Amer. J. Bot. 74(8): 1280–1288. 1987.

EFFECT OF SEED DIMORPHISM ON THE DENSITY-DEPENDENT DYNAMICS OF EXPERIMENTAL POPULATIONS OF ATRIPLEX TRIANGULARIS (CHENOPODIACEAE)[1]

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ABSTRACT

The importance of seed size and density in determining individual plant performance and plant population dynamics in experimental populations of the halophyte *Atriplex triangularis* was studied. Two distinct seed morphs—large, light seeds and small, dark seeds—are produced by individual *A. triangularis* plants. Experimental populations consisting of seed size monocultures (large or small seeds) and seed size mixtures were established at three different densities, and the time of germination, plant size, plant survivorship, and plant fecundity were monitored. Marked variation in time of germination was observed among treatments and between seed sizes, but germination within any given treatment occurred over a five- to ten-day period. Large seeds produced larger plants than small seeds did, and this dichotomy was maintained over the course of the entire experiment. Germination date and seed size interacted such that larger plants grew from seeds which germinated earlier than those which germinated later, regardless of seed size. Germination date had a more pronounced effect than seed size did on plant mortality in high density populations. At high density, large seed monocultures experienced greater mortality than small seed monocultures did, but in seed size mixtures, the mortality was evenly distributed between plants from the two seed sizes. Regardless of density conditions and parentage, large and small seeds were produced in equal proportion by the plants. Total seed production, however, was dramatically affected by plant density, and to a lesser degree by germination date. Although seed size effects alone did not appear to affect directly final plant biomass and fecundity, effects of seed size early in ontogeny may have contributed to differences in fecundity.

UNTIL RECENTLY, investigations into the importance of variation in seed size in studies of plant population dynamics and plant competition have been neglected in the ecological literature (Silvertown, 1984; Stanton, 1984a, b; Venable, 1985a; Venable and Levin, 1985a, b). Stanton (1984a) has summarized many of the reasons for the lack of attention directed towards ascertaining the ecological importance of seed size. For example, in contrast to the small (5- to 10-fold) variation in seed size within or among individual plants (Harper, Lovell, and Moore, 1970), plant population density may vary over several orders of magnitude in natural situations (Harper, 1977). Historically, therefore, many studies of plant growth and plant population dynamics have focused on the role played by plant population density (see Harper, 1977; Antonovics and Levin, 1980, for reviews). In such studies, the emphasis has been on variation in plant size (e.g., Koyama and Kira, 1956; White and Harper, 1970; Turner and Rabinowitz, 1983; Weiner, 1985; Ellison, 1987), variation in plant growth rate (e.g., Ford, 1975; Turner and Rabinowitz, 1983; Hara, 1984; Weiner, 1985; Ellison, 1987), variation in plant architecture (e.g., Lonsdale and Watkinson, 1983; Ellison, 1987), and variation in seed production (e.g., Clay and Shaw, 1981). All of these factors, however, could be influenced by initial variation in seed size.

Recent investigations have examined explicitly the role of seed size variation in plant growth and plant population dynamics (Rabinowitz, 1978; Philipupillai and Ungar, 1984; Stanton, 1984a, b; Venable, 1985a; Venable and Levin, 1985a, b). Only two studies, however, have studied the interaction of seed size and population density. Black (1957, 1958) studied the influence of seed size on the population dynamics of *Trifolium subterraneum* at densities at which significant mortality occurs. Stanton (1984a) studied the influence of

[1] Received for publication 21 March 1986; revision accepted 29 December 1986.

I thank the residents of Rumstick Cove for permission to use the marsh. Fred Hulme provided assistance in the greenhouse, E. Farnsworth assisted in planting, and W. S. Metcalfe assisted in data collection. J. Antonovics, M. D. Bertness, E. Farnsworth, W. S. Metcalfe, J. Schmitt, and one anonymous reviewer provided helpful comments on early versions of the manuscript. P. Dixon provided statistical advice. This research was supported by a Sigma-Xi grant-in-aid to A. M. Ellison and NSF Grant DEB-82-05747 to M. D. Bertness.

