

# THE EFFECT OF SALINITY AND TEMPERATURE ON THE GERMINATION OF POLYMORPHIC SEEDS AND GROWTH OF *ATRIPLEX TRIANGULARIS* WILLD.<sup>1</sup>

M. A. KHAN AND I. A. UNGAR

Department of Botany, Ohio University, Athens, Ohio 45701

## ABSTRACT

Polymorphic seeds of *Atriplex triangularis* were germinated at various temperatures (5–15 C, 5–25 C, 10–20 C, 20–30 C) and salinity regimes (0 to 1.5% NaCl) in order to determine their germinability and early seedling growth under these conditions. Larger seeds generally had a higher germination percentage in saline medium. The rate and percentage of germination decreased with increased salinity stress. A thermoperiod of 25 C day and 5 C night, 12 hr/12 hr, temperature enhanced germination of seeds. Early seedling growth is promoted in larger seeds at lower salinity, and at high-day and low-night temperatures. Polymorphic seeds have different physiological requirements which provide alternative situations for seed germination in natural habitats.

*ATRIPLEX TRIANGULARIS* WILLD. (Chenopodiaceae) is an annual species of halophyte which is widely distributed in coastal and inland salt marshes of North America (Chapman, 1974; Ungar, 1974; Osmond, Bjorkman and Anderson, 1980).

Our field studies in a Rittman, Ohio salt marsh indicated that the normal germination period for *Atriplex triangularis* is from February through June, with some germination occurring as late as October. Recent investigations of seed germination in the genus *Atriplex* (Springfield, 1966; Sharma, 1976; Ignaciuk and Lee, 1980) have treated all seed sizes together and have not attempted to determine if seed size affects germination behavior and seedling growth under various temperature and salinity treatments. Beadle (1952) found that seeds of different size had similar responses to changes in temperature. Koller (1957) found that "flat" types of *Atriplex dimorphostegia* seed germinate very early as compared to a "humped" type that started germinating at a later stage. Uchiyama (1981) found that the germination ability of heavier seeds was much higher (93%) than lighter seeds (10%).

Previous studies indicated that there was an interaction between temperature and salinity concentrations affecting halophyte seed germination (Ungar, 1978, 1982), but no studies have been done with species of *Atriplex* which

have polymorphic seeds to determine if seed size and germination responses of seeds to salinity and temperature are correlated. Germination percentage of several *Atriplex* species was greater in the range of 12–25 C at various osmotic concentrations but declined beyond this range, i.e., the tolerance of osmotic stress was greater at the optimum temperature (Beadle, 1952; Springfield, 1966; Ignaciuk and Lee, 1980). Sharma (1976) demonstrated that the optimum conditions for germination of *Atriplex vesicaria* and *Atriplex nummularia* shifted to slightly higher temperatures at low soil water potentials, but the effects of lowering of water potential was not marked at temperatures above and below the optimum. Similar results were obtained with seeds of coastal species (Binet, 1965, 1966), but cold pretreatment (30 days at 5 C) of these seeds resulted in better germination. Ward (1967) found that dormancy of *Atriplex hastata* seeds was removed by cold pretreatments (4 C) for 2 wk and germination decreased steadily with increased salinity, with 2% (w/v) NaCl completely inhibiting germination.

Sankary and Barbour (1972) found that the percentage germination of *Atriplex polycarpa* seeds was similar at alternating and constant temperatures. In contrast to these findings, several species of *Atriplex* had low germination percentages at constant temperature regimes, while alternating temperature regimes were effective in inducing germination (Ignaciuk and Lee, 1980; Young et al., 1980). *Atriplex glabriuscula* and *A. laciniata* were less sensitive to increased salinity concentrations at optimal alternating temperature regimes (Ignaciuk and Lee, 1980).

<sup>1</sup> Received for publication 28 May 1983; revision accepted 3 October 1983.

The authors acknowledge the support of National Science Foundation Grant DEB-79-27236. We wish to thank Dr. Warren A. Wistendahl for his comments on the manuscript. Our appreciation to Shahina Khan for her assistance in the laboratory.

Seed size appears to be a significant factor in determining the time of germination and survival of seedlings in the salt-marsh environments. In this study we examined the effect of the interaction between salinity and temperature on the germination of polymorphic seeds and seedling growth of *Atriplex triangularis*.

**MATERIALS AND METHODS**—Seeds of *Atriplex triangularis* were collected in 1981 from plants growing in saline marshes at Rittman, Ohio. They were stored dry at 4 C. Germination and growth studies were initiated during 1982. Seeds were separated from inflorescences and sorted into large, medium, and small seeds. The large seeds were >2.0 mm, medium seeds ranged between 2.0–1.5 mm and small seeds were <1.5 mm in diameter.

