# SEED POLYMORPHISM AND GERMINATION RESPONSES TO SALINITY STRESS IN ATRIPLEX TRIANGULARIS WILLD.

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Seeds of *Atriplex triangularis* exhibited a very pronounced morphological and physiological seed polymorphism. Seed size varied from 1.0 to 2.8 mm and predicted the likelihood of successful establishment through its effect on germination and seedling vigor. Large seeds had a mean dry weight of  $2.44 \pm 0.16$  mg and a mean length of  $2.45 \pm 0.24$  mm; medium seeds, mean dry weight of  $1.21 \pm 0.10$  mg and mean length of  $1.78 \pm 0.19$  mm; small seeds, mean dry weight of  $0.64 \pm 0.04$  mg and mean length of  $1.27 \pm 0.10$  mm. The degree of salt tolerance increased progressively with increasing seed size. Seeds from all size classes that were initially treated with 2%-5% NaCl had from 85% to 100% germination after being immersed in distilled water for 6 days, indicating a transitory adverse effect of salt stress on germination. The amount of water absorbed by all seeds is influenced by change in media salinity but not by hormonal treatments. Small seeds contain more Na<sup>+</sup> and Cl<sup>-</sup> than medium and large seeds. Seedling dry weight was related to initial seed size. Salt stress inhibited seedling growth. Gibberellic acid alleviated some of the dormancy in seeds induced by high salt concentrations.

#### Introduction

The halophyte Atriplex triangularis Willd. (A. patula var. hastata [L.] Gray) (Chenopodiaceae) is an annual of wide distribution, commonly found in inland saline and coastal marshes (OSMOND et al. 1980). Both light and dark seeds were found in bracteoles: the dark seeds had a hard black testa, while light seeds appeared yellowish brown (Frankton and Bassett 1968; Ungar 1971). TASCHEREAU (1972) reported seed dimorphism, indicating a greater abundance of black seeds. DRYS-DALE (1973), however, reported that seed size is lognormally continuous rather than bimodal; he also indicated that seed polymorphism may be developmental as seeds of both colors and major categories are found on the same plants. BAKER (1974) found that A. triangularis plants arising from large seeds had faster root and shoot growth than seedlings from small seeds that germinated at the same time.

Change in the properties of membranes plays a prominent role in controlling seed germination by affecting the rate of hydration, enzyme release, ion transport and concentration, pH, and inhibitor content (TAO and KHAN 1977). Gibberellic acid (GA<sub>3</sub>), kinetin, and fusicoccin promote proton extrusion, K<sup>+</sup> uptake, and a decrease in transmembrane electric potential in seeds (ILAN et al. 1971; WOOD and PALEG 1972; MARRÈ et al. 1974). Seed germination in various halophytes was enhanced by GA<sub>3</sub> treatment (UNGAR and BINET 1975; UNGAR and

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BOUCAUD 1975; BOUCAUD and UNGAR 1976; UNGAR 1978).

We investigated the germination responses of A. triangularis seeds to various environmental factors. Water uptake and ion content of seeds were measured under various salt concentrations and growth regulator treatments. The effect of seed size and salinity on seedling growth was also determined.

# Material and methods

Seeds were collected in October 1981 from an inland salt marsh on the property of the Morton Salt Company, Rittman, Ohio. The lengths of 747 seeds were measured with an ocular micrometer, and seeds were sorted into three groups: small, <1.5 mm; medium, between 1.5 and 2.0 mm; and large, > 2 mm. Air-dry weights of 25 mature seeds were determined using 25 replicates each of small, medium, and large seeds. For all germination and growth experiments, seeds were placed in  $50 \times 9$ mm Gelman no. 7234 sterile, tight-fitting plastic petri dishes containing 6 ml of test solution. Each dish was placed in a 9-cm-diameter glass petri dish to reduce water evaporation. These dishes were placed in programmed refrigerated incubators using a 12-h photoperiod and alternating regime of 5/25 C with a 12-h night/12-h day temperature.

Effects of salinity on the germination of various size classes of *Atriplex triangularis* seeds and subsequent seedling growth were studied in light. Four replicates of 25 seeds each were used under six salinity regimes of 0%, 1%, 2%, 3%, 4%, and 5% NaCl (wt/vol). Germination was recorded at 2-day intervals for 20 days, and the percentage of germination was calculated. After 20 days, seedling growth was measured, and ungerminated seeds from the 2%, 3%, 4%, and 5% NaCl treatments were transferred to distilled water to study the recovery

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Manuscript received September 1983; revised manuscript received May 1984.

of germination, which was also recorded at 2-day intervals for 6 days.