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seed size and competition in wild radishes under greenhouse and natural conditions. In both clover and wild radish, however, seeds span a range of sizes; the distribution of sizes is continuous and the division of the seeds into size classes is necessarily artificial.

In contrast, dramatic seed polymorphism is common in the Chenopodiaceae (Harper et al., 1970). In halophytic genera such as *Atriplex* (Ungar, 1971) and *Salicornia* (Ungar, 1979), seeds occur in discrete morphs within individual plants. It has been proposed that possessing different seed morphs is adaptive (e.g., Harper, 1977; Ungar, 1978, 1982; Silvertown, 1984; Venable, 1985b) because the different morphs may respond differently to environmental conditions, and/or germination will occur when conditions for growth are optimal. Models incorporating these ideas have been developed which examine explicitly the evolution and evolutionary stability of seed polymorphism (Silvertown, 1984; Venable, 1985b).

Ungar and his coworkers have carefully investigated the germination requirements of seeds of different sizes in *Atriplex* and *Salicornia* species (Ungar, 1962, 1978, 1982; Ungar and Riehl, 1980; Khan and Ungar, 1984a, b; Philipupillai and Ungar, 1984). There are no data available, however, on how plants derived from seeds of different sizes perform in seed size monocultures vs. those in stands grown from seeds of varying sizes under identical conditions. Here, I present the results from a study of the effects of seed size on the dynamics of experimental populations of *Atriplex triangularis* Willd. under varying density conditions.

MATERIALS AND METHODS—I collected mature *Atriplex triangularis* (henceforth referred to as *Atriplex*) plants in October 1984 from Rumstick Cove, a protected embayment of Smith Cove in Barrington, Bristol County, Rhode Island. (A complete description of Rumstick Cove is given in Bertness [1984].) Plants were returned to the laboratory where I removed the seeds from the bracteoles using forceps. As Ungar (1971) did, I distinguished two varieties of seeds which occur on any given plant: small, dark-colored seeds with a hard black testa and large, light-colored, soft seeds. I weighed a random sample of 400 seeds (±0.00001 g) and found the biomass distribution to be roughly bimodal (Fig. 1). The coefficient of bimodality (b) is given by the formula $(m_3^2 + 1)/(m_4 + 3)$, where m_3 is the skewness and m_4 is the kurtosis of the size distribution. Significant bimodality is indicated if $b > 0.555$ (SAS, 1982), and for the seed

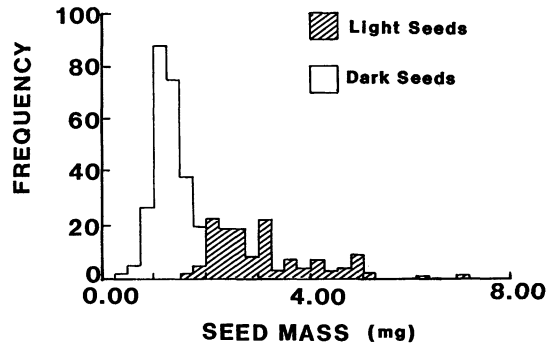

Fig. 1. Frequency of seeds of different biomass (mg); 400 randomly chosen seeds were weighed. Soft, light seeds were significantly larger than seeds with a hard, dark testa.

biomass distribution, $b = 0.628$. The mean biomass of the small dark seeds was 1.10 mg and that of the large light seeds, 2.65 mg (significantly different; $P < 0.0001$, ANOVA). A third, intermediate-sized morph (Khan and Ungar, 1984a, b) was not present in the Rumstick Cove population.

The seeds were stored dry at 4 C for five months prior to use. Before planting, seeds were rinsed with a 10% Clorox solution and then deionized water to surface sterilize them. I planted the seeds directly into a 50–50 mix of coarse sand and potting soil. Because Khan and Ungar (1984a) found that germination success was highest and most rapid when seeds were watered with fresh water, I watered the experimental populations with tap water throughout the course of the experiment.

