Propagule size, dispersal ability, and seedling performance in *Asclepias syriaca*

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Summary. Using the propagules of common milkweed (*Asclepias syriaca* L.) we tested the predictions that decreasing size may increase dispersal ability, but also decrease the probability of seedling success, of wind-dispersed seeds. In 1982 and 1983 we released seeds from four milkweed clones at two heights in an open field and measured their dispersal distances. In the laboratory we measured falling times in a dead air space, seed mass and area, and coma mass and length of the same seeds. The seeds were later planted in a greenhouse and germination, mortality, and seedling dry mass were recorded.

Seed mass was negatively correlated with dispersal distance in 1982, but not in 1983 under highly variable wind conditions. Coma mass/seed mass ratio was positively correlated with dispersal distance in 1982. During both years seed mass and coma mass/seed mass ratio were highly significantly correlated with falling time in dead air space. However, heavy seeds had superior germination, survivorship, and seedling mass at harvest, and seeds that germinated fell faster in dead air than those that did not. We found substantial variation in seed morphology both among clones and among pods within clones. Propagule falling times in dead air and (in 1982) dispersal distances in the field also differed significantly among clones and pods. The potential therefore exists for differential dispersal and establishment of milkweed genotypes.

Plants exhibit a remarkable variety of seed dispersal mechanisms, which are usually assumed to enhance fitness. Proposed selective advantages for such mechanisms include escape from high juvenile mortality near the parent plant, colonization of newly-disturbed habitats, and the possibility of directed dispersal to microhabitats suitable for seedling establishment (see Howe and Smallwood 1982 for a review).

However, adaptations for dispersal may require trade-offs with other fitness components. For example, in wind-dispersed species, dispersal distances are greatest for propagules with the slowest rate of fall in still air (Sheldon and Burrows 1973). In a comparative study of plumed composite propagules, Sheldon and Burrows (1973) showed that terminal velocity decreases as the ratio of pappus mass to achene mass increases. Thus, selection for dispersal ability may often favor small seeds. On the other hand, large seeds

frequently are superior in seedling establishment or growth (e.g., Schaal 1980; Howe and Richter 1982; Cicidiyan and Malloch 1982; Wulff 1982; Stanton 1984; Waller 1984). We can therefore predict a negative relationship between dispersal ability and seedling fitness traits in plants with wind-dispersed seeds.

At present few data are available that relate intraspecific variation in seed morphology to dispersal in the field, and to our knowledge no studies have explicitly investigated seedling performance as a possible constraint on dispersal ability for wind-dispersed seeds. We therefore report here on intraspecific variation in seed morphology and its consequences for dispersal ability and seedling success in the common milkweed, *Asclepias syriaca* L. (Asclepiadaceae).

Asclepias syriaca, a common weed throughout most of eastern North America, can be considered a colonizing species. Populations east of the undisturbed prairie until recently were probably confined to temporary habitats, such as areas created by windthrow, forest fires, and catastrophic flooding (Morse and Fritz 1983; Janzen 1984). Today *A. syriaca* is common in areas of human disturbance, such as fields, pastures, and roadsides, which quickly revert to forest if not maintained. By producing wind-dispersed, plumed seeds, milkweeds are capable of spreading from an existing population to colonize a newly disturbed site. Milkweed pods are usually found on stems 70–100 cm in height, and typically contain 100–200 seeds which are dispersed in mid-autumn. *A. syriaca* also propagates extensively by vegetative means, and the stems are often found in distinct patches, corresponding to individual clones.

Here we address the following questions: 1) How do milkweed seed size and propagule morphology affect dispersal ability? 2) How do the same characteristics affect seedling performance? 3) Are dispersal ability and seedling performance related? 4) What are the patterns of variation in seed size and morphology, dispersal ability, and seedling performance within and between milkweed clones? The answers to these questions will shed light on the selective pressures and constraints influencing the evolution of seed traits and dispersal mechanisms.

Methods

Seed dispersal in the field

We measured seed dispersal in late October 1982 and 1983 in an old field on the Haffenreffer Reserve of Brown University in Bristol, Bristol Co., Rhode Island. In both years

all field observations were made in a single afternoon. In 1982 a light wind (2–8 km/h) blew from the southwest between 13:30 and 16:00, the time during which the flight experiments were carried out. In 1983 a gusty and intermittently stronger wind (1–14 km/h) blew from the northeast. The field itself contained large grassy patches and sizeable areas covered with a variety of forbs, dominated by *Aster novae-angliae* and several *Solidago* spp. Several clones of common milkweed also grew in this field.

In both years we randomly selected four clones, all within 200 m of each other. Different clones were used in 1982 (Clones A–D) and 1983 (Clones E–H). From each clone we randomly chose three unpredated pods from those that had split open and were beginning to release seeds. We obtained 16 seeds from each pod, the next seeds that would have been released under undisturbed conditions. Thus, we used neither the first nor the last of the seeds as they would normally be released. The seeds all appeared normal and viable and showed no signs of predation or other damage.