Small, medium, and large seeds were germinated in a 12-h photoperiod with 0%, 1%, 1.5%, and 2.0% NaCl with or without 100, 500, and the 1,000 mg/liter GA<sub>3</sub>; percentage of germination was recorded every other day for 20 days. Small, medium, and large seeds also were germinated in complete darkness in 0%, 1%, 1.5%, and 2.0% NaCl with or without 1,000 mg/liter GA<sub>3</sub> at 5/25 C for 20 days, and germination was recorded at the end of 20 days.

The rate of absorption of water and NaCl solutions (1% and 3%) by small, medium, and large seeds with and without GA<sub>3</sub> was studied. Seeds were treated with 100 mg/liter GA<sub>3</sub> for 24 h in the presence of 0%, 1%, and 3% NaCl. Each treatment had four replicates with 25 seeds each. Dry weight for each replicate was estimated initially. Difference in seed weight before and after treatments was considered to be the amount of water absorbed. To determine the ion content, seed replicates were ground in 10 ml of distilled water with a mortar and pestle. Sodium and potassium were estimated with a Perkin Elmer Model 360 Atomic Absorption Spectrophotometer, and chloride ions were estimated with a Beckman specific ion electrode.

The kinetics of absorption by seeds from NaCl solutions was studied with small, medium, and large seeds, which were incubated in 1% and 3% NaCl for 6, 24, 48, and 72 h; the differences in their dry weight were recorded. Ionic content (Na<sup>+</sup>, K<sup>+</sup>, and Cl<sup>-</sup>) was estimated by the methods described above.

Small, medium, and large seeds were allowed to absorb distilled water for 6, 12, and 24 h, were transferred to 2% NaCl, and germinated at 5/25 C with 12-h photoperiod. Percentage of germination was recorded at 2-day intervals for 20 days. Velocity of germination was determined by using an index of germination velocity (KHAN and UNGAR 1984).

Statistical analyses of all data used the computer programs of Statistical Analysis System (RAY 1982) on an IBM 370 computer. Data were analyzed with the CHART, GLM, LSD (P=.05), and MEANS procedures.

### Results

## SEED SIZE AND WEIGHT

Seed length ranged from 1 to 2.8 mm. The frequency distribution indicated a trimodal distribution (fig. 1). Large seeds had a mean length of 2.45  $\pm$  0.24 m; medium seeds, 1.78  $\pm$  0.19 mm; and small seeds, 1.27  $\pm$  0.10 mm. Weight of air-dried seeds also fitted a trimodal distribution (fig. 2). Large seeds had a mean dry weight of 2.44  $\pm$  0.16 mg; medium seeds, 1.21  $\pm$  0.10 mg; and small seeds, 0.64  $\pm$  0.04 mg. Average testa weight for

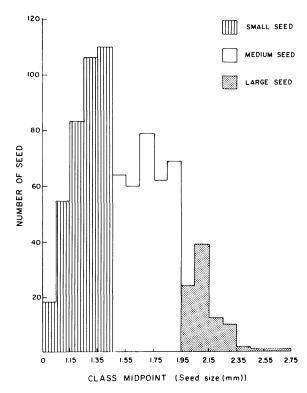


Fig. 1.—Variation in seed length of Atriplex triangularis

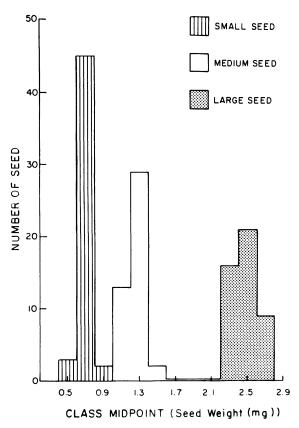


Fig. 2.—Variation in seed weight of Atriplex triangularis

 $\begin{array}{c} TABLE \ 1 \\ \\ Absorption \ of \ water \ (mg) \ from \ NaCl \ solutions \ by \\ \\ Atriplex \ triangularis \ seeds \end{array}$ 

NaCl	Seed weight (mg)	6 h <sup>a</sup>	24 h <sup>a</sup>	48 h <sup>a</sup>	72 h
1%:					
Small	.64	.05	.17	.01	.04
Medium	1.21	.21	.13	.04	01
Large	2.44	.48	.62	.23	.04
3%:					
Small	.64	.04	.12	.11	.01
Medium	1.21	.27	.19	.08	.06
Large	2.44	.44	.40	.41	.02

Note.—LSD (salinity) = 0.04; LSD (time) = 0.05; LSD (seed size) = 0.04.

small seeds was 0.22 mg; for medium seeds, 0.35 mg; and for large seeds, 0.37 mg.