To assess the effect of seed size and density on the growth and survival of *Atriplex,* I planted seeds at three densities, equivalent to 100, 1,000, and 10,000 plants/m^2. Seedling densities in excess of 5,000/m^2 are common in natural populations in New England (Ellison, personal observation). The low density treatment consisted of single seeds in 10 × 10 × 10 cm pots. Fifty replicate pots of each seed size were planted. I planted the higher density treatments in 65 × 30 × 6 cm flats. Within each flat, I arranged eight 12 × 12 cm quadrats with 5 cm between quadrats. I planted two flats with large seeds only (one with 25 seeds/quadrat, one with 144 seeds/quadrat), two flats with small seeds only and two flats of seed size mixtures. In the intermediate density flats, I planted the seeds in regular hexagonal arrays in each quadrat. In the high density flats, I planted the seeds in a checkerboard design. In mixtures, I planted the quadrats such that large and small seeds alternated within the arrays. In this way, the nearest neighbors of any given large seed (for example) were small seeds and vice versa.

TABLE 1. *Comparison of germination time of large and small seeds*

Density	Planting type	Mean time of germination (days after planting)		
		Large seeds		Small seeds
1	monoculture	13.6	ns	14.7
10	monoculture	14.4	***	16.3
	mixture	14.1	**	16.1
100	monoculture	15.9	****	14.6
	mixture	16.2	ns	16.1

** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.0001$.

TABLE 2. *Results of the ANOVA for germination date (days after planting). The overall ANOVA table is given on top and the contributions of each of the independent variables is given in the lower table. In the lower table, S = seed size, D = density, T = planting type (mixture or monoculture)*

Source	df	SS	MS	F	Probability > F
Overall analysis of variance					
Model	11	1,090.168	99.106	11.12	0.0001
Error	1,764	15,723.597	8.914		
Total	1,775	16,813.765			
Partitioned sums of squares					
S	1	75.869		8.51	0.0036
D	2	125.426		7.04	0.0009
T	1	13.618		1.53	0.2163
S*D	2	351.791		19.17	0.0001
S*T	1	16.598		1.86	0.1728
D*T	2	44.375		2.49	0.0821
S*D*T	2	11.870		0.67	0.2121

Identical patterns were used for the flats of seed size monocultures, and within each quadrat I could follow the fate of individual plants of known seed size.

All pots and flats were maintained in long-day (15 hr light), alternating thermoperiod (30 C day, 16 C night) conditions in the growth chambers of the Brown University greenhouses. To minimize the effects of local conditions, I randomly redistributed the flats and pots in the growth chambers weekly throughout the course of the experiment.

To determine the effect of seed size, sowing pattern, and density on seed germination date, I monitored germination every day for 25 days after planting. To determine the effect of seed size, sowing pattern, and density on *Atriplex* growth and survivorship, 8 solitary plants of each seed size and two quadrats of each of the intermediate and high density treatments were harvested 25, 67, and 110 days after planting. To avoid edge effects in the intermediate and high density quadrats, I harvested only the inner 100 cm^2 of each quadrat. All harvested plants were individually dried and weighed (± 0.01 g). The remaining plants were left to set seed. All seeds produced by each plant were collected, sorted by size, and counted.

There are two complications with the experimental design. Although large and small seeds alternated within rows in the mixture plantings so that a large seed (for example) is bounded on either side by a small one, the nearest diagonal neighbor is a large seed (i.e., a seed of identical size to the "target seed"). However, in both the hexagonal and checkerboard arrays, the four *nearest* neighbor seeds of any given seed are seeds of the opposite size, while the two (in a hexagonal array) or four (in a checkerboard) further neighbors are seeds of the same size. The implicit assumption in using this design is that near neighbors have a greater effect on a given plant's performance than far neighbors do, even on a scale of only a few centimeters. The second complication results from putting multiple quadrats into single flats. All of the intermediate and high density quadrats of a given treatment are in a single flat; i.e., the design is formally a three-way factorial (density × seed size × planting type [seed size mixture or monoculture]) without replication, but with repeated measures (harvests) within each flat. This design was chosen because of the number of available seeds and growth chamber space. In the lowest density treatment, there is no seed size mixture, so there is an empty cell in the factorial design. Interpretation of statistical analyses (see below) reflects the planting design.