We released the seeds in a grassy area in the middle of the field, near a milkweed clone that was also releasing seeds. In each flight trial we released four seeds simultaneously: two seeds from each of two clones. The two seeds from each clone were released 50 and 100 cm above the ground, approximating the extremes of pod height found in that field. The two clones contributing seeds to a trial were alternated with each trial, and within a clone the pod contributing seeds was rotated with each trial.

A spotter followed each seed released until it fell to the ground, collected the seed, and measured the dispersal distance. The collected seeds were then taken back to the laboratory in individual paper cups. In all, 384 seeds were used.

Falling times in the laboratory

We released the same seeds in a dead air space in the laboratory, recording the time required to fall from the top to the bottom of a paper or acetate cylinder 150 cm high and 15 cm in diameter. In view of the results of Sheldon and Burrows (1973), we assumed that the seeds reached terminal velocity very quickly. Thus our measurement of falling time was inversely related to terminal velocity, an index of potential for dispersal: the slower the rate of fall, the greater the dispersal potential (Sheldon and Burrows 1973).

Measurements of seeds

Four measurements of seeds and comas were made after the seeds were dropped in the dead air column: mass of seed, mass of coma, area of seed, and length of the longest fibers of the coma. Seeds (air-dried) were weighed to the nearest 0.1 mg on a Cahn electrobalance. Seed area was estimated by measuring maximum length and width under a dissecting microscope and then applying the equation for an ellipse. Since the seeds are basically flat, area should be closely correlated with volume. Length of fiber was measured under a dissecting microscope. To estimate the loading of propagules and relative contribution to dispersal and seed production, we also calculated the ratio of coma mass to seed mass.

Germination of seeds and growth of seedlings

Seeds from the 1982 experiment were stored outdoors until early April, when growth begins in the field. They were then planted in a greenhouse in a randomized array, one to a 7.5 cm pot filled with standard potting mixture. Seeds were placed 2 cm deep in this mixture, hilum up, and monitored daily for germination and mortality. All seeds that germinated and survived to early July were harvested at ground level, oven-dried, and weighed.

Results

Effect of propagule size and morphology on dispersal ability

Dispersal distances of propagules in the field were highly skewed and leptokurtic in both 1982 and 1983 (Fig. 1). Propagules released at 100 cm traveled significantly farther than those released at 50 cm in both years (Fig. 1). Morphological characters were much more important in expaining flight distance in 1982 than in 1983, perhaps because of the greater variability in wind speed and turbulence in 1983. In 1982 coma mass/seed mass ratio was positively correlated with dispersal distance (Table 1, Fig. 2). Thus, lightly-loaded propagules travelled farther in 1982, although the effect was not detectable in 1983. Both seed mass and seed area were negatively correlated with dispersal distance, indicating that small seeds flew farther than large ones, in 1982 but not in 1983 (Table 1); coma length had a slight positive effect for high-released seeds in 1983 (Table 1). Seed mass and seed area were significantly correlated in both 1982 (Spearman $r_s = 0.60$, $n = 142$, $P < 0.001$) and 1983 ($r_s = 0.52$, $n = 157$, $P < 0.0001$); relationships among the other characters were more variable between years.

Morphological characters exerted a much greater influence on the falling time of propagules in a dead air space than they did on dispersal in the field. In both years the coma mass/seed mass ratio was positively correlated with falling time (Table 2, Fig. 3). The relationship was not linear; as coma mass/seed mass ratio increased, falling time initially increased rapidly and then began to level off (Fig. 3). Seed mass had a strong negative effect on falling time (Table 2, Fig. 4) and seed area a weaker negative effect; coma length was positively correlated with falling time in both years (Table 2). Lightly-loaded propagules fell more slowly, suggesting a high potential for dispersal. Seed mass was clearly the most important factor increasing falling time, while coma length apparently contributed to the drag forces slowing the rate of descent.

Falling time in the dead air space was significantly correlated with dispersal distance in the field for propagules released at 100 cm in 1982 ($r_s = 0.348$, $n = 82$, $P = 0.0014$), but not in 1983 ($r_s = -0.090$, $n = 78$, $P = 0.43$), and not for propagules released at 50 cm in either 1982 ($r_s = 0.134$, $n = 71$, $P = 0.26$) or in 1983 ($r_s = 0.090$, $n = 68$, $P = 0.47$). Thus, when seeds were released close to the ground or under gusty wind conditions, the aerodynamic properties of individual seeds were poor predictors of dispersal in the field.

