Amer. J. Bot. 75(6): 859–863. 1988.

MORPHOLOGY AND DISPERSAL OF ONE- AND TWO-SEEDED DIASPORES OF CRYPTANTHA FLAVA[1]

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ABSTRACT

The wind-dispersed diaspore of the herbaceous perennial *Cryptantha flava* (Boraginaceae) consists of one, or occasionally two, nutlets (seeds) enclosed in a pubescent calyx. Physical characteristics of one- and two-seeded diaspores and their rates of descent in still air were compared. Natural dispersal distances in the field of calyces containing 0, 1, or 2 seeds were also measured. Two-seeded diaspores are wider at the ovary and have a greater total mass, a greater mass of the ovary, and a higher rate of descent in still air than one-seeded diaspores. Under field conditions, however, there is no difference in how far calyces containing 0, 1, or 2 seeds disperse. Thus rate of descent is not a good predictor of relative dispersal distances in this species. Much of the dispersal in the field must occur as movement along the surface of the ground, and during such secondary dispersal, the greater width of two-seeded diaspores may compensate for the potentially opposing effect of their greater mass.

ALTHOUGH ALL FOUR OVULES within flowers of *Cryptantha flava* (A. Nels.) Payson (Boraginaceae) may be fertilized, usually only one (sometimes two) matures (Casper and Wiens, 1981). The nutlets (hereafter, seeds) of congeneric species that mature all four ovules are individually deciduous, but in *C. flava* the mature seed(s) and aborted ovules remain attached to the gynobasic style. The large pubescent calyx and the enclosed ovary abscise from the plant as a unit. Wind is the main dispersal agent (Casper, 1987), and Casper and Wiens (1981) suggested that by decreasing the mass of the diaspore, the reduction in seed number results in increased dispersal distance of propagules.

A similar pattern of seed reduction occurs in several species of tropical trees in the Leguminosae (Augspurger and Hogan, 1983). Although flowers have more than one ovule, they produce indehiscent, wind-dispersed fruits that usually contain a single seed. Augspurger and Hogan (1983) and Augspurger (1986) have shown that in *Lonchocarpus pentaphyllus* and *Platypodium elegans* the few multiseeded fruits disperse shorter distances than single-seeded fruits.

In this study, the size, mass, and dispersal characteristics of one- and two-seeded diaspores of *C. flava* are compared. Their rate of descent in still air (indoors) and the distances they disperse naturally in the field are measured. Natural dispersal distances of calcyes that contain no mature seeds are also determined.

STUDY SPECIES—*Cryptantha flava* is a perennial herbaceous species that grows in sandy soil throughout the semiarid Colorado Plateau in communities dominated by sagebrush and juniper. Typically, plants are 10 to 40 cm tall and produce from one to more than 40 flowering stalks, each with at least 25 flowers. Inflorescences are made up of several cymules (lateral branches) and flowering progresses sequentially along the cymules beginning with positions proximal to the main stalk. Fruit ripening also occurs sequentially by position, but mature diaspores may be retained on the plant for several days if there is not sufficient wind to cause their abscission.

In Uintah Co. in northern Utah where the two sites for this study are located, seed dispersal begins in late June or early July. In one of the populations, the mean percentage of two-seeded diaspores per plant was 10.4 ($N = 19$) and 4.6 ($N = 17$) in 1979 and 1980, respectively (Casper, 1984). Both sites have extensive areas of bare ground between shrubs; they are described more fully in Casper (1987).

METHODS—Features that might affect dispersal potential were measured for 21 one-seeded and 19 two-seeded diaspores collected from the same field-grown plants: the mass of the entire diaspore, its length, the width of the calyx at the widest point (the tip), and the width of the calyx at the ovary (Fig. 1). Because mea-

[1] Received for publication 20 October 1986; revision accepted 26 August 1987.

We thank J. Haynes and W. Moise for help in dropping seeds down the stairwell and two anonymous reviewers for their comments on an earlier version of the manuscript. The study was supported by NSF Grant BSR 83-07888.