**Salinity-temperature effect on germination and seedling growth**—The seeds were surface sterilized with 0.1-strength Clorox (0.52% sodium hypochlorite) for 1 min and then washed 2 to 3 times with distilled water. Germination was carried out in 50 × 9-mm Gelman No. 7232 tight-fitting plastic petri dishes with 6 ml of test solution. Each dish was placed in a 9-cm-diam glass petri dish as an added precaution against loss of water by evaporation. Four replicates of 25 seeds each were used for each treatment. Seeds were considered to be germinated with the emergence of the radicle.

To determine the effect of temperature on germination and seedling growth, alternating temperature regimes of 5–15 C, 5–25 C, 10–20 C, and 20–30 C, based on a 24-hr cycle were used, where the higher temperature (15, 20, 25, and 30 C) coincided with a 12-hr light period (2,000-lux Sylvania cool-white fluorescent lamps) and the lower temperature (5, 10, and 20 C) coincided with a 12-hr dark period.

Seeds were germinated in distilled water, 0.5, 1.0, and 1.5% NaCl solutions under the above mentioned temperature regimes. Percent germination was recorded every alternate day for 20 days. The rate of germination was estimated by using a modification of the Timson (1965) index of germination velocity =  $\Sigma G/t$ , where  $G$  = percentage of seeds germinated at 2-day intervals,  $t$  = total germination period. The maximum value possible using this index for our data was 50, that is (1,000/20). Higher values represent a more rapid rate of germination. Hypocotyl and root length were measured to the nearest millimeter after 20 days and weights were determined by drying the seedlings 80 ± 2 C for 48 hr.

**Statistical analysis**—Statistical analysis of all data was done using the computer programs of "Statistical Analysis System" (Ray, 1982) on the IBM 370 computer. Data were analyzed with the CHART, GLM(ANOVA), LSD and MEAN procedures.

**RESULTS**—**Salinity-temperature effects on germination**—The germination percentage of *Atriplex triangularis* progressively decreased with increases in salinity. Germination of smaller seeds was usually more adversely affected by salinity while larger seeds appeared to be more salt tolerant. Alternating temperature regimes of 5–25 C yielded maximum germination at salinities tested (Fig. 1–3). Temperature regimes of 20–30 C also frequently showed high germination but 5–15-C and 10–20-C temperature treatments often resulted in substantially reduced germination percentage for all seed sizes (Fig. 1–3). Rates of germination estimated by using an index of germination velocity indicate that rate of germination of seed sizes in the various salinity treatments is usually higher at the 5–25-C temperature regime (Table 1). Velocity of germination of large seeds is higher at salinities and various temperatures except at 5–15 C.

Effect of salinity and temperature on the final germination percentage of *Atriplex* indicated a general reduction in germination percentages with increasing salinity (Fig. 1–3). Sixty percent of the large seeds germinated at 5–25 C and 1.5% salinity as compared to small seeds treat-

TABLE 1. Index of germination velocity of *Atriplex triangularis* seeds from various salinity and temperature treatments

Temperature night-day	Salinity (%)	Seed size		
		Small	Medium	Large
5–15 C	0.0	18.95	20.90	15.70
	0.5	12.22	15.50	11.60
	1.0	9.70	9.85	4.40
	1.5	1.50	8.00	1.15
5–25 C	0.0	37.15	33.90	43.95
	0.5	24.50	26.25	41.75
	1.0	9.30	21.10	41.30
	1.5	1.90	12.35	31.75
20–30 C	0.0	33.00	40.10	44.05
	0.5	18.65	28.15	42.00
	1.0	7.90	17.11	15.60
	1.5	4.05	12.75	16.10
10–20 C	0.0	18.80	24.25	32.95
	0.5	12.05	16.65	23.85
	1.0	2.60	9.85	13.95
	1.5	1.40	8.90	8.20