Statistical analysis—To analyze the results, I used statistical procedures from the Statistical Analysis System (version 82.3, SAS Institute, Cary, NC). I analyzed the germination data using the FREQ(uency) and GLM procedures, the biomass data with the GLM procedure, and seed production data using the Wilcoxon signed-rank test and the GLM procedure. Although the design is technically a repeated-measures design without replication, quadrats within flats were spaced as far apart as possible to minimize between-quadrat interactions. A strict repeated-measures ANOVA where date of harvest is incorporated as a main effect (Rowell and Walters, 1976) gives misleading results because plant size increases dramatically over time, and because the absence of replicated flats reduces severely the available degrees of freedom. Consequently, results for each harvest were analyzed separately. Seed germination data analysis was performed on

TABLE 3. *Mean biomass (g) (±1 SE) of individual plants harvested over the course of the experiment. Number of plants harvested at each sample date is given in parentheses. For the plants grown in seed size mixtures, I present both the overall mean biomass ("All seeds" column) as well as the mean biomasses for plants of each seed size. An asterisk (*) between a pair of values indicates that the means of that pair are significantly different ($P < 0.05$, Scheffé test)*

Days after planting	Density	Monocultures			Mixtures			
		Large seeds		Small seeds	All seeds	Large seeds		Small seeds
25	1	0.10 ± 0.018 (9)	*	0.04 ± 0.009 (8)	—	—		—
	10	0.02 ± 0.004 (13)		0.01 ± 0.002 (11)	0.02 ± 0.003 (14)	0.02 ± 0.005 (7)		0.01 ± 0.007 (7)
	100	0.01 ± 0.001 (64)		0.01 ± 0.001 (190)	0.01 ± 0.001 (136)	0.01 ± 0.002 (68)		0.01 ± 0.001 (68)
67	1	0.58 ± 0.098 (8)		0.42 ± 0.104 (8)	—	—		—
	10	0.58 ± 0.174 (14)	*	0.21 ± 0.054 (16)	0.38 ± 0.131 (13)	0.52 ± 0.259 (6)		0.26 ± 0.103 (7)
	100	0.04 ± 0.007 (86)		0.10 ± 0.016 (164)	0.07 ± 0.018 (116)	0.11 ± 0.033 (58)		0.03 ± 0.008 (58)
110	1	2.20 ± 0.262 (8)	*	0.81 ± 0.374 (8)	—	—		—
	10	2.21 ± 0.401 (16)	*	2.97 ± 0.707 (12)	2.60 ± 0.731 (13)	3.31 ± 1.454 (5)		2.16 ± 0.816 (8)
	100	0.14 ± 0.085 (19)		0.34 ± 0.052 (122)	0.45 ± 0.063 (98)	0.61 ± 0.118 (45)	*	0.31 ± 0.057 (53)

individual responses, while biomass and seed production analyses were performed on treatment means. All variables were transformed prior to analysis when necessary to equalize variances (Sokal and Rohlf, 1981). All results are presented untransformed.

RESULTS—*Germination*—In the low density treatment, large seeds did not germinate sooner than small ones ($P > 0.05$, Table 1). In the intermediate density treatment, large seeds germinated sooner than small seeds both in seed size monocultures ($P < 0.001$) and in seed size mixtures ($P < 0.01$) (Table 1). However, there was no difference in the germination time of a given seed size in mixture or in monoculture at the intermediate density ($P > 0.05$); i.e., large seeds germinated as rapidly in the large seed monocultures as they did in the seed size mixtures, and similarly for small seeds. In the high density treatment, large and small seeds germinated at the same average time in seed size mixtures (Table 1), but in monocultures, small seeds germinated more rapidly than large ones did ($P < 0.0001$; Table 1), the reverse of that observed for intermediate-density treatments.