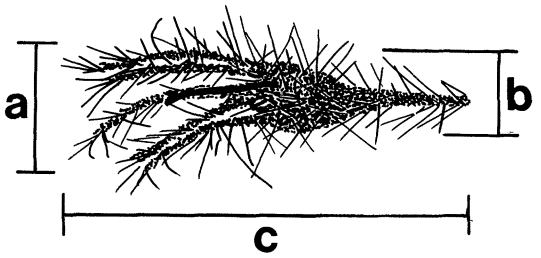

Fig. 1. Calyx and enclosed seed showing dimensions measured. Measurements were exclusive of epidermal hairs. a = width of calyx at widest point; b = width of diaspore at ovary; c = total length of diaspore.

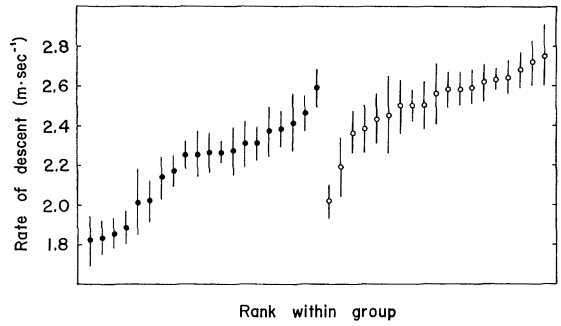

Fig. 2. Rate of descent in still air (mean of 12 trials ± SD) for one- (closed circles) and two-seeded (open circles) diaspores graphed by rank within group. Diaspores were dropped 12.3 m.

surements were made in Philadelphia where the humidity is much higher than at the field sites, the diaspores were first dried to constant mass over $CaSO_4$. After their rates of descent in still air were determined, they were dried again, and the masses of the calyx and the ovary (mature and aborted ovules) measured separately for each diaspore.

Rate of descent was calculated by dropping the diaspores from a height of 12.3 m in an open indoor stairwell. Because they should reach terminal velocity soon after their release, rate of descent should be approximately equal to terminal velocity (Sheldon and Burrows, 1973). The 40 diaspores were dropped in a random order, and the entire set was dropped 12 times. The 12 trials were used to calculate the mean rate of fall per diaspore in order to reduce the effect of experimental error in tracking and timing the small objects.

Natural dispersal in the field was examined by spray painting nearly mature infructescences with a light coat of Glowz brand Dayglo UV fluorescent paint and recovering painted diaspores after dissemination. Painting is necessary because seed shadows from different individuals overlap greatly, and unpainted diaspores are difficult to relocate. To a test sample of dry, mature diaspores, paint added an additional 3.2 mg ± 0.20 (SD) (N = 20) or 3.7% to the mass of one-seeded diaspores and 4.4 ± 0.29 (SD) (N = 17) or 4.7% to two-seeded diaspores. We reasoned that if painting decreases dispersal distance, it should affect two-seeded diaspores more.

Six plants that seemed to have relatively large numbers of two-seeded fruits were selected for the experiment. The probability that a flower will yield two seeds is correlated with its proximity to the main stalk (Casper, 1984). Since seeds near the main stalk are also the first to ripen, two-seeded diaspores might disperse at different times and under different wind conditions than many one-seeded diaspores; therefore, only the proximal halves of the cymules were painted. Locations of one- and two-seeded diaspores do not differ in height above ground. There is no relationship between the location of a flower on the plant and the probability that it will fail to produce a seed (Casper, 1984).

Four days later, strong winds preceding a rainstorm dispersed most of the painted diaspores on five plants. The marked diaspores were recovered the following day in order to minimize their exposure to seed predators. Secondary as well as primary dispersal was expected to have occurred because diaspores seem to be blown about until they lodge against small plants or other obstructions or come to rest in depressions in the soil (Casper, personal observation). Distances up to 8 m were searched in all directions from each plant, but because of the highly directional seed shadows, greater distances were searched downwind from the plants. Maximum dispersal was considered to be the farthest distance at which a marked diaspore was found with no others within the next 8 m (see Augspurger and Hogan, 1983). The numbers of diaspores within 0.5 m, some of which had obviously fallen from the plants without dispersing horizontally, were noted and the exact distance from the source plant was measured for those located beyond 0.5 m. The diaspores of the sixth plant were recovered 18 days later.

