennial species of *Cryptantha* having both fixed ovule abortion and single-seeded dispersal units evolved from species in which all four ovules were capable of maturing. The assumption is based on (1) four ovules being characteristic of the family Boraginaceae (Cronquist 1968), and (2) most species of *Cryptantha* producing one to four deciduous nutlets. Sibling competition could have played a role in the evolution of single-seededness only if the use of the calyx as the dispersal unit evolved prior to the fixed ovule abortion, but it is not possible to discern from extant species the order in which these traits arose. There are no obvious intermediates among the nearly 60 perennial species in North America (Higgins 1971), although at least one species has a dispersal dimorphism; *Cryptantha johnstonii* produces three deciduous nutlets and one persistent nutlet that is dispersed with the calyx (Casper pers. obs.). The current study does not discount the possibility that single-seededness

could have evolved prior to the use of the calyx as the dispersal unit. Packaging nutlets within the calyx is itself adaptive because it both facilitates dispersal by wind and greatly reduces granivory by ants (Casper 1987).

Although nutlets of *C. flava* are smaller when two mature (Casper and Grant 1988), current size differences alone also do not necessarily provide evidence for an evolutionary trade-off in nutlet number and size. The species considered most closely related to *C. flava*, *Cryptantha confertiflora* (Higgins 1971), produces up to four deciduous nutlets that are larger than those of *C. flava*, but *C. confertiflora* has far fewer flowers per inflorescence (Casper unpubl. data).

In general, the microhabitat in which nutlets were planted more strongly affected fitness traits than did planting density. At both sites, plants in the open microhabitat were less likely to survive than those under shrubs, and at site 1, plants in the open produced considerably more inflorescences. Shrubs may increase longevity by mediating temperature extremes, reducing evaporative water loss, or improving soil nutrient levels (Fowler 1986). However, reproductive output under shrubs may be light limited. Consistent with demographic responses found here, seedlings are naturally more common in the open, but adults are equally abundant in the two microhabitats (Casper unpubl. data).

Large differences also exist between populations in the overall performance of plants and in the importance of planting density as a factor affecting fitness. Both study sites support large natural populations of *C. flava*, but site 2, where no effects of density were detected, appears a less suitable habitat for this species. Individuals in the natural population at site 2 are also much smaller and produce far fewer inflorescences than do those at site 1 (Casper unpubl. data). Nutlets used in this experiment were all collected at site 1, allowing for the possibility that adaptation to the local habitat accounted for the differences between sites in plant performance, but that seems unlikely because natural populations exhibit parallel differences.

The strong association between indehiscent fruits and single-seededness in other taxa (Casper et al. 1992) suggests that postdispersal sibling competition could have widespread importance in the evolution of single-seededness. It is likely that the grasslike growth form of *C. flava* minimizes aboveground interactions, limiting competition to belowground. Postdispersal compe-

tion among plants arising from the same dispersal unit might well prove more severe for species where canopies of adjacent plants overlap, or for those occurring in more productive habitats, where competition may be generally more important (Keddy 1989).

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