#### RATE OF ABSORPTION

During 6 h of soaking there was very little absorption by small seeds (7% of dry weight), whereas large seeds soaking in 1% NaCl increased to ca. 20% of their dry weight (table 1). There was a slightly lower absorption in the 3% NaCl treatment, but the two treatments were not significantly different from each other. Small seeds soaking in 1% and 3% NaCl for 24 h showed a significant enhancement in the amount of absorption: 33% in 1% NaCl and 24% in 3% NaCl. Medium and large seeds also had a significant increase in the amount of absorption (P = .01). No significant absorption occurred in small and medium seeds soaking in 1% NaCl for 48 and 72 h, whereas absorption was considerably reduced in large seeds after 48 h. However, for medium seeds imbibing in 3% NaCl, the amount of absorption decreased substantially after 48 h.

Only the results of the 3% NaCl treatments are reported in table 2 since the 1% NaCl treatment did not yield significantly different results. Small seeds had a higher concentration of Na<sup>+</sup> than medium and large seeds (table 2). When soaked for 6 h in 1% NaCl, the sodium ion concentration substantially increased, but it progressively decreased to the level of the nontreated seeds after soaking for 72 h. In medium and large seeds, there was some increase in Na<sup>+</sup> concentration when seeds were presoaked for 6 h in NaCl, but this was not as prominent as that of small seeds, and it also decreased after 72 h of soaking. Change in media salinity does not seem to have any effect on Na<sup>+</sup> content of seeds.

When the amount of Na<sup>+</sup> was expressed as a percentage of tissue water, there was a very high concentration of Na<sup>+</sup> in the small seeds when soaked for 6 h in 1% NaCl, but, as the soaking time increased, the Na<sup>+</sup> concentration decreased substantially after 24 h of soaking. The Na<sup>+</sup> concentration was also higher after 6 h in medium and large seeds,

TABLE 2  $\label{eq:Concentration} \mbox{Concentration (\% $\pm$ SE) of $Na^+$, $Cl^-$, and $K^+$ in polymorphic seeds of Atriplex triangularis after soaking in 3% NaCl from 6 to 72 h$ 

Ion	Air-dry seed <sup>a</sup>	6 h <sup>a</sup>	24 h <sup>a</sup>	48 h <sup>a</sup>	72 h <sup>a</sup>
Small seed:					
Na <sup>+</sup>	$.67 \pm .04$	$1.02 \pm .03$	$.93 \pm .08$	$.73 \pm .04$	$.61 \pm .05$
K <sup>+</sup>	$.37 \pm .02$	$.27 \pm .01$	$.27 \pm .04$	$.19 \pm .01$	$.19 \pm .02$
Cl <sup>-</sup>	$1.56 \pm .13$	$1.34 \pm .19$	$.83 \pm .06$	$.76 \pm .10$	$.86 \pm .12$
Medium seed:					
Na <sup>+</sup>	$.43 \pm .02$	$.64 \pm .02$	$.53 \pm .03$	$.46 \pm .02$	$.52 \pm .03$
K <sup>+</sup>	$.37 \pm .01$	$.30 \pm .02$	$.31 \pm .03$	$.29 \pm .01$	$.27 \pm .03$
Cl <sup>-</sup>	$.72 \pm .03$	$.91 \pm .05$	$.40 \pm .05$	$.48 \pm .06$	$.81 \pm .19$
Large seed:					
Na <sup>+</sup>	$.38 \pm .04$	$.35 \pm .05$	$.29 \pm .02$	$.33 \pm .01$	$.32 \pm .01$
K <sup>+</sup>	$.32 \pm .02$	$.37 \pm .01$	$.33 \pm .02$	$.39 \pm .01$	$.36 \pm .02$
Cl <sup>-</sup>	$.98 \pm .02$	$.42 \pm .12$	$.32 \pm .02$	$.33 \pm .01$	$.50 \pm .08$

NOTE.—Na<sup>+</sup>: LSD (time) = 0.09; LSD (seed size) = 0.07; K<sup>+</sup>: LSD (time) = 0.03; LSD (seed size) = 0.02; Cl<sup>-</sup>: LSD (time) = 0.03; LSD (seed size) = 0.11.

<sup>&</sup>lt;sup>a</sup> = Increase in seed weight (mg) during respective time.

<sup>&</sup>lt;sup>a</sup> = Ion content from a 1:1 (seed:distilled water) extract.

TABLE 3  $Percentage \ increase \ in \ weight \ (mg \ \pm \ SE) \ and \ concentration \ (\% \ \pm \ SE) \ of \ Na^+, \ Cl^-, \ and \ K^+ \ in \ seeds \ treated \ with \ GA_3 \ and \ NaCl \ for \ 24 \ h$ 