Effect of seed morphology on germination and seedling success

Slightly over 50% of the 1982 seeds germinated. Germinating seeds were significantly heavier than those not germinating ($t = 4.41$, $n = 165$, $P < 0.0001$). None of the other morphological characters varied with germination. Emergence date was not correlated with any measurement of propagule morphology ($-0.08 \leq r_s \leq -0.01$, $n \geq 72$, $P \geq 0.47$). Eight of
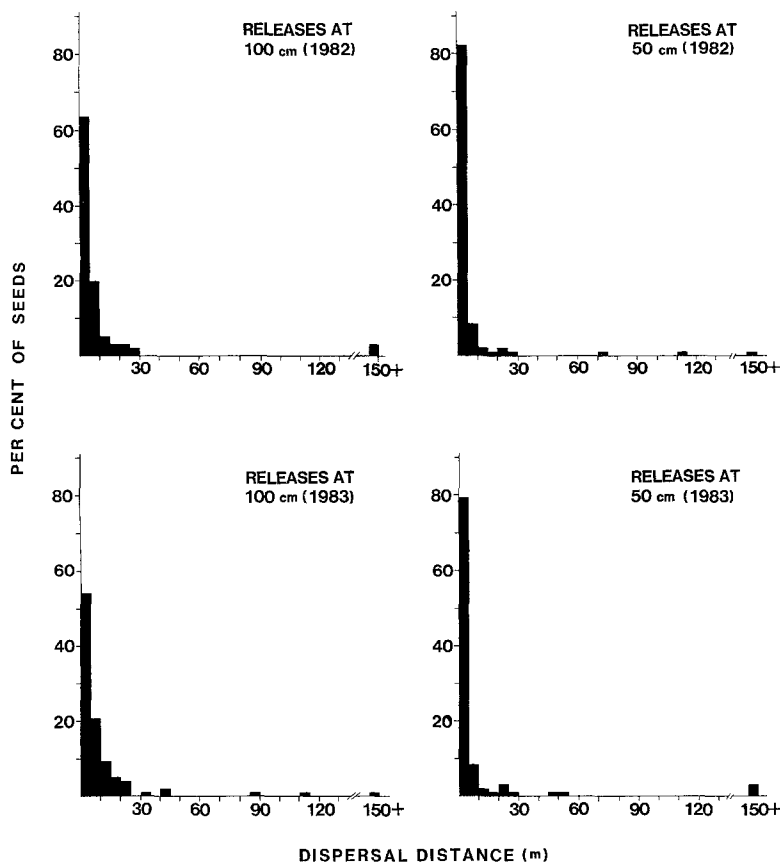
Fig. 1. Distribution of dispersal distances in 1982 and 1983 for propagules released at heights of 100 and 50 cm. High-released seeds traveled significantly farther in both 1982 (Wilcoxon two-sample test, $z = 4.76$, $P < 0.0001$) and 1983 (Wilcoxon two-sample test, $z = 5.86$, $P < 0.0001$). $N = 96$ for each release

the 86 seedlings died before harvest. Seeds producing seedlings that died were significantly lighter than seeds producing seedlings that survived ($t = -2.739$, $P < 0.01$ in a one-tailed t-test). A multiple regression of seedling mass at harvest on seed mass and emergence date was highly significant ($R^2 = 0.208$, df $= 69$, $P = 0.0004$). The regression equation was (seedling mass) $= -0.006$ (days to emergence) $+ 0.038$ (seed mass) $+ 0.143$, indicating that large seeds and early emergence times tended to produce large seedlings. Both seed mass ($R^2 = 0.104$) and date of emergence ($R^2 = 0.120$) made similar contributions to this result (partial regression coefficients). None of the other morphological characters added to the significance of the regression. Thus, seed mass was the only morphological character measured that affected seed performance. It influenced all three measures of seed success; germination, survivorship, and accumulation of biomass.