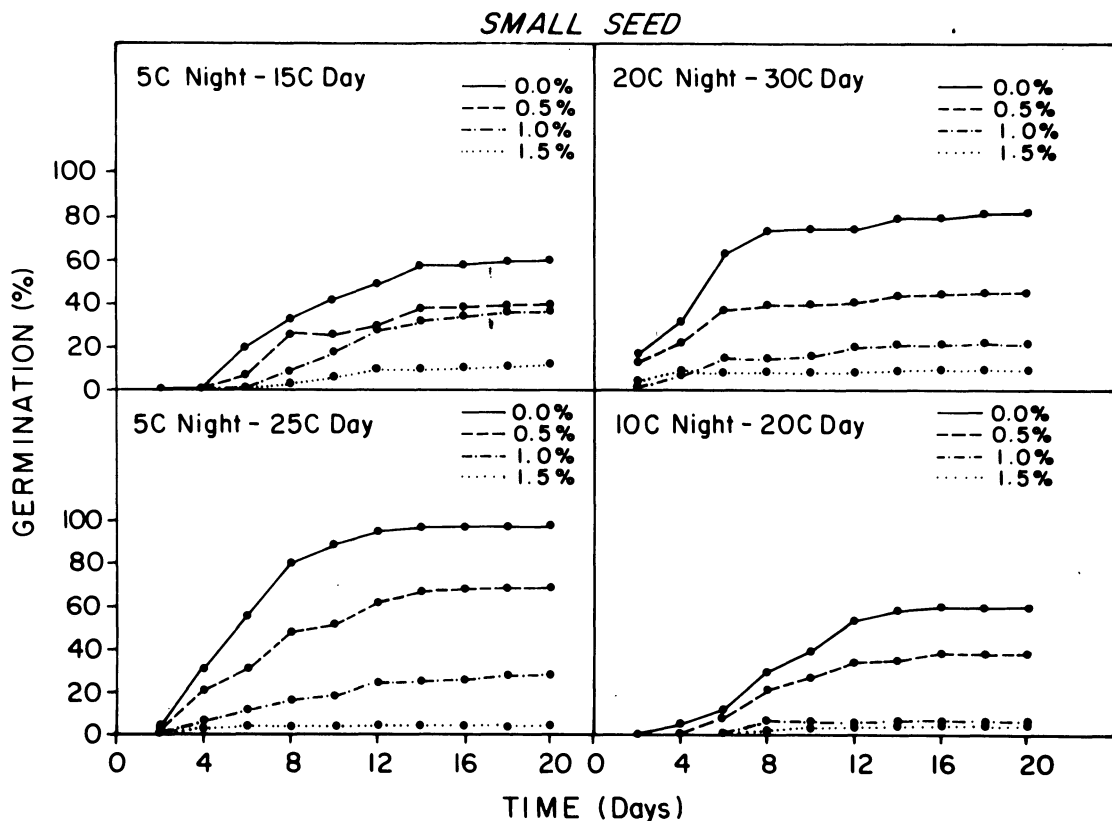


Fig. 1. Effect of temperature and salinity (0.0, 0.5, 1.0 and 1.5% NaCl) on the rate of germination of *Atriplex triangularis* small seeds.

ments where only 5% of the seeds germinated under the same conditions. Individual effects of temperature, salinity, seed size and their interactions in affecting germination were very highly significant (Table 2).

**Salinity-temperature effects on growth**—Seedlings raised from different seed sizes differ in their response to temperature and salinity. Hypocotyl growth in the non-saline control was usually greater than that at all salinity concentrations (Table 3). Greatest inhibition of growth was obtained in the 1.5% NaCl treatment. The hypocotyl was in general significantly longer at 5–25-C temperature regimes in all seed sizes, whereas, 5–15-C and 10–20-C temperatures were very inhibitory to hypocotyl growth. Individual effects of salinity, seed size, temperature and their interaction were highly significant in effecting hypocotyl growth (Table 2).

*Atriplex triangularis* seedlings had a significant reduction in root growth with increases in salinity for all seed sizes tested (Table 4). Alternating temperature regimes of 5–15 C in-

hibited root growth substantially as compared to other temperature treatments. Best root growth for large seeds was obtained at the 5–25-C temperature regimes in all salinities (Table 4). The effect of salinity, temperature, seed size and their interactions in affecting root growth were very highly significant (Tables 3, 4).

Dry weight of seedlings grown from various seed sizes in most cases was significantly higher in low salinity treatments than in the non-saline control (Table 3). The dry weight of seedlings at the highest salinity was significantly different from the control at all temperature treatments. Seedlings at temperature regimes of 5–25 C and 20–30 C had comparatively higher dry weight for all seed sizes compared to that of the 5–15-C and 10–20-C temperature regimes. Temperature regimes of 5–15 C were found to be most inhibitory for dry weight of large seedlings when compared to any other temperature regime used (Tables 3, 4). Individual effects of salinity, temperature and seed size, and their interactions on the dry weight