RESULTS—The mass of the ovary, total mass, and the width at the ovary are greater in two-seeded than in one-seeded diaspores (Table 1; Fig. 2). Calyces of one- and two-seeded diaspores do not differ either in width at the tip or total length (Table 1). As expected from the

TABLE 1. *Mass, dimensions, and mean rate of descent compared for one- and two-seeded diaspores. Values represent mean (SD)*

Measured trait	One-seeded ($N = 21$)	Two-seeded ($N = 19$)	F statistic
Mass of entire diaspore (mg)	8.81 (0.67)	11.32 (1.07)	80.519***[b]
Mass of ovary (mg)	3.13[a] (0.28)	5.21 (0.76)	131.275***
Mass of calyx (mg)	5.61[a] (0.67)	6.11 (0.80)	2.925
Width of calyx at widest point (mm)	5.30 (1.28)	5.69 (1.39)	0.830
Width of calyx at ovary (mm)	2.33 (0.23)	2.87 (1.17)	35.599***
Length of diaspore (mm)	12.72 (0.94)	12.81 (1.17)	0.058
Mean rate of descent ($cm \cdot sec^{-1}$)	219.1[a] (22.3)	251.1 (18.1)	25.601***

[a] $N = 20$ for these values only. One diaspore was lost during the seed dropping experiment.
[b] $***P < 0.001$.

TABLE 2. *Distributions of calyces enclosing 0, 1, or 2 seeds and calyces from which seed(s) had been removed by predators. Numbers dispersing beyond 0.5 m compared with numbers dispersing within 0.5 m*

Plant	Distance	No. calyces with N seeds: $N = 0$	1	2	No. calyces with seeds removed
A	Within	2	8	5	4
	Beyond	22	46	13	6
B	Within	5	14	4	1
	Beyond	1	9	9	0
C	Within	13	48	8	32
	Beyond	5	15	7	9
D	Within	11	13	3	0
	Beyond	5	15	7	0
E	Within	0	3	1	0
	Beyond	3	16	3	1
Total A–E	Within	31	86	21	37
	Beyond	36	108	41	15
F	Within	0	34	0	0
	Beyond	0	55	0	0

differences in mass, two-seeded diaspores also have a higher rate of descent in still air. A linear regression of total mass on rate of descent for the entire set of one- and two-seeded diaspores yields $R^2 = 0.32$; $P < 0.001$.

Five of the marked plants in the field produced some two-seeded diaspores. A total of 375 diaspores were recovered from these plants. Predators (presumably rodents) had removed the seeds from 52 of them. Of the remainder, 19.2% contained two seeds, 51.7% contained one, and 17.9% had no mature seed. Maximum distances achieved by diaspores with at least one seed ranged from 7.05 m to 17.50 m for the five plants. There was no difference in the proportion of one- and two-seeded diaspores located within 0.5 m of the source plants either when the plants were considered individually or together (Table 2; χ^2, Fisher Exact Test where appropriate; $P > 0.05$). For the subset located farther than 0.5 m from the source plants, there was no difference in the distance that one- and two-seeded diaspores dispersed (Table 3; Mann-Whitney U Test on individual plants; $P > 0.05$). Combined across all plants, the mean distance achieved by diaspores located farther than 0.5 m was 3.96 m ± 3.40 (SD), $N = 108$ for one-seeded and 4.25 m ± 3.90 (SD), $N = 41$ for two-seeded.

Likewise, calyces containing no mature seeds did not differ significantly in their dispersal distances from those containing one seed (or from those containing either one or two seeds). For those calyces containing no seeds that traveled beyond 0.5 m, the mean dispersal distance was 5.33 m ± 4.19 (SD), $N = 36$, and their maximum dispersal distance per plant ranged from 2.09 to 18.92 m.

DISCUSSION—One- and two-seeded diaspores of *C. flava* differ in mass and rate of descent, traits that should affect their dispersal potential, yet no differences were detected in the dispersal distances of calyces containing 1, 2, or 0 seeds in the field. There are at least two possible explanations for why dispersal distance does not vary with seed number.