Relationship between seedling success and dispersal

Germinating seeds had significantly shorter falling times than did those that failed to germinate ($F = 16.91$, $n = 148$, $P < 0.0001$ in an ANOVA). However, field dispersal distance did not differ between germinating and non-germinating classes for either high-released (Wilcoxon, $z = 1.16$, $P = 0.25$) or low-released (Wilcoxon, $z = -0.97$, $P = 0.33$) seeds. Emergence date was not correlated with flight distance in the field ($r_s = -0.03$, $n = 38$, $P = 0.88$ for high release, $r_s = -0.23$, $n = 47$, $P = 0.13$ for low release) or with falling time ($r_s = -0.01$, $n = 73$, $P = 0.95$). The small number of seedlings that died did not differ significantly from those that survived to harvest in either flight distance (Wilcoxon, $z = -1.03$, $P = 0.30$ for high release, Wilcoxon, $z = 0.50$, $P = 0.62$
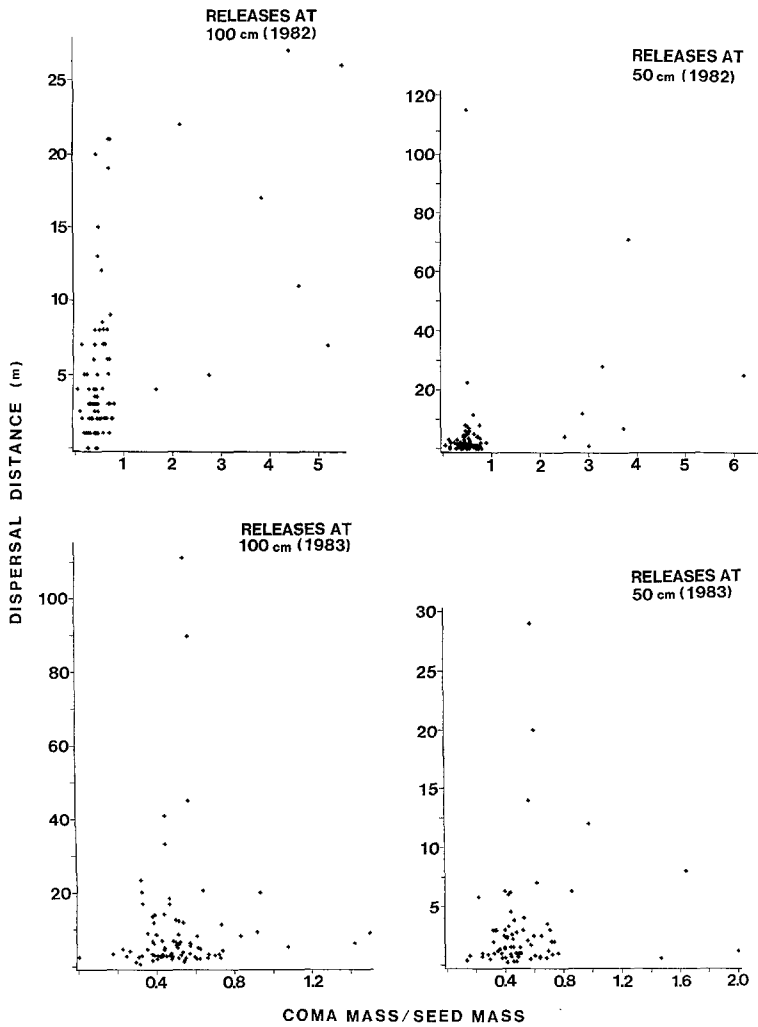
Table 1. Relationships between morphological characters and dispersal distance in field. Spearman correlation coefficients; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$

Year	Release height (cm)	N	Seed mass	Seed area	Coma mass	Coma length	Coma mass/ seed mass
1982	100	79	−0.27*	−0.32***	0.12	−0.05	0.38***
	50	67	−0.18	−0.34**	0.10	0.02	0.27*
1983	100	85	−0.01	−0.05	0.04	0.26*	0.12
	50	76	−0.02	−0.03	0.07	0.18	0.17

for low release) or in falling time ($t = 1.22$, $n = 67, 7$, $P > 0.2$). Seedling mass at harvest was not correlated with falling time ($r_s = 0.045$, $n = 65$, $P = 0.72$) or with flight distance in the field for either high ($r_s = 0.05$, $n = 32$, $P = 0.78$) or low ($r_s = 0.13$, $n = 43$, $P = 0.42$) release. In stepwise multiple regression with emergence date, neither measure of dispersal ability contributed significantly to predictions of seedling mass. Thus, of the several measures of seedling performance, only germination exhibited a significant correlation with dispersal ability, and this relationship occurred only under controlled laboratory conditions, not in the field.

Differences in propagule morphology among clones and pods

Nested ANOVA revealed significant differences in seed mass, seed area, coma mass, and coma length both among clones and among pods within clones in both years (Tables 3, 4). The coma mass/seed mass ratio could not be transformed to meet the normality assumption necessary

Fig. 2. Effect of coma mass/seed mass ratio on dispersal distance in 1982 and 1983 at 100 cm and 50 cm releases. Seeds that travelled >150 m and could not be followed were not collected and therefore not weighed. Note that all of the axes are not the same
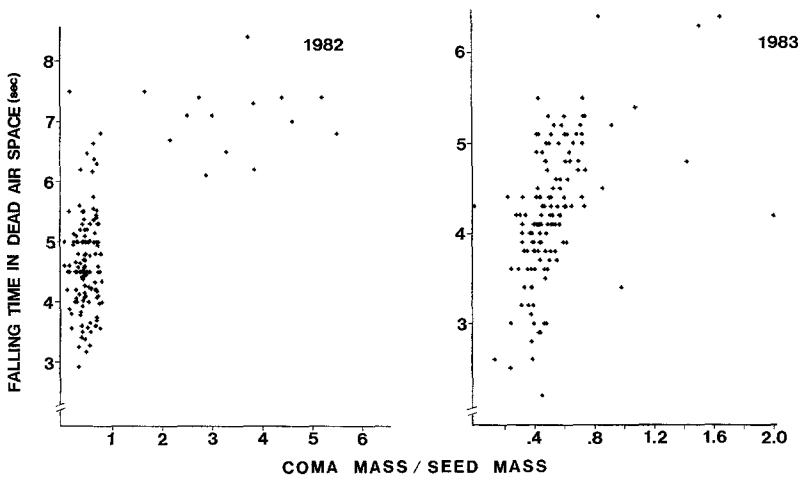
Fig. 3. Effect of coma mass/seed mass ratio on time to fall 150 cm in dead air. In 1982 $r_s = 0.32$, $n = 148$, $P < 0.0001$; in 1983 $r_s = 0.61$, $n = 140$, $P < 0.0001$. Note that all of the axes are not the same