TREAT-		0% Na	Cl			3% N	laCl	
MENT	Wt	Na <sup>+</sup>	Cl <sup>-</sup>	K <sup>+</sup>	Wt	Na <sup>+</sup>	Cl <sup>-</sup>	K <sup>+</sup>
Small seed:								
Н <sub>2</sub> О	$77.70 \pm 5.85$	$.61 \pm .16$	$.80 \pm .11$	$.43 \pm .14$	$45.30 \pm .00$	$.68 \pm .15$	$.90 \pm .04$	$.23 \pm .02$
GA <sub>3</sub>	$64.70 \pm 5.10$	$.24 \pm .03$	$.78 \pm .08$	$.30 \pm .08$	$36.80 \pm 6.15$	$.22 \pm .03$	$.57 \pm .15$	$.29 \pm .04$
Medium seed	i:							
H <sub>2</sub> O	$44.40 \pm 2.52$	$.49 \pm .16$	$.87 \pm .26$	$.41 \pm .03$	$46.00 \pm 1.09$	$.35 \pm .08$	$.42 \pm .02$	$.29 \pm .02$
GA <sub>3</sub>	$48.40 \pm 1.81$	$.28 \pm .06$	$.44 \pm .03$	$.59 \pm .09$	$44.40 \pm 2.63$	$.52 \pm .17$	$.47 \pm .02$	$.35 \pm .02$
Large seed:								
Н₀О	$50.60 \pm 4.60$	$.28 \pm .11$	$.23 \pm .02$	$.44 \pm .03$	$39.00 \pm 1.38$	$.26 \pm .04$	$.23 \pm .01$	$.38 \pm .02$
-		$.22 \pm .09$	$.17 \pm .01$	$.44 \pm .01$	$37.80 \pm 1.79$	$.32 \pm .09$	$.36 \pm .15$	$.46 \pm .07$

Note.—Wt: LSD (seed size) = 2.98; LSD (treatment) = 3.44; LSD (salinity) = 2.98; Na $^+$ : LSD (seed size) = 0.15; LSD (treatment) = 0.17; LSD (salinity) = 0.15; Cl $^-$ : LSD (seed size) = 0.17; LSD (treatment) = 0.19; LSD (salinity) = 0.19; K $^+$ : LSD (seed size) = 0.04; LSD (treatment) = 0.05; LSD (salinity) = 0.04.

but much lower than in small seeds, and ion content decreased significantly with an increased soaking time.

Chloride, as a percentage of dry weight, was initially (6 h) unchanged and then progressively decreased with time for small, medium, and large seeds that were soaked in 1% and 2% NaCl (table 2). Chloride as a percentage of tissue water was very high in small seeds during the 6-h treatment (28%) but decreased to 2% after 72 h of soaking in 1% NaCl. Similar results were obtained when seeds were exposed to 3% NaCl. In medium and large seeds, initial Cl<sup>-</sup> concentration was much lower than that of small seeds, but the Cl<sup>-</sup> concentration, when calculated as a percentage of tissue water, progressively decreased with increasing exposure time.

Potassium as a percentage of tissue water decreased with increase in soaking time for small, medium, and large seeds in various concentrations of NaCl. When K<sup>+</sup> is expressed as percentage of dry weight for small and medium seeds, it de-

creased in concentration with increase in soaking time in both salinity treatments. However, in large seeds, the concentration did not change in either salinity treatment (table 2).

# EFFECT OF GA<sub>3</sub> ON THE ABSORPTION OF NaCl SOLUTION

 $GA_3$  treatments applied to small seeds reduced their absorption with or without salt, whereas in medium and large seeds there was no significant hormonal effect on the absorption of water and NaCl solution (table 3). Seeds in nonsaline medium, when soaked for 24 h without  $GA_3$ , contained more  $Na^+$  than seeds treated with  $GA_3$  at all salinities and seed sizes (table 3). Small seeds had higher  $Na^+$  concentrations than medium and large seeds. In  $Cl^-$ , the pattern was similar to that in  $Na^+$  (table 3). Concentration of  $K^+$  decreased with an increase in NaCl in the medium. Inclusion of  $GA_3$  did not have any effect on the  $K^+$  concentration of seeds (table 3).

TABLE 4 Effect of presoaking of seeds in distilled water on their subsequent germination (%  $\pm$  SE) in 2% NaCl

Time of soaking (h)	2 days	10 days	20 days	Velocity of germination
Small seed:				
6	$0. \pm 0.$	$18.0 \pm .3$	$41.0 \pm 1.0$	$8.5 \pm .5$
12	$0. \pm 0.$	$24.0 \pm 3.7$	$47.0 \pm 5.5$	$11.6 \pm 1.8$
24	$1.0 \pm 1.0$	$20.0 \pm 1.6$	$48.0 \pm 3.7$	$10.2 \pm 1.1$
Medium seed:				
6	$0. \pm 0.$	$16.0 \pm 2.8$	$30.0 \pm 3.5$	$7.5 \pm 1.2$
12	$4.0 \pm 2.8$	$10.0 \pm 2.6$	$33.0 \pm 1.9$	$7.1 \pm 1.7$
24	$4.0 \pm .6$	$18.7 \pm .03$	$33.3 \pm .9$	$9.1 \pm .4$
Large seed:				
6	$0. \pm 0.$	$9.0 \pm 1.9$	$27.0 \pm 3.0$	$6.1 \pm 1.3$
12	$6.0 \pm 3.5$	$18.0 \pm 3.5$	$41.0 \pm 2.6$	$10.6 \pm 1.6$
24	$10.0 \pm 2.6$	$24.0 \pm 1.6$	$31.0 \pm 1.0$	$11.7 \pm 1.3$