Table 2 shows the results of the overall ANOVA of factors affecting germination; the partitioned sums of squares show the significance of each model term in the full model (Type IV sums of squares; Freund and Littell, 1981). The ANOVA shows that seed size had a strong effect on the time of germination (Table 2). Overall, if all densities and replicates are pooled, small seeds germinated ½ day earlier than large ones (small seeds: $\bar{x} = 15.2 \pm 0.24$ [SE] days after planting, $N = 950$; large seeds: $\bar{x} = 15.7 \pm 0.19$ [SE] days after planting, $N = 826$, $P < 0.05$, t test). Although this result is significant, it may be biased by the larger number of seeds in the high density treatments. Planting density also affected germination time (Table 2). Seeds in low density quadrats germinated earlier than those in high density ones (Table 1). By the first harvest, 77% of the large seeds and 89% of the small seeds had germinated and no germination was observed beyond 22 days after planting. The total number of seeds germinated did not differ significantly between seed sizes within treatments ($P > 0.10$) or among treatments ($P > 0.10$).

Individual plant performance—In virtually all cases, plants growing at low densities were larger than plants growing at higher densities at all harvest dates (Table 3). Within a given density, however, plants grown from large seeds were larger than plants grown from small seeds only in a small number of cases (Table 3). The importance of germination date in determining final plant biomass is illustrated in Fig. 2. This figure shows the mean biomass (±1 SE) of plants from large and small seeds for each density and planting type. Only the results from the third harvest are presented, as the results

TABLE 4. *Results of the ANCOVA for shoot biomass from the final harvest. The significance of each of the model terms is determined using the last factor as the error term. D = density, S = seed size, T = planting type (mixture or monoculture), G = germination date (days after planting)*

Source	df	SS	*F*	Probability *F*
D	2	74.709	51.24	0.022
S	1	1.394	1.91	0.483
T	1	0.048	0.07	0.792
D*S	2	2.224	0.76	0.629
D*T	2	0.133	0.04	0.813
S*T	1	2.278	3.12	0.325
G	1	14.162	19.40	0.049
D*S*T	2	1.459		

from the previous two harvests are qualitatively identical. Plants which germinated early were larger than later germinating ones, and with one exception (intermediate density seed size monocultures), plants from large seeds were larger than plants from small ones which germinated on the same day (Fig. 2).

An analysis of covariance (ANCOVA) was used to examine some of the factors influencing plant biomass. Density had an overriding effect on plant performance ($P < 0.02$; Table 4). Seed size and planting type did not affect final plant biomass (Table 4). However, time of germination influenced final plant biomass ($P < 0.05$; Table 4). Although seed size does not, in a statistical sense, interact with germination time (the covariate), it should be recalled that seed size was a significant factor in determining germination date (Table 2; see also Khan and Ungar, 1984a, b).

In order to determine if germination effects were overshadowing seed size effects in the ANCOVA, the analysis was run without the covariate (germination date). If seed size was a significant effect in the reanalysis, then it can be stated cautiously that seed size effects were affecting individual plant performance indirectly through their effect on germination time. A more direct statistical approach would be path analysis (as in Waller, 1985), but many of the necessary statistical assumptions are not satisfied by these data. When the data were reanalyzed without germination date in the model, seed size effects were marginally significant ($F_{1,2} = 9.0635$, $0.1 < P < 0.05$), indicating that indirect effects of seed size may have been a factor in determining final plant size.