Table 2. Relationships between morphological characters and time to fall 150 cm in dead air space. Spearman correlation coefficients; * $P < 0.05$; ** $P < 0.005$; *** $P < 0.001$; **** $P < 0.0001$

Year	N	Seed mass	Seed area	Coma mass	Coma length	Coma mass/ seed mass
1982	126	−0.51****	−0.25**	−0.18*	0.31***	0.32****
1983	137	−0.27***	−0.10	0.26**	0.31***	0.61****

for nested ANOVA; however, a Kruskal-Wallis test showed significant differences in this ratio among clones in both 1982 ($x^2 = 34.69$, df = 3, $P < 0.001$) and in 1983 ($x^2 = 46.68$, df = 3, $P < 0.0001$). When pods were compared within clones in separate Kruskal-Wallis tests, significant differences among them were found for 3 of the 4 clones in 1982 ($x^2 \geq 6.27$, df = 2, $P \leq 0.044$) and for 2 of the 4 clones in 1983 ($x^2 \geq 7.04$, df = 2, $P \leq 0.030$). Thus, morphological variation was high, and it occurred in all characters measured, both among and within clones, including characters
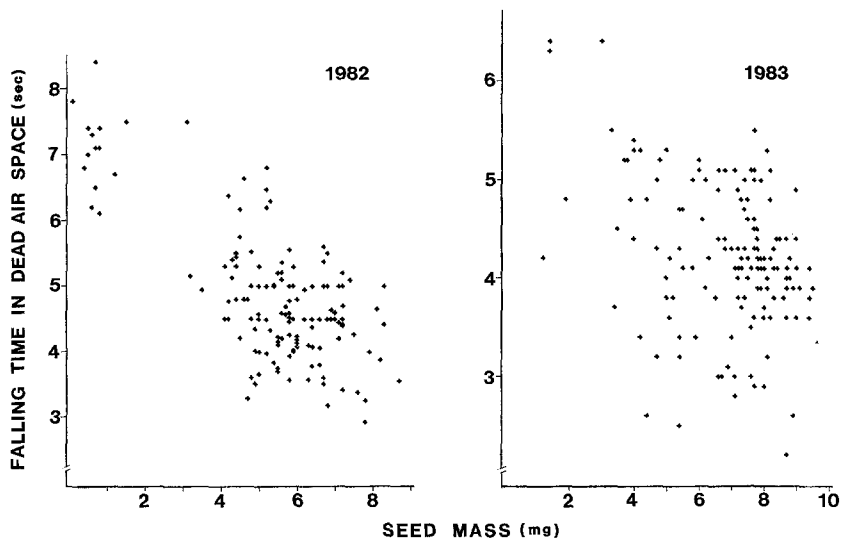
Fig. 4. Effect of seed mass on falling time in dead air. In 1982 $r_s = -0.73$, $n = 148$, $P < 0.0001$; in 1983 $r_s = -0.35$, $n = 142$, $P < 0.0001$. Note that all of the axes are not the same

Table 3. Morphological characteristics, flight performance, and germination-seedling performance of milkweed seeds from different clones and pods. $N = 10$–16 for each pod. Letters refer to clones (A–D from 1982, E–H from 1983), numbers to pods within clones. $\bar{x} \pm$ S.D.

Morphological characteristics of propagules				Flight distances		Falling times in dead air (S)	Germination-seedling performance			
Clone and pod	Seed mass (mg)	Seed area (mm²)	Coma mass (mg)	Coma length (mm)	Released at 100 cm (m)	Released at 50 cm (m)		Number germin-ating	Number not germ-inating	Number dying	Mass, ovendried seedlings (g)
A1	6.2±0.6	24.0±5.0	2.8±0.5	41.0±7.6	3.8± 2.9	3.4± 2.7	4.5±0.5	12	3	0	0.25±0.12
A2	6.3±2.4	23.7±6.2	2.6±0.6	37.0±6.2	7.1± 8.9	16.7±39.9	4.2±1.3	8	7	1	0.32±0.14
A3	4.9±0.6	21.2±3.0	2.7±0.8	42.1±6.8	3.8± 2.9	1.7± 1.2	5.8±0.7	7	9	1	0.21±0.12
B1	6.1±2.1	27.3±3.1	2.4±1.3	42.4±3.8	24.0±51.2	2.9± 2.2	5.7±1.0	6	5	0	0.20±0.11
B2	5.9±1.6	27.3±6.3	2.6±1.1	36.8±4.1	4.4± 2.0	5.1± 8.4	4.6±0.4	8	8	0	0.29±0.09
B3	6.5±0.9	29.3±3.6	2.0±0.9	40.0±6.5	1.5± 1.0	0.5± 0.6	4.3±0.5	1	13	0	0.20
C1	5.3±1.0	22.3±2.1	2.3±0.3	29.4±5.4	4.3± 2.8	2.1± 1.2	4.3±0.5	10	3	0	0.22±0.17
C2	5.7±0.6	22.7±2.2	3.8±0.4	31.7±2.9	9.9± 7.5	4.0± 3.7	4.1±0.3	10	5	1	0.21±0.11
C3	6.5±1.0	25.7±2.0	2.8±0.7	32.9±4.1	5.0± 6.9	2.5± 3.7	4.8±0.4	9	5	0	0.16±0.14
D1	0.6±0.3	11.2±4.1	2.2±0.4	32.2±6.6	31.6±41.4	35.5±51.8	7.1±0.6	0	12	0	–
D2	5.1±0.5	19.5±4.9	2.6±0.8	35.2±5.7	6.0± 3.2	4.8± 7.3	4.6±0.5	10	4	3	0.17±0.10
D3	4.5±0.3	19.1±1.2	2.8±0.8	36.4±9.0	22.1±51.7	1.6± 1.3	4.9±0.7	5	9	2	0.28±0.15