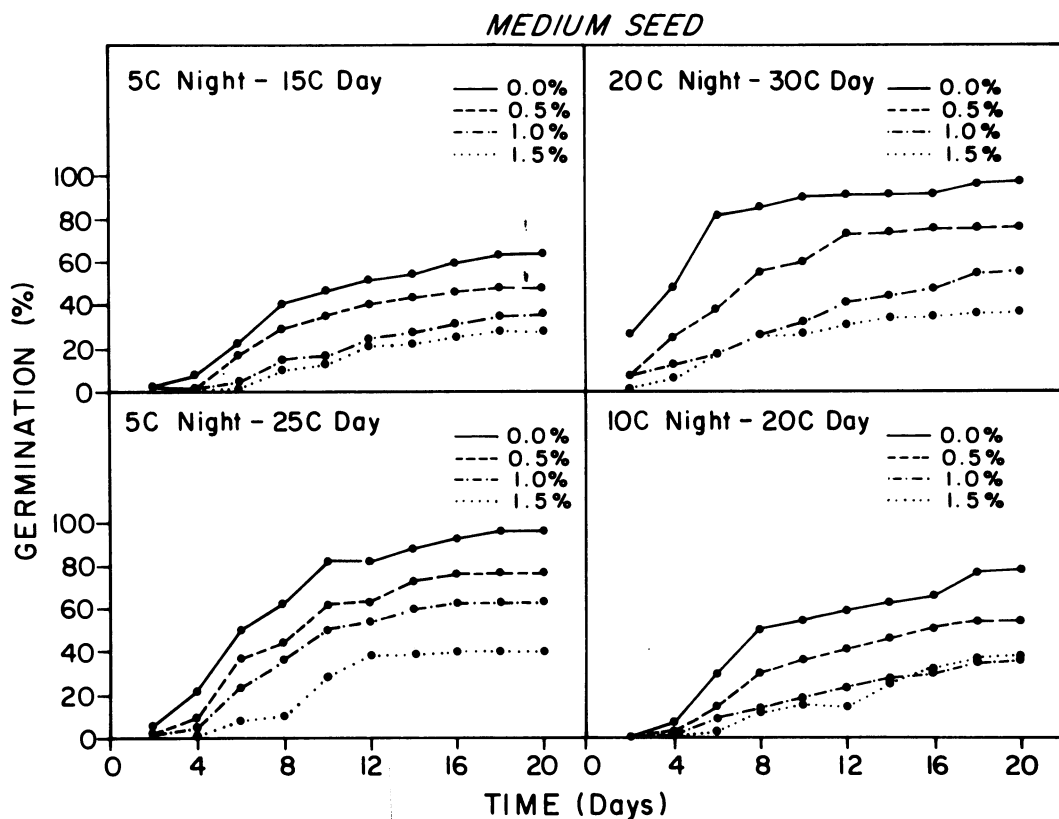


Fig. 2. Effect of temperature and salinity (0.0, 0.5, 1.0, and 1.5% NaCl) on the rate of germination of *Atriplex triangularis* medium seeds.

of seedlings were very highly significant (Table 2).

**DISCUSSION**—Germination regulating mechanisms with which *Atriplex triangularis* seeds are equipped may be utilized as strategies for survival. A number of environmental and biological variables, and their interactions, may be used as signals by which germination is triggered so as to take advantage of ecological situations that maximize the probability for successful establishment. Most of the seed population remains dormant in the absence of such signals. Morphological differences among the polymorphic seed types of *Atriplex triangularis* are significantly correlated with the variations in the germinability of seeds, with small seeds being more dormant than large seeds. Laboratory studies indicate that large seeds of *Atriplex triangularis* do not have any requirements for cold pretreatments. In late fall 1982 they were found germinating under field conditions. However, increases in salinity concentrations seemed to induce dormancy, and this effect of salinity was more pronounced in small seeds than in large seeds.

Low temperatures probably maintain dormancy in seeds during the winter and early spring. High germination percentages occur in the laboratory experiments only under alternating temperatures. The low temperatures and small amplitude of the diurnal temperature cycle in winter may therefore be a major factor contributing to the inhibition of germination.

Similar interactions between increased salinity and alternating temperatures were found by Ignaciuk and Lee (1980). They reported that seeds of *Atriplex glabriuscula* and *A. laciniata* germinated well under alternating temperature regimes in the laboratory. The alternating temperature requirements of species of *Atriplex* thus provide not only a means of delaying germination until the proper season, but also in the case of *Atriplex triangularis* causes smaller seeds to remain dormant in the moderately saline conditions and thus maintains a seed bank. Similar alternating temperature requirements have been reported for other halophytes (Binet, 1964, 1965; Ungar, 1974; Okusanya, 1977; Young et al., 1980). However, alternating temperatures did not promote germination