Mortality—The influence of seed size on mortality varied among treatments. No mortality was observed among the low density plants or in the intermediate density quadrats, and no significant mortality occurred by either of the first two harvest dates in the high density quadrats. The pattern of mortality in the high density quadrats harvested at the end of the experiment was consistent across treatments; early-germinating seedlings were more likely to survive than late-germinating ones. In high density large seed monocultures, 20% of seeds that germinated 12–13 days after planting survived, and less than 10% survived that germinated greater than 14 days after planting. In small seed monocultures, greater than 65% of seeds germinating 12–13 days after planting survived, while less than 35% survived that germinated more than 17 days after planting. Similar patterns were observed in seed size mixtures, where 75% of the large seeds and 60% of the small seeds that germinated on days 12–13 survived while only 25% of the large seeds and 44% of the small seeds that germinated five days later survived to the end of the experiment. As noted earlier, large seeds often produced larger plants than small seeds did. Competition may have been more intense in large seed monocultures, and could have resulted in greater mortality in the large seed monocultures than in the small seed monocultures. In seed size mixtures, however, plants which germinated on a given day from large and small seeds did not differ in survivability. It is not clear from these data, however, whether germination date or seed size was more important in determining seedling survivorship, or if germination date and seed size interacted in any appreciable fashion to determine seedling survivorship. Differences among treatments may also reflect the small sample sizes used. This aspect of seed size effects merits further study.

Seed production—In virtually all combinations of planting type and density, seed size did not affect directly seed production. Most plants produced very few seeds, but of those that did, most produced equal numbers of large and small seeds (Table 5). In seed size monocultures, the plants produced large and small seeds in equal numbers ($P > 0.05$, Wilcoxon signed-rank test; Table 5). In high density seed size mixtures, plants from small seeds produced significantly more large seeds than small ones ($P < 0.05$, Wilcoxon signed-rank test; Table 5), but plants from large seeds produced equal numbers of large and small seeds ($P > 0.05$, Table 5). In contrast, in intermediate density seed size mixtures, plants from large seeds produced significantly more large seeds than small ones ($P < 0.05$, Wilcoxon signed-rank test; Table 5), and plants from small seeds pro-