First, given the high rates of descent, the height of release may be insufficient to result in measurable differences in horizontal distance during primary dispersal. The rates of descent are comparable to those for one- and two-seeded wind-dispersed fruits of *Platypodium elegans* (Augspurger, 1986), but they are much greater than values reported for fruits of many herbaceous Compositae (Sheldon and Burrows, 1973) and grasses (Rabinowitz and Rapp, 1981). The plants of *C. flava* are obviously much shorter than tropical trees from which one- and multiseeded fruits disperse different distances (Augspurger and Hogan, 1983; Augspurger, 1986).

In a similar study comparing diaspore characteristics among seven species of grasses, Rabinowitz and Rapp (1981) found that mass, terminal velocity, and plant height were not good predictors of relative primary dispersal distances among the species. The shapes of the diaspores, however, differ greatly.

Secondly, considerable secondary dispersal must have occurred in the dissemination of

TABLE 3. *Mean distance (cm) traveled from source plant (SD) for calyces enclosing 0, 1, or 2 seeds and dispersing farther than 0.5 m. Sample sizes are in Table 2*

Plant	Mean distance		
	No. seeds = 0	1	2
A	611.0 (341.3)	508.6 (317.0)	552.7 (346.2)
B	189.2 (0)	371.4 (211.4)	617.2 (584.0)
C	97.8 (62.6)	146.6 (86.1)	143.7 (64.7)
D	466.8 (384.8)	634.5 (502.0)	432.6 (250.3)
E	346.3 (135.7)	208.2 (174.1)	123.0 (52.1)
Mean A–E	533.2 (419.0)	396.4 (340.3)	425.1 (390.9)
F	—	803.9 (529.9)	—

marked diaspores in the field, and traits other than terminal velocity and mass may be important during secondary movement. In modeling the trajectory of Compositae fruits, Sheldon and Burrows (1973) note that only when the terminal velocity is less than about 80 cm · sec^{-1}, and thus the resistance to falling is high, do fruits move with the local horizontal wind speed. Because the diaspores of *C. flava* have a high rate of descent, they must not remain airborne very long, and much of their horizontal movement must occur along the surface of the ground. The greater width of the two-seeded diaspores might increase their ability to be moved by wind across a horizontal substrate and possibly compensate for the opposing effect of mass.

Thus, this study offers no evidence that the reduction in seed number per flower increases dispersal distance in wind-dispersed *C. flava*. There may be other advantages to maturing only one seed that are unrelated to the mode of dispersal. Clearly, there are indehiscent multiovulate fruits, like those of oaks and almonds, that commonly mature a single seed but are not wind-dispersed (Mogensen, 1975; Pimienta and Polito, 1982; Garrison and Augspurger, 1983). The abortion of all but one ovule in such species prevents more than one seed from landing in the same location and avoids sibling competition that could occur if more than one seedling emerged from the same fruit (Stebbins, 1967; Cronquist, 1968; Casper and Wiens, 1981). Greenhouse studies suggest this could be an additional factor selecting for single-seededness in wind-dispersed *Platypodium elegans* (Augspurger, 1986).

The mature ovaries of most borages split into single-ovulate subunits. Although the fruits are not technically dehiscent, they are functionally dehiscent since the seeds disperse individually. In *C. flava* (and congeneric species that usually mature a single seed) the calyx acts as additional packaging material. In *C. flava,* it protects the seed from granivorous ants (Casper, 1987) and probably increases dispersal distance beyond that of a naked seed (Casper, 1982). Because the calyx completely encloses the ovary, it functions as an indehiscent fruit. Just as in species with true indehiscent fruits, abortion of all but one seed per ovary in *C. flava* will normally reduce the incidence of competition among siblings.

The extra ovules produced in species with fixed ovule abortion could permit selective elimination of viable embryos based on some assessment of quality or genotype (Casper and Wiens, 1981; Casper, 1984), or they could simply serve as a backup system, increasing the probability that a flower will yield a viable seed.

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