Morphological characteristics of propagules					Flight distances		Falling times in cylinder
Clone and pod	Seed mass	Seed area	Coma mass	Coma length	Released at 100 cm	Released at 50 cm	
E1	6.7±0.9	26.5±3.7	4.1±0.8	33.4±2.2	10.9±14.2	21.9±51.9	4.5±0.4
E2	4.0±0.6	24.6±2.5	2.9±0.6	31.8±3.4	25.3±50.8	10.8±11.3	5.3±0.6
E3	7.1±2.1	28.0±4.4	3.9±0.7	35.8±2.6	9.6±10.9	8.0±15.8	4.2±0.4
F1	6.9±2.1	23.6±4.7	2.7±0.5	31.9±2.1	4.9± 5.0	22.7±52.1	3.7±0.5
F2	8.2±0.9	28.8±5.3	3.7±0.9	35.0±4.3	5.8± 5.0	7.2±17.7	4.2±0.7
F3	7.6±2.1	25.8±4.1	3.3±0.7	32.5±4.0	11.3± 8.5	4.9± 4.8	4.3±0.8
G1	8.0±1.9	36.4±4.4	3.7±0.6	33.1±3.0	12.4±12.4	3.1± 2.5	4.0±0.8
G2	6.7±0.9	29.6±2.5	2.8±0.7	27.7±4.3	4.2± 1.7	4.7± 8.2	4.1±0.3
G3	5.1±0.8	21.1±3.4	1.6±0.6	22.9±3.1	4.0± 3.2	1.1± 0.9	3.5±0.6
H1	7.9±0.7	29.2±2.9	3.6±0.8	31.6±7.0	21.6±31.7	2.5± 1.5	4.1±0.8
H2	7.1±1.7	28.3±2.3	3.4±1.1	28.9±7.3	6.2± 6.1	1.8± 1.1	4.3±0.7
H3	7.1±1.1	27.7±3.0	3.7±0.9	35.0±3.8	15.8±30.3	20.1±52.5	4.7±0.5

shown to affect both dispersal ability and seedling performance.

Dispersal of seeds from different clones and pods

Our observations of seed dispersal distance did not meet the assumptions necessary for nested ANOVA even after logarithmic transformation. In 1982 the high-released seeds differed significantly among clones in dispersal distance (Kruskal-Wallis $x^2 = 9.60$, df $= 3$, $P = 0.022$), although the low-released seeds did not (Kruskal-Wallis $x^2 = 5.19$, df $= 3$, $P = 0.158$). At both high (Kruskal-Wallis $x^2 = 30.16$, df $= 11$, $P = 0.002$) and low (Kruskal-Wallis $x^2 = 22.95$, df $= 11$, $P = 0.018$) release heights, significant differences in dispersal

Table 4. Variation in morphological characters. Nested ANOVA analysis. Sample sizes = 146–179. * $P<0.05$; *** $P<0.001$; **** $P<0.0001$

Year	Source of variation	df	F Seed mass	Seed area	Coma mass	Coma length
1982	among clones	3	41.16****	39.47****	5.76***	19.28****
	among pods	8	15.66****	4.33****	5.04****	2.06*
1983	among clones	3	11.08****	10.12****	13.76****	15.77****
	among pods	8	9.67****	15.66****	11.63****	8.65****

Table 5. Time required for milkweed propagules to fall 150 cm in a dead air space. Nested ANOVA analysis. $P<0.0001$ for all F values

Year	Source of variation	df	SS	F
1982	among clones	3	27.58	21.40
	among pods within clones	8	82.94	24.14
	error	141	60.55	
	total	152	171.07	
1983	among clones	3	20.01	16.29
	among pods within clones	8	14.42	4.40
	error	134	54.89	
	total	145	89.33	

distance occurred among all pods taken together. Significant differences were found among pods within clones in two of the four clones at both release heights (Kruskal-Wallis $x^2 \geq 6.66$, df = 3, $P \leq 0.036$). In 1983 we found no significant differences among clones or among pods in dispersal distance at either release height. However, at least in 1982, different genotypes and different pods produced seeds with clearly different dispersal properties in the field. Falling times of the propagules in a dead air space varied significantly among both clones and among pods within clones in both years (Table 5). Propagules of the fastest and slowest falling clones differed by over 20%, the most extreme pods by 35–40%, in both years (Table 3). These differences, from which the variables of release height and wind speed were eliminated, were considerably stronger than the differences in flight distances recorded under field conditions.