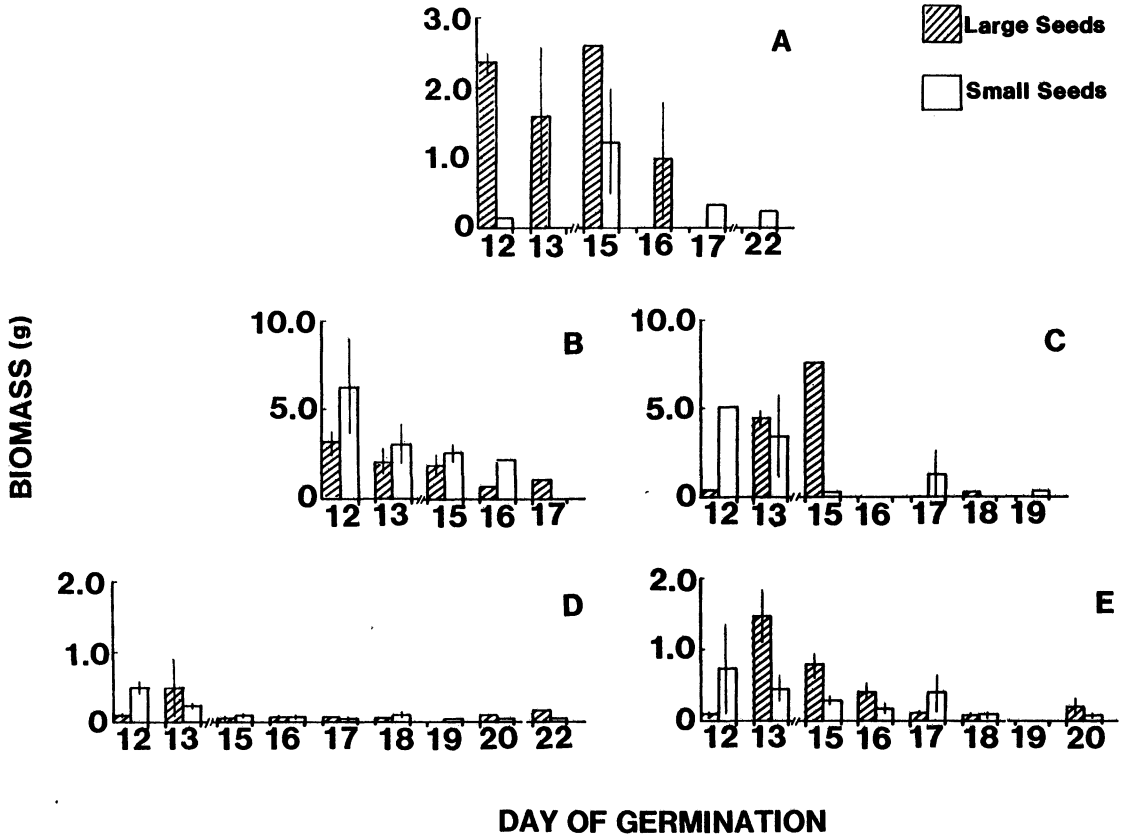

Fig. 2. Mean biomass of plants from large seeds (shaded bars) and small seeds (open bars) (±1 SE where calculable; bars lacking an error represent only a single plant) at the final harvest date. Each pair of bars in each histogram represents the large and small seeds which germinated on a given day (days after planting). **A,** low density plants; **B,** intermediate density plants in seed size monocultures; **C,** intermediate density plants in seed size mixtures; **D,** high density plants in seed size monocultures; **E,** high density plants in seed size mixtures.

duced equal numbers of large and small seeds ($P > 0.05$, Table 5).

Total seed production was affected predominantly by plant density ($P < 0.0001$; Table 6). Seed size alone had no effect on total seed production. Germination date, on the other hand, significantly affected seed output ($P < 0.0001$, ANCOVA; Table 6). As with the data on plant biomass, the ANCOVA was run without germination date in the model to see if germination date masked seed size effects in the model. Although the F statistic increased in the reanalysis ($F_{1,84} = 1.31$; compare with Table 6), seed size effects remained not significant ($P > 0.25$). Plant biomass is known to be a good predictor of fecundity (Harper, 1977), and early germinating plants were larger than late germinating ones (Fig. 2, Table 4) and produced more seeds than late germinating ones. Although seed size alone did not affect fecundity, its direct effect on plant germination time and its indirect effect on plant biomass illustrate that seed size effects early in ontogeny can affect plant success later in time.

DISCUSSION—Many investigators have shown that seed size affects the subsequent performance of the plant produced from that seed (Black, 1957, 1958; Harper, 1977; Stanton, 1984a, b; Venable, 1985a; Venable and Levin, 1985a, b). In the experimental populations of *Atriplex* described here, seed size primarily affected plant germination, and through the effect of seed size on germination, may have affected plant biomass and mortality. The relationship between seed size and each of these factors is consquently complex. Density-dependent effects were most important in determining plant fecundity, and plants usually produced equal numbers of large and small seeds regardless of the size of the seed from which they were grown. Through its interaction with germination date, however, seed size affected plant performance throughout the life of the plants.

TABLE 5. *Mean seed production (±1 SE) by plants grown from different-sized seeds in seed size monocultures and seed size mixtures for each density treatment. Mean seed production was calculated from only those plants which actually produced seeds*

Density	Planting type	Parent seed size	Number of large seeds produced		Number of small seeds produced
1	monoculture	L	126.7 ± 23.55	ns	124.3 ± 27.74
		S	77.1 ± 22.13	ns	117.0 ± 40.96
10	monoculture	L	137.8 ± 16.61	ns	150.4 ± 55.08
		S	55.1 ± 17.98	ns	50.9 ± 18.36
	mixture	L	169.8 ± 47.47	*	18.6 ± 2.50
		S	67.5 ± 31.49	ns	29.8 ± 16.27
100	monoculture	L	24.3 ± 10.27	ns	15.0 ± 9.94
		S	21.5 ± 6.35	ns	20.4 ± 7.45
	mixture	L	17.4 ± 4.29	ns	17.4 ± 5.15
		S	15.0 ± 3.90	*	9.1 ± 2.21

* $P < 0.05$.