SMALL SEED

MEDIUM SEED

TABLE 5

EFFECT OF SALINITY ON THE VELOCITY OF GERMINATION
OF POLYMORPHIC SEEDS

NaCl (%)	Small seed	Medium seed	Large seed
0.0	36.5	40.1	44.1
1.0	18.7	24.9	40.3
2.0	9.0	14.3	18.7
3.0	.0	3.1	3.8
4.0	.0	2.6	1.1
5.0	.0	.3	.9

NOTE.—Velocity of germination =  $\Sigma G/t$ , where G = percentage of germination at 2-day intervals, t = total germination period (20 days).

#### EFFECT OF PRESOAKING ON GERMINATION

Presoaking for 12 and 24 h resulted in a faster rate of germination than 6 h of soaking (table 4). Final germination percentages for all seed sizes in all treatments were not significantly different from each other. Presoaking significantly increased the final germination percentage of small seeds compared with the nonsoaked controls.

#### SALT TOLERANCE

The velocity of germination of small seeds substantially decreased with increase in salinity (table 5). No small seeds germinated in 3%, 4%, and 5% NaCl. Medium seeds appeared to be a little more tolerant and have a higher velocity of germination than small seeds at all NaCl treatments, with medium seeds germinating in 5% NaCl. Large seeds were most tolerant to salinity. Velocity of germination for large seeds was higher at all NaCl concentrations than for small and medium seeds. However, an increase in salinity concentrations progressively decreased germination percentages for all seed sizes.

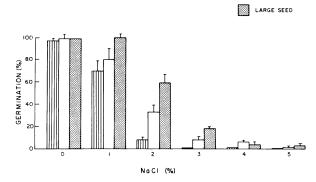


FIG. 3.—Final germination percentage of *Atriplex triangularis* seeds after a 20-day treatment with 1%, 2%, 3%, 4%, and 5% NaCl.

Without salt, seeds of all sizes had ca. 100% germination (fig. 3). Salt in the medium induced dormancy, which increased with increased salt concentration. Salinity is more effective in inducing dormancy in small seeds than in large seeds. Seeds of all sizes in all treatments recovered very quickly (table 6). Germination was above 90% in almost all treatments after 6 days except for the small seeds that were initially treated with 5% salt, which had an 87% recovery of germination. Increase in salt stress inhibited the growth of seedlings, more in small seeds than in large seeds (table 7).

# EFFECT OF SALINITY AND GA<sub>3</sub> ON GERMINATION

GA<sub>3</sub> promoted the germination of small, medium, and large seeds compared to the controls in distilled water and the dark (table 8). GA<sub>3</sub> completely reversed the inhibitory effect of 1% NaCl on germination in all three seed sizes. With an in-

TABLE 6

GERMINATION (%  $\pm$  SE) PERCENTAGE OF ATRIPLEX TRIANGULARIS SEEDS IN DISTILLED WATER AFTER A 20-day NaCl treatment

NaCl (%)	2 days	4 days	6 days	Total germination
Small seed:				
2	$79.5 \pm 3.3$	$94.5 \pm 2.9$	$97.7 \pm 2.9$	$98.0 \pm 2.0$
3	$69.0 \pm 6.4$	$82.0 \pm 5.3$	$98.0 \pm 1.0$	$98.0 \pm 2.0$
4	$62.0 \pm 5.3$	$82.0 \pm 3.5$	$98.0 \pm 1.0$	$98.0 \pm 2.3$
5	$52.0 \pm 9.1$	$78.0 \pm 8.1$	$87.0 \pm 5.5$	$87.0 \pm 11.0$
Medium seed:				
2	$53.7 \pm 3.5$	$78.1 \pm 7.8$	$100.0 \pm .0$	$100.0 \pm .0$
3	$71.7 \pm 3.5$	$88.0 \pm 3.3$	$97.8 \pm 1.2$	$98.0 \pm 2.3$
4	$61.7 \pm 5.2$	$88.3 \pm 4.8$	$96.8 \pm 1.2$	$97.0 \pm 4.0$
5	$62.6 \pm 6.4$	$86.8 \pm 5.1$	$97.9 \pm 2.0$	$98.0 \pm 4.0$
Large seed:				
2	$65.9 \pm 7.1$	$97.6 \pm 2.3$	$100.0 \pm .0$	$100.0 \pm .0$
3	$79.3 \pm 3.5$	$97.6 \pm 5.3$	$100.0 \pm .0$	$100.0 \pm .0$
4	$72.2 \pm 3.5$	$91.8 \pm 1.8$	$97.9 \pm 1.2$	$98.0 \pm 2.0$
5	$71.1 \pm 8.7$	$93.8 \pm 5.2$	$95.9 \pm 1.6$	$96.0 \pm 3.2$