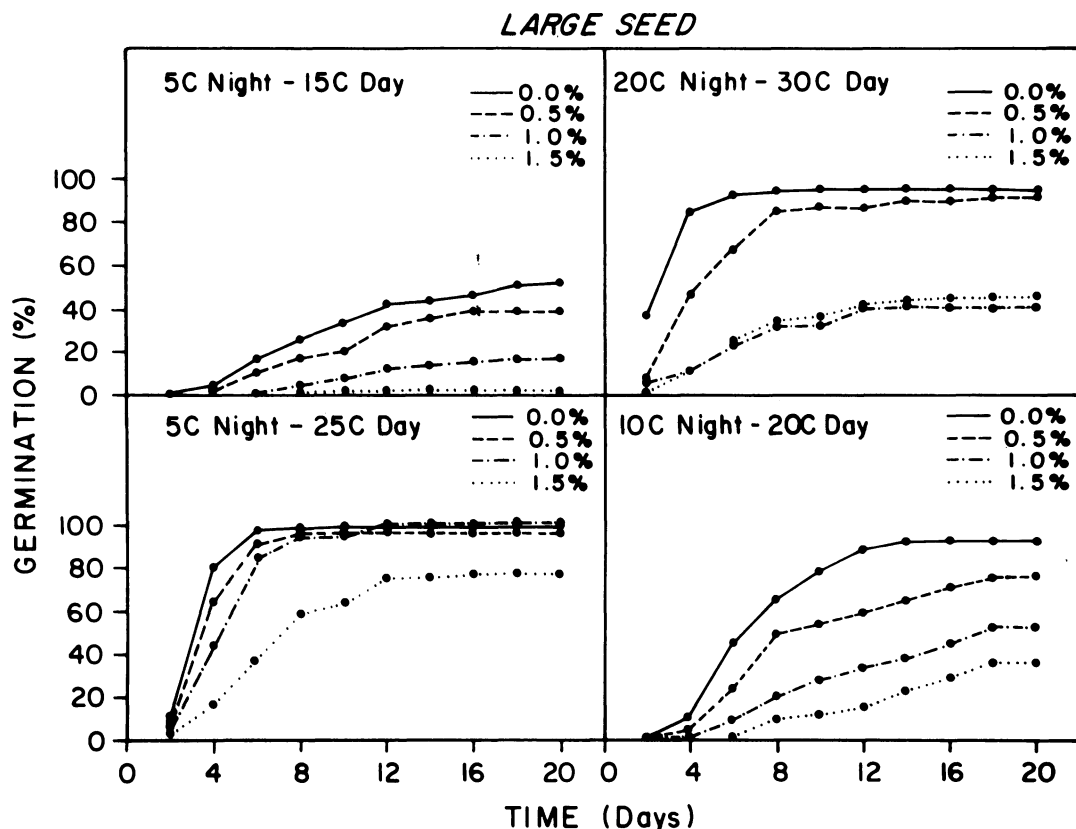


Fig. 3. Effect of temperature and salinity (0.0, 0.5, 1.0, and 1.5% NaCl) on the rate of germination of *Atriplex triangularis* large seeds.

more than constant temperatures in some other species of *Atriplex* (Sankary and Barbour, 1972; Uchiyama, 1981).

*Atriplex triangularis* was most tolerant to increasing salinity at the optimal temperature (5–25 C) for germination. The present study also demonstrated a very highly significant ( $P < 0.0001$ ) interaction between temperature and salinity in affecting germination. Similar interactions have been reported by Ungar and Hogan (1970) for *Iva annua*, Binet and Combes (1961) for *Cochlearea anglica*, and Khan and Khan (1978) for *Triticum aestivum* and *Corchorus capsularis*.

High day temperatures appeared to be playing a significant role in promoting germination. This promotion could be due to increased water uptake by seeds (Koller and Hadas, 1982; Uchiyama, 1981), changes in membrane permeability (Taylorson and Hendricks, 1977), leakage of organelle membranes and enhanced metabolic activity over that at low temperatures (Koller and Hadas, 1982) and a synergistic effect with Pfr (Taylorson and Hendricks, 1977). However, the exact nature of these

mechanisms is not yet properly understood (Ungar, 1982).

Germination of halophyte species can occur in salinities ranging from 200 to 1,700 mM. However, germination of many halophytic species occurs at concentrations of NaCl less than that of sea water (600 mM) (Ungar, 1978). *Atriplex triangularis* falls into this latter group. With increasing salinity there was a consistent decrease in the percent of germination, a noticeable delay in rate of germination, and a decrease in seedling length. Optimal germination occurs under reduced salinity stress even in the case of the most highly salt tolerant species (Binet, 1964; Ungar, 1962, 1974, 1977, 1978). This could be of ecological significance since germination of seeds in early spring, when salinity stress is reduced by high soil moisture levels, probably assures that some individuals would survive until the end of the growing season (Ungar, 1977). Later in the summer salt stress would be too high on inland saline pans for germination of seeds to occur and subsequent seedling mortality would be high.

Seed dimorphism and polymorphism have

TABLE 2. Summary of analysis of variance for germination, hypocotyl length, root length and dry weight

Dependent variable	Source	df	ss	F	P
Germination (%)	Salinity (S)	3	4,555.9	193.5	<0.0001
	Seed size (SS)	2	1,672.4	106.6	<0.0001
	Temperature (T)	3	1,898.9	80.7	<0.0001
	SS × T	6	1,089.5	23.1	<0.0001
	SS × S	6	205.7	4.4	<0.0004
	T × S	9	204.4	2.8	<0.0036
	SS × T × S	18	431.4	3.1	<0.0001
Hypocotyl length (mm)	Salinity (S)	3	7,317.6	103.7	<0.0001
	Seed size (SS)	2	1,250.6	26.6	<0.0001
	Temperature (T)	3	6,428.2	91.1	<0.0001
	SS × T	6	1,390.4	9.9	<0.0001
	SS × S	6	183.1	1.3	<0.2619
	T × S	9	1,403.9	6.6	<0.0001
	SS × T × S	18	835.1	1.9	<0.0147
Root length (mm)	Salinity (S)	3	4,159.5	244.1	<0.0001
	Seed size (SS)	2	59.2	5.2	<0.0066
	Temperature (T)	3	2,002.6	117.5	<0.0001
	SS × T	6	432.1	12.7	<0.0001
	SS × S	6	110.7	3.3	<0.0050
	T × S	9	1,148.8	22.5	<0.0001
	SS × T × S	18	465.5	4.6	<0.0001
Dry weight (mg)	Salinity (S)	3	4.9	42.9	<0.0001
	Seed size (SS)	2	25.3	329.5	<0.0001
	Temperature (T)	3	9.1	78.9	<0.0001
	SS × T	6	6.4	27.8	<0.0001
	SS × S	6	2.2	9.7	<0.0001
	T × S	9	2.1	6.0	<0.0001
	SS × T × S	18	1.3	1.9	<0.0223