Polymorphic seeds of halophytes show wide variation in germination requirements and timing both in laboratory studies (Ungar, 1962, 1978, 1979, 1982; Khan and Ungar, 1984a, b) and in the field (Ungar and Riehl, 1980; Philipupillai and Ungar, 1984). These investigators have shown that small seeds tend to germinate later than large ones under saline conditions. Under freshwater conditions (as used in this study), there are no appreciable differences in germination rate between the two seed morphs (Khan and Ungar, 1984b). Further studies of density and seed size effects in *Atriplex* across a salinity gradient could illuminate further the importance of seed polymorphism in this species. Ross and Harper (1972) have shown how critical emergence time is in determining plant performance. The data presented here illustrate that germination time and seed size may interact to determine final plant size and fecundity. Overall, small seeds germinated a fraction of a day earlier than large seeds did, but small seeds generally produced smaller plants than large seeds did both in seed size monocultures and in seed size mixtures (Tables 3, 4; Fig. 2). Large and small seeds, however, both germinated over a lengthy period of time, and the effects of germination time of seeds of a particular size on plant performance overshadowed seed size effects alone (Fig. 2; Table 4). Density-dependent effects and germination date were the most important determinants of plant biomass and fecundity (Tables 4–6). Although seed size affected germination date (Tables 1, 2), seed size alone appeared to have little effect on fecundity (Table 6).

Stanton (1984a) found that in wild radishes (*Raphanus raphanistrum*), seed size did not affect overall plant performance beyond the early seedling stage. In her study, however, low density plants were studied in the greenhouse while competing plants were studied in the field. The effects of seed size in the field may differ from that in the greenhouse and competitive effects due to density may have overshadowed seed size effects (as they did in the *Atriplex* populations studied here).

Somatic seed polymorphisms are common in many plant families (Harper et al., 1970). Two hypotheses have been advanced as explanations for the existence of seed polymorphisms: differential germination and differential dispersal among the different seed morphs (Harper et al., 1970; Ungar, 1979; Cavers, 1983). Germination differences among seed morphs are common in halophytes (reviews in Ungar, 1978, 1982), and it has been suggested that these germination polymorphisms are an adaptive response to seasonal variations in salinity and flooding in coastal (and other saline) habitats (Ungar, 1978, 1979, 1982). The results of this study support other data showing germination differences among *Atriplex* seed morphs (Khan and Ungar, 1984a, b), but do

TABLE 6. *Results of the ANCOVA for total seed production. Notation as in Table 4*

Source	df	SS	MS	*F*	Probability *F*
Overall analysis of covariance					
Model	12	43.431	3.619	9.916	0.0001
Error	72	26.277	0.365		
Total	84	69.708			
Partitioned sums of squares					
D	2	29.275		41.22	0.0001
S	1	0.201		0.57	0.4538
T	1	1.437		4.05	0.0479
D*S	2	0.444		0.23	0.5377
D*T	2	0.029		0.04	0.8426
S*T	1	0.057		0.16	0.6896
D*S*T	2	0.213		0.30	0.7441
G	1	8.222		23.16	0.0001

not address the adaptive nature of this response. The latter would be best approached through controlled field investigations. The dispersability of the different seed morphs also merits future sudy.

The results presented here illustrate that seed size can affect plant population parameters throughout plant development in a cascading way. Time of germination was affected by seed size, and germination time subsequently affected plant size and fecundity. Considered alone, seed size effects diminish through time, but germination effects do not (Tables 1, 2, 4, 6). Plant size, also an important determinant of plant population dynamics and plant fecundity, was influenced weakly by seed size. Seed size interactions with population density and planting background further influenced plant size and fecundity, and contributed to the overall population dynamics of these experimental *Atriplex* populations. These results show that seed size effects, both directly and indirectly through their influence on germination time, can be important determinants of individual plant performance, but density effects on plant fecundity likely dominate overall population dynamics.

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