TABLE 7

EFFECT OF SALINITY ON THE GROWTH OF SEEDLINGS FROM POLYMORPHIC SEEDS OF ATRIPLEX TRIANGULARIS

	Salinity (%)				
VARIABLE	.0	.5	1.0	1.5	
Small seed:					
Hypocotyl length (mm $\pm$ SE)	$25.2 \pm .8$	$20.1 \pm .9$	$12.8 \pm .5$	$5.0 \pm .1$	
Root length (mm ± SE)	$20.6 \pm .6$	$8.7 \pm .7$	$4.2 \pm .4$	$4.0 \pm .8$	
Dry weight (mg $\pm$ SE)	$.4 \pm .1$	$1.2 \pm .2$	$.7 \pm .2$	$.6 \pm .1$	
Medium seed:					
Hypocotyl length (mm $\pm$ SE)	$24.9 \pm 1.0$	$25.1 \pm 1.3$	$16.6 \pm 1.1$	$12.8 \pm 2.9$	
Root length (mm $\pm$ SE)	$23.1 \pm 1.2$	$15.8 \pm 2.2$	$2.8 \pm .2$	$2.6 \pm .8$	
Dry weight (mg $\pm$ SE)	$.7 \pm .1$	$0.8 \pm .1$	$.6 \pm .1$	.4 ± .1	
Large seed:					
Hypocotyl length (mm ± SE)	$32.9 \pm 1.1$	$35.8 \pm 1.3$	$18.8 \pm 2.0$	$18.4 \pm 1.8$	
Root length (mm ± SE)	$27.0 \pm 1.1$	$17.7 \pm 1.7$	$8.7 \pm .5$	$8.5 \pm .9$	
Dry weight (mg $\pm$ SE)	$1.9 \pm .1$	$2.9 \pm .1$	$2.2 \pm .0$	$1.6 \pm .1$	

crease in salinity, germination was progressively reduced, but inclusion of GA<sub>3</sub> improved germination

#### Discussion

Several Atriplex species growing under saline conditions were reported to have seed dimorphism and polymorphism (KOLLER 1957; FRANKTON and BASSETT 1968; UNGAR 1971; DRYSDALE 1973; GUSTAFSSON 1973; BAKER 1974). GUSTAFSSON (1973) reported that the rate and percentage germination of black and brown seeds of A. triangularis and A. longipes were scarcely different, and black seeds of A. longipes showed greater germination percentages in some experiments. UNGAR (1984) indicated that plant size affects both the number of seed produced per plant and the ratio of small to large seeds.

Polymorphic seeds of A. triangularis are physiologically different in their response to salinity. Germination of small seeds is prevented by NaCl exposure, but this is clearly temporary. Distilled

TABLE 8 Effect of salinity and  $GA_3$  (1,000 mg/liter) on the Germination (%  $\pm$  SE) of polymorphic seeds of Atriplex triangularis in the dark

NaCl	Small Seeds	Medium seeds	Large seeds
0%:			
$-GA_3$	$14 \pm 2.6$	$28 \pm 2.8$	$63 \pm 6.6$
$+GA_3$	$30 \pm 8.1$	$34 \pm 1.2$	$76 \pm 3.3$
1%:			
$-GA_3$	$1 \pm 1$	$7 \pm 3$	$36 \pm 2.5$
+GA <sub>3</sub>	$18 \pm 3$	$35 \pm 6$	$61 \pm 7.2$
1.5%:			
$-GA_3$	0	0	20 + 4.3
+GA <sub>3</sub>	$9 \pm 3$	$15 \pm 1.9$	$27 \pm 4.4$
2%:			
$-GA_3$	0	$1 \pm 1$	$12 \pm 3.7$
$+GA_3$	$2 \pm 2$	$3 \pm .5$	$14 \pm 5.3$

water removes the inhibition of seed germination caused by NaCl. Seeds of several species, including *A. halimus* and *Salicornia europaea*, remain dormant at low water potential, and these seeds do not lose their viability and will germinate when returned to distilled water treatment (ZID and BOUKHRIS 1977; UNGAR 1982).

Germination in A. halimus was not permanently inhibited by 4% and 5% NaCl, and seeds germinated when returned to distilled water (ZID and BOUKHRIS 1977). IGNACIUK and LEE (1980) found that germination of A. glabriuscula and A. laciniata was not inhibited after 30 days of soaking in 600 mM NaCl. This common response among halophytes implies that it is of some ecological significance within highly saline environments, reflecting a physiological response that is strongly selected for during the evolution of these species.