Seedling performance among clones and pods

Using the SAS FUNCAT procedure (SAS Institute, Inc., 1982) in a nested model, we found significant variation in percentage of germination, both among clones ($x^2 = 13.38$, df = 3, $P = 0.004$) and among pods ($x^2 = 18.68$, df = 8, $P = 0.017$), in part due to the poor germination of seeds from two pods. One of these pods (D1) had extremely small seeds, none of which germinated. However, only one of 14 seeds germinated from a pod (B3) with relatively large seeds and small comas. Germination percentages for the other pods ranged from 35% to 80% (Table 3). Seedlings from the different clones and pods did not differ in germination time (nested ANOVA; df = 3, 7; $P>0.05$ for both be-

tween pods and between pods within clones). Five of the eight seedling deaths came from Clone D, suggesting that mortality was non-random, although too few seedlings died to permit detailed statistical analysis. Combining germination and survivorship data, we found a significant difference among clones ($x^2 = 15.83$, df = 3, $P = 0.001$) and among pods ($x^2 = 17.75$, df = 8, $P = 0.023$) in the proportion of seedlings alive at harvest (nested FUNCAT). Seedlings from different clones and pods did not differ significantly in above-ground dry mass at final harvest (nested ANOVA; df = 3, 7, $P>0.05$ for both between pods and between pods within clones), although individual seedlings varied widely in size. Thus, differences in seedling performance among clones and pods were primarily a consequence of success in germination, and probably secondarily in survival of seedlings.

Discussion

Our results show that propagule morphology, including seed size, can affect dispersal ability in milkweeds. Yet, although small seeds tended to have greater dispersal ability than large ones, they were at a disadvantage in germination and survivorship. These two trends were reflected in the negative relationship between dispersal ability, as measured by falling time in the laboratory, and germination success. However, we detected no direct relationship between dispersal distance in the field and any measure of seed success. Since a direct tradeoff must exist under field conditions to have any evolutionary significance, our results are suggestive but not conclusive. We also found considerable variation among clones in propagule morphology, with consequent variation in both dispersal ability and germination success. If this variation is genetically based, the potential might exist for natural selection on propagule size through the differential dispersal and survivorship of genotypes.

Factors affecting dispersal ability

It is well known that propagule size and morphology are important to dispersal (e.g., Sheldon and Burrows 1973; Werner and Platt 1976; Green 1980; Rabinowitz and Rapp 1981; Augspurger and Hogan 1983). However, most of the available information comes from comparative studies of several species. Less is known about the distributions of propagules of different sizes and weights within a single plant's seed shadow (but see Augspurger and Hogan 1983). Our results suggest that intraspecific variation in seed size and morphology can produce substantial variation in dispersability both within and between milkweed sibships. Seeds with a high ratio of coma mass to seed mass tended to disperse farther in the field and fall slower in dead air than those with a low ratio, a finding in agreement with the results of Sheldon and Burrows (1973) for Compositae propagules. Moreover, seed mass itself affected falling time in dead air and (in 1982) dispersal distance in the field, supporting our initial prediction that a tradeoff might occur between dispersal ability and seedling starting capital.

Dispersal in the field was, however, also strongly influenced by factors unrelated to propagule morphology, including height of release and wind speed. Propagules released 100 cm above the ground traveled significantly farther than did those released at 50 cm. Moreover, propagule morphology had a greater effect on the field dispersal per-

formance of seeds released at the greater height than at the lower. Thus, selection for seed dispersal might act on pod and stem height as well as on seed morphology. However, taller stems may be more vulnerable to windthrow than short ones, especially when bearing heavy loads of pods (Morse, unpublished). Thus, an increase in the danger of falling over as stem height increases may constrain selection for seed release at a greater height.