been reported for a number of *Atriplex* species growing under saline conditions (Kadman-Zahavi, 1955; Koller, 1957; Ward, 1967; Frankton and Bassett, 1968; Ungar, 1971; Drysdale, 1973). The ecological significance of seed polymorphism in plants growing in saline environments is not clearly understood. Larger seeds of *Atriplex triangularis* were found to be less dormant than the smaller seeds, and germination percentages and the index of germination velocity of large seeds were much higher at optimal temperatures (5–25 C) than for the medium and small seeds. Seeds of *Atriplex triangularis* have an extended germination period, lasting from February to June, with some germination occurring even in late fall (Ungar

and Khan, unpublished data). Wertis (1982) showed a nearly complete germination of large seeds in the seed bank early in the germination period, while small seeds provided a long-term seed bank. This behaviour is most likely related to the differences in physiological responses of polymorphic seeds and to the fluctuation in soil salinity conditions during the growing season which limits the periods when seeds can germinate.

The present study suggests that there is a physiological polymorphism in *Atriplex triangularis* seeds. Large seeds, less sensitive to salinity, germinate earlier in the spring when soil salinity levels are less than 1.5%, whereas small seeds are more sensitive to salt and temperature. Some of the small seeds germinate as temperatures reach the optimum while the remainder form part of the seed bank. Soil salinities in July and August averaged 3.8% and 4.9%, beyond the range that small seeds of *A. triangularis* can germinate.

Seedling length of *Atriplex triangularis* was significantly reduced with increased salinity. However, seedlings grown from larger seeds were more tolerant to salinity at all temperatures. Alternating temperature regimes of 5–25 C and 20–30 C produced comparatively

TABLE 3. LSD values for germination, hypocotyl length, root length, and dry weight ( $P < 0.05$ )

Dependent variable	Independent variable		
	Seed size	Salinity	Temperature
Germination (%)	3.91	5.52	4.52
Hypocotyl length (mm)	1.69	1.96	1.96
Root length (mm)	0.83	0.96	0.96
Dry weight (mg)	0.07	0.08	0.08

TABLE 4. Mean hypocotyl length, root length, and dry weight of *Atriplex triangularis* seedlings after 20 days from various salinity and temperature regimes. Mean  $\pm$  S.E.