 $GA_3$  was effective in promoting germination of A. triangularis seeds in 1% NaCl but stimulated less than 5% germination at higher salinities. This inability to reverse the inhibitory effect of NaCl at very high salinities indicates that metabolic processes are being directly affected by salt stress. The more effective promotion of seed germination by  $GA_3$  in the dark than in light also was reported by BOUCAUD and UNGAR (1973, 1976) and UNGAR and BINET (1975).

Presoaking of polymorphic seeds improved the rate of germination, particularly of small seeds. Similar effects of presoaking on germination were reported in *A. semibaccata* and *A. lentiformis* (YOUNG et al. 1980). UCHIYAMA (1981) related seed germination to the rate of absorption of water. He believed that, irrespective of temperature, when the water content of the seeds of *A. nummularia* reached 70%, seeds would germinate.

In A. triangularis the absorption rate of seeds from NaCl solutions was affected by an increase in the salinity of the medium. Uptake of water by the dry seeds is characterized by an initial phase

of rapid uptake by saturation kinetics, followed by a transition phase with a very gradual or negligible uptake, and this in turn is followed by a third phase of rapid and exponentially rapid uptake (KOLLER and HADAS 1982).

Springfield (1970) showed that imbibition in A. canescens depends on whether seeds are winged or dewinged. Winged seeds increased in weight by 92% and appeared fully imbibed within 24 h. Dewinged seeds imbibed water faster, increased in weight by 59%, and were fully imbibed within 15 h. Nobs and Hagar (1974) showed that, during the first 5 h, the large brown seeds of A. hortensis had a very rapid rate of water imbibition and reached saturation at 48 h. The small black seeds showed a considerably slower rate of water uptake. They had not reached saturation by day 10.

OSMOND et al. (1980) reported that, under similar conditions, uptake was 100 times faster in brown than in black seeds of *A. hortensis*. The absorption of water by black seeds was more limited by the conductance of the seed coat than by the addition of NaCl to the solution (Nobs and Hagar 1974; OSMOND et al. 1980). A similar insensitivity to NaCl was observed with the black seeds of *A. holocarpa* (COURTICE 1971).

Small seeds of A. triangularis contained more Na<sup>+</sup> and Cl<sup>-</sup> than did medium and large seeds, but the K<sup>+</sup> concentration did not vary with seed size. POULIN et al. (1978) found 0.77% Na<sup>+</sup> in S. eu-

ropea seeds collected from saline environments. HOCKING (1982) showed that seeds of Cakile maritima had an Na<sup>+</sup> content of 0.02% and a chloride content of 0.07% compared with high leaf Cl<sup>-</sup> concentrations. UNGAR (1984) found that field-grown A. triangularis had an average salt content of 2.1% in seeds from the high-salt environment and 1.7% total salts from the low-salt environment.

Our results clearly demonstrate morphological and physiological seed polymorphism in *A. triangularis*. Small seeds are more dormant than the large seeds at higher salinity, but when small seeds are returned to distilled water, they have germination percentages that are not significantly different from the control. GA<sub>3</sub> promotes germination at lower salinity treatments. Seedlings grown from large seeds are larger than seedlings originating from small and medium seeds. The amount of water absorbed by the small, medium, and large seeds is influenced by change in media salinity but not by GA<sub>3</sub> treatments.

# Acknowledgments

We acknowledge the support of National Science Foundation grant DEB-79-27236. We thank Dr. WARREN A. WISTENDAHL for his comments on the manuscript and SHAHINA A. KHAN for her assistance.

#### LITERATURE CITED

- Baker, H. G. 1974. The evolution of weeds. Annu. Rev. Ecol. Syst. 5:1–24.
- BOUCAUD, J., and I. A. UNGAR. 1973. The role of hormones in controlling the mechanically induced dormancy of *Suaeda* spp. Physiol. Plantarum **29:97**–102.
- ——. 1976. Hormonal control of germination under saline conditions of three halophytic taxa in the genus *Suaeda*. Physiol. Plantarum **37:**143–148.
- COURTICE, A. 1971. Fluctuating plant numbers in three species of *Atriplex L. Ph.D.* diss. University of Sydney.
- DRYSDALE, F. 1973. Variation of seed size in *Atriplex patula* var. *hastata* (L.) Gray. Rhodora 75:106-110. FRANKTON, C., and I. J. BASSETT. 1968. The genus *Atriplex*
- FRANKTON, C., and I. J. BASSETT. 1968. The genus Atriplex (Chenopodiaceae) in Canada. I. Three introduced species: A. heterosperma, A. oblongifolia, and A. hortensis. Can. J. Bot. 46:1309–1313.
- GUSTAFSSON, M. 1973. Evolutionary trends in *Atriplex triangularis* group in Scandinavia. I. Hybrid sterility and chromosomal differentiation. Bot. Notiser **126**:345–392.
- HOCKING, P. J. 1982. Salt and mineral nutrient levels in fruits of two strand species, *Cakile maritima* and *Arctotheca populifolia*, with special reference to the effect of salt on the germination of *Cakile*. Ann. Bot. **50**:335–343.
- IGNACIUK, R., and J. A. LEE. 1980. The germination of four annual strand-line species. New Phytol. 84:581-591.
- ILAN, I., T. GILAD, and L. REINHOLD. 1971. Specific effect of kinetin on the uptake of monovalent cations by sunflower cotyledons. Physiol. Plantarum 24:337-341.
- KHAN, M. A., and I. A. UNGAR. 1984. The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. Amer. J. Bot. 71:481–489.