The leptokurtic distribution of seed dispersal distances observed in this study, with many seeds falling close to the parent and a few traveling very far, is typical for plants (Levin and Kerster 1974). We should note, however, that the dispersal distances we observed may underestimate those of many naturally-released propagules, because milkweed seeds require a minimum wind speed to be pulled from their pods, and most are released at wind speeds of 8 km/h or more (Morse, unpublished). Our dispersal distances were somewhat lower than those described by Platt and Weis (1977) as "close to the maximum expected", obtained at wind speeds of 10–15 km/h. However, we obtained our results in a relatively open area; for clones surrounded by taller vegetation, wind speeds may be much lower below the canopy and, in addition, seeds can easily become trapped in foliage. Probably relatively few milkweed seeds escape the immediate vicinity of the parental clone. Of the 384 seeds followed in two years, only eight travelled farther than the spotters could follow (over 150 m). For a colonizing species such as milkweed, these few seeds may be the most important in evolutionary terms. If, as seems likely, the morphological characters favoring such extreme long-distance dispersal are the same as those enhancing dispersal ability in our study, then seeds escaping a population may be significantly lighter, or have higher coma mass/seed mass than average seeds produced within that population.

Effect of seed size on seedling performance

The importance of seed size to seedling performance is also well documented (e.g., Schaal 1980; Cicidiyan and Malloch 1982; Howe and Richter 1982; Wulff 1982; Stanton 1984; Waller 1984). In our milkweeds, seed size had a particularly important effect at germination; much of the variation in seed size was eliminated by the germination failure of the smaller seeds. Additionally, seedlings from large seeds survived better and reached a greater mass than those produced from small seeds, although variation in emergence date (which was unrelated to seed morphology) was as important as seed size in determining seedling mass at harvest. These results were for plants grown singly in pots; differences between large and small seeds might be intensified in competition with other vegetation, as would be likely in many field situations.

Relationship between dispersal ability and seedling success

Comins et al. (1980) predicted that the ESS migration rate should increase with growing probability of site extinction, or with decreasing hazards of migration. The evolution of dispersal distributions has also been discussed in terms of safe site availability (e.g., Green 1980, 1983; Geritz et al. 1984). However, these useful discussions do not take into account potential tradeoffs between dispersal ability and probability of establishment, although propagule size and morphology are known to be important for both phenom-

ena (e.g., Werner and Platt 1976; Howe and Richter 1982). Selection for dispersability may in itself increase the hazard of migration or decrease the range of safe sites in which a propagule is capable of establishment. Our findings suggest that the individual seeds most successful in leaving a milkweed population or reaching a distant safe site may be those least capable of establishment and growth. Small seeds fell slower in dead air and flew farther in the field, but also had lower probabilities of germination. Seeds that later germinated fell significantly faster in dead air than did seeds that later failed to germinate. This observation suggests a direct negative relationship between dispersal ability and seedling establishment, although under more variable field conditions we could not detect such a relationship. Despite the ambiguity of the field data, the finding that seed morphology can simultaneously affect both dispersal and seedling performance is quite suggestive. A suggestion of a similar tradeoff between establishment and dispersal has been reported in an animal-dispersed species (Howe and Richter 1982), and the general phenomenon may in fact be quite widespread and ecologically important.

Differences among clones and pods

We found substantial differences among clones in propagule morphology and seed size, with consequent differences in both dispersal ability and germination success. We do not know to what extent these differences reflect underlying genetic variation between clones, as opposed to maternal effects resulting from environmental factors. However, our results do suggest that propagules from different milkweed genotypes exhibit different dispersal and establishment patterns. Such phenomena could have important consequences for the genetic population structure of A. syriaca. If the differences are at least partially genetically based, they present an opportunity for natural selection to operate on dispersal.

The differences observed between pods within a clone also present the opportunity for differential dispersal and establishment of genotypes. Since milkweeds are fertilized by pollinia, the seeds within a pod may frequently be full siblings (Bookman 1984), but seeds in different pods on a stem quite possibly have different pollen parents. Our results suggest that different full-sib groups within a clone may have different dispersal ability and germination success, although we do not know whether these differences are due to paternal genotype or simply to developmental constraints or differences in resource availability to pods in different positions on stem. If paternal genotype affects dispersal and germination, natural selection may discriminate among full-sibling groups.

The extreme variation observed both within and between milkweed genotypes in propagule morphology does not suggest that selection has acted to produce any one "optimal" propagule morphology. Nor should such selection be expected. Probably the evolution of dispersal strategies depends more upon the variance and shape of dispersal curves than upon some optimal mean (e.g., Green 1983). If seed dispersal and establishment are in fact important and opposing selective forces for milkweed propagule morphology, they may shape seed shadows by acting on the variance in seed and coma characters.

In summary, our results indicate that variation in propagule morphology between and within clones can affect both

dispersability and seedling performance, although a direct tradeoff between these two characters could only be detected under laboratory conditions. For propagule morphology to be shaped jointly by selection pressures for dispersal and seed performance, some of the variation in morphology must be genetically based, and the tradeoff between the two pressures must be evident under natural conditions. We also do not yet know whether seedling fitness in milkweeds increases with dispersal distance (e.g., Augspurger 1983), another necessary condition for an evolutionary tradeoff. Nevertheless, our findings are important because this study is the first to consider dispersal and seedling success simultaneously. The results suggest that future investigations of the evolution of dispersal should consider the fitness consequences of seed size as a constraint, and vice versa.

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