Variables	Temperature night-day	Salinity (%)			
		0.0	0.5	1.0	1.5
SMALL SEED					
Hypocotyl length (mm)	5–15 C	11.60 ± 2.35	6.32 ± 0.08	0.00 ± 0.00	0.00 ± 0.00
	5–25 C	23.16 ± 0.71	19.86 ± 0.95	11.99 ± 1.45	5.00 ± 0.06
	10–20 C	14.70 ± 3.16	18.30 ± 2.16	6.67 ± 1.66	0.00 ± 0.00
	20–30 C	20.31 ± 0.92	19.47 ± 0.69	12.36 ± 1.22	8.60 ± 2.15
Root length (mm)	5–15 C	7.75 ± 0.89	4.38 ± 0.20	0.00 ± 0.00	0.00 ± 0.00
	5–25 C	19.85 ± 0.56	7.40 ± 0.60	3.73 ± 0.33	3.00 ± 0.75
	10–20 C	12.66 ± 1.57	8.05 ± 0.81	3.33 ± 0.83	0.00 ± 0.00
	20–30 C	18.68 ± 1.42	8.79 ± 1.05	4.24 ± 0.13	2.00 ± 0.50
Dry weight (mg)	5–15 C	0.41 ± 0.05	0.33 ± 0.03	0.29 ± 0.06	0.00 ± 0.00
	5–25 C	0.44 ± 0.07	0.93 ± 0.30	0.73 ± 0.16	0.50 ± 0.13
	10–20 C	0.35 ± 0.03	0.48 ± 0.03	0.33 ± 0.08	0.00 ± 0.00
	20–30 C	0.46 ± 0.09	0.47 ± 0.04	0.36 ± 0.02	0.40 ± 0.10
MEDIUM SEED					
Hypocotyl length (mm)	5–15 C	13.36 ± 1.14	8.50 ± 1.51	0.00 ± 0.00	0.00 ± 0.00
	5–25 C	26.02 ± 0.91	23.09 ± 0.99	14.25 ± 0.94	12.75 ± 2.06
	10–20 C	16.79 ± 1.34	15.16 ± 1.14	8.16 ± 1.33	3.40 ± 0.68
	20–30 C	22.19 ± 0.72	18.25 ± 1.50	16.91 ± 0.98	8.00 ± 1.06
Root length (mm)	5–15 C	3.91 ± 0.56	1.94 ± 0.14	1.69 ± 0.13	1.64 ± 0.14
	5–25 C	25.90 ± 1.34	13.84 ± 0.91	2.74 ± 0.35	3.19 ± 0.81
	10–20 C	9.93 ± 0.84	4.02 ± 0.32	3.12 ± 0.36	1.84 ± 0.18
	20–30 C	18.02 ± 0.63	5.47 ± 0.44	4.53 ± 0.35	4.26 ± 0.64
Dry weight (mg)	5–15 C	0.44 ± 0.03	0.45 ± 0.06	0.42 ± 0.03	0.38 ± 0.01
	5–25 C	0.57 ± 0.08	0.73 ± 0.08	0.52 ± 0.08	0.42 ± 0.06
	10–20 C	0.51 ± 0.04	0.31 ± 0.08	0.30 ± 0.08	0.35 ± 0.14
	20–30 C	0.72 ± 0.04	0.83 ± 0.09	0.67 ± 0.09	0.56 ± 0.06
LARGE SEED					
Hypocotyl length (mm)	5–15 C	7.00 ± 1.53	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	5–25 C	31.69 ± 0.98	33.96 ± 1.67	17.73 ± 1.67	18.39 ± 1.47
	10–20 C	29.38 ± 1.27	23.09 ± 2.09	12.60 ± 1.42	5.00 ± 0.45
	20–30 C	26.22 ± 1.59	31.29 ± 1.61	20.33 ± 2.95	9.11 ± 1.06
Root length (mm)	5–15 C	2.35 ± 0.23	2.05 ± 0.20	1.43 ± 0.17	1.00 ± 0.00
	5–25 C	26.05 ± 1.20	16.87 ± 1.16	6.27 ± 0.56	8.49 ± 0.56
	10–20 C	17.09 ± 1.12	6.54 ± 0.67	4.44 ± 0.37	2.94 ± 0.30
	20–30 C	11.25 ± 1.00	6.81 ± 0.60	3.85 ± 0.39	3.13 ± 0.31
Dry weight (mg)	5–15 C	0.21 ± 0.09	0.24 ± 0.14	0.21 ± 0.00	0.07 ± 0.00
	5–25 C	1.80 ± 0.08	2.33 ± 0.08	2.03 ± 0.09	1.62 ± 0.16
	10–20 C	1.63 ± 0.08	1.80 ± 0.12	1.50 ± 0.24	1.12 ± 0.08
	20–30 C	1.91 ± 0.05	2.14 ± 0.23	2.29 ± 0.02	1.54 ± 0.45

better seedling growth at all salinities than that of 10-20-C and 5-15-C treatments.

Chatterton and McKell (1969) found that growth of the established seedling of *Atriplex polycarpa* was reduced by NaCl solutions (-25 bars). Root growth was somewhat correlated with shoot growth; however, salt restricted shoot growth more than root growth as the level of salinity increased. Only the highest concentrations of NaCl used reduced the root length. Results of our study support these findings. Black (1956) has shown that *Atriplex hastata* tolerates NaCl concentrations of 0.6 M, but growth was severely inhibited at concen-

trations above 0.3 M. Sankary and Barbour (1972) found that optimal conditions for vegetative growth of *Atriplex polycarpa* were an 18-hr photoperiod and 24 C, whereas growth at 12 C was considerably reduced.

Abdulrahman and Williams (1981) studied the effect of temperature and various NaCl concentrations on the growth of *Salicornia frutescens*. They found maximum growth at 171 mM NaCl under cool growth conditions (20-10 C) and at 342 mM NaCl under warm conditions (30-15 C) with minimum growth in the 0 mM NaCl (control). The significantly higher shoot and root weights for *Puccinellia nuttal-*

*liana* seedlings in -4-bar solution than in nutrient solution controls indicated that growth was favored by small increments of sodium sulphate. A reduction of seedling growth was obtained with increased salinity beyond -4 bars, with a sharp decline in root length, and fresh and dry weight of shoots and roots between -8 and -16 bars (Macke and Ungar, 1971). Osmond et al. (1980) indicated that *Atriplex* growth was stimulated at external NaCl concentrations which were inhibitory to the growth of glycophytes. This result was also evident in the earlier work of Ashby and Beadle (1957). However, Billard and Binet (1975) showed a progressive decrease in dry weight with an increase in salinity in all *Atriplex* species studied. Dry weight of *Atriplex triangularis* seedlings was not significantly different in various temperature regimes in the absence of NaCl, whereas, addition of 0.5% and 1.0% NaCl significantly promoted seedling growth in all temperatures as compared to non-saline controls. Maximum dry weights were obtained for seedlings grown in alternating regimes of 5-25 C.

Our study clearly suggests an ecological significance of the polymorphic seeds in *Atriplex triangularis*. The various seed sizes have different tolerance limits to salinity, with all of the larger seeds germinating early in the growing season (Ungar and Khan, unpublished data). Smaller seeds which germinate throughout the growing season are more dormant and these seeds have more specific temperature requirements for germination under saline conditions. Small seeds form a seed bank while large seeds remain dormant only over winter. Polymorphic seeds have different physiological requirements which provide alternate temporal and spatial situations for seed germination and growth in a habitat which experiences a gradient of salinity and temperature changes throughout the period of germination and seedling growth.

#### LITERATURE CITED

- ABDULRAHMAN, F. S., AND G. J. WILLIAMS III. 1981. Temperature and salinity regulation of growth and gas exchange of *Salicornia fruticosa* (L.) L. *Oecologia* 48: 346-352.
- ASHBY, W. C., AND N. C. W. BEADLE. 1957. Studies on halophytes III. Salinity factors in the growth of Australian saltbush. *Ecology* 38: 344-352.
- BEADLE, N. C. W. 1952. Studies in halophytes. I. The germination of the seed and establishment of the seedling of five species of *Atriplex* in Australia. *Ecology* 33: 49-52.
- BILLARD, J. P., AND P. BINET. 1975. Physio-écologie des *Atriplex* des milieux sableux littoraux. *Bull. Soc. Bot. Fr.* 122: 51-64.
- BINET, P. 1964. La germination des semences des halophytes. *Bull. Soc. Fr. Physiol. Végét.* 10: 253-263.
- . 1965. Etude de quelques aspects physiologiques de la germination chez *Atriplex tornabeni* Tin. *Bull. Soc. Bot. Nord. Fr.* 18: 40-55.
- . 1966. Propriétés physiologiques fondamentales des semences d'*Atriplex babingtonii* Wood. *Bull. Soc. Bot. Nord. Fr.* 19: 121-137.
- , AND M. R. COMBES. 1961. Action de la température et de l'eau de mer sur la germination des graines de *Cochlearia anglica* L. C. R. Acad. Sci. 253: 895-897.
- BLACK, R. F. 1956. Effect of NaCl in water culture on the ion uptake and growth of *Atriplex hastata* L. *Aust. J. Biol. Sci.* 9: 67-80.
- CHAPMAN, V. J. 1974. Salt marshes and salt deserts of the world. J. Cramer, Bremerhaven, West Germany.
- CHATTERTON, N. J., AND C. M. MCKELL. 1969. *Atriplex polycarpa*. I. Germination and growth as affected by sodium chloride in water cultures. *Agron. J.* 61: 448-450.
- 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* (Chenopodiaceae) in Canada. I. Three introduced species: *A. heterosperma*, *A. oblongifolia*, and *A. hortensis*. *Can. J. Bot.* 46: 1309-1313.
- IGNACIUK, R., AND J. A. LEE. 1980. The germination of four annual strand-line species. *New Phytol.* 84: 581-591.
- KADMAN-ZAHAVI, A. 1955. Notes on germination of *Atriplex rosea*. *Bull. Res. Council. Israel* 4: 375-388.
- KHAN, M. A., AND M. I. KHAN. 1978. Effect of light and temperature on seedlings raised under sodium chloride salinity. *Pak. J. Bot.* 10: 167-172.
- KOLLER, D. 1957. Germination mechanisms in some desert seeds. I. *Atriplex dimorphostegia* Kar et Kir. *Ecology* 38: 1-13.
- KOLLER, D., AND A. HADAS. 1982. Water relations in the germination of seed. In O. L. Lange, P. S. Noble, C. B. Osmond, and H. Ziegler [eds.], *Encyclopedia of plant physiology: physiological plant ecology*, pp. 402-431. Springer-Verlag, Berlin.
- MACKE, A., AND I. A. UNGAR. 1971. The effect of salinity on seed germination and early growth of *Puccinellia nuttalliana*. *Can. J. Bot.* 49: 515-520.
- OKUNSANYA, O. T. 1977. The effect of sea water and temperature on the germination behaviour of *Crithmum maritimum*. *Physiol. Plant.* 41: 265-267.
- OSMOND, C. B., O. BJORKMAN, AND D. J. ANDERSON. 1980. *Physiological processes in plant ecology*. Springer-Verlag, Berlin.
- RAY, A. A. (ed.) 1982. SAS user guide. SAS institute Inc. Cary, N.C., USA.
- SANKARY, M. N., AND M. G