- KOLLER, D. 1957. Germination regulating mechanisms in some desert seeds. IV. Atriplex dimorphostegia Kar et Kir. Ecology 38:1-13.
- KOLLER, D., and A. HADAS. 1982. Water relations in the germination of seed. Pages 402-431 in O. L. LANGE, P. D. NOBEL, C. B. OSMOND, and H. ZIEGLER, eds. Physiological plant ecology. Vol. 2. Encyclopedia of plant physiology. Springer, Berlin.
- MARRÈ, E., R. COLUMBO, and A. BALLARIN-DENTI. 1974. Transmembrane potential increase induced by auxin, benzyladenine and fusicoccin. Correlation with proton extrusion and cell enlargement. Plant Sci. Lett. 2:139–150.
- Nobs, M. A., and W. A. Hagar. 1974. Analysis of germination and flowering rates of dimorphic seeds of *Atriplex hortensis*. Carnegie Inst. Wash. Yearbook **73:**859–864.
- OSMOND, C. B., O. BJORKMAN, and D. J. ANDERSON. 1980. Physiological processes in plant ecology. Springer, Berlin. 468 pp.
- POULIN, G., D. BOURQUE, S. EID, and K. JANKOWSKI. 1978. Composition chimique de *Salicornia europaea* L. Natur. Can. 105:473-478.
- RAY, A. A., ed. 1982. SAS user guide. SAS Institute, Cary, N. C. 920 pp.
- SPRINGFIELD, H. W. 1970. Germination characteristics of Atriplex canescens seed. XI Int. Grassland Cong. Proc. 11:586– 589.
- TAO, K., and A. A. KHAN. 1977. Hormonal regulation of nucleic acids and proteins in germination. Pages 413–433 in A. A. KHAN, ed. The physiology and biochemistry of seed dormancy and germination. Elsevier/North-Holland, New York.
- TASCHEREAU, P. M. 1972. Taxonomy and distribution of Atri-

- plex species in Nova Scotia. Can. J. Bot. **50**:1571–1594.
- UCHIYAMA, Y. 1981. Studies on the germination of saltbushes. I. The relationship between temperature and germination of *Atriplex nummularia* Lindl. Jap. J. Trop. Agr. 25:62-67. UNGAR, I. A. 1971. *Atriplex patula* var. *hastata* seed dimor-

UNGAR, I. A. 1971. Atriplex patula var. hastata seed dimorphism. Rhodora 73:548–551.

- 1978. Halophyte seed germination. Bot. Rev. **44:**233–264.
- 1982. Germination ecology of halophytes. Pages 143–154 in D. N. Sen and K. S. Rajpurohit, eds. Contribution to the ecology of halophytes, Vol. 2. Junk, The Hague.
- ------. 1984. Autecological studies with Atriplex triangularis. Pages 40–52 in A. R. TIEDEMANN, E. D. MCARTHUR, H. C. STUTZ, R. STEVENS, and K. L. JOHNSON, eds. Proceedings—Symposium on the biology of Atriplex and related chenopods. USDA Forest Service Technical Report INT-172.
- UNGAR, I. A., and P. BINET. 1975. Factors influencing seed

- dormancy in *Spergularia media* (L.) C. Presl. Aquatic Bot. 1:45-55.
- UNGAR, I. A., and J. BOUCAUD. 1975. Action des fortes teneurs en NaCl sur l'évolution des cytokinines au cours de la germination d'un halophyte: le Suaeda maritima (L.) Dum. var. macrocarpa Moq. Compt. Rend. Acad. Sci. Paris 281:1239– 1242.
- Wood, A., and L. G. Paleg. 1972. The influence of gibberellic acid on the permeability of model membrane systems. Plant Physiol. **50**:103–108.
- YOUNG, J. A., B. L. KAY, H. GEORGE, and R. A. EVANS. 1980. Germination of three species of Atriplex. Agron. J. 72:705–709.
- ZID, E., and M. BOUKHRIS. 1977. Quelques aspects de la tolérance de l'*Atriplex halimus* L. au chlorure de sodium, multiplication, croissance, composition minérale. Oecol. Plantarum 12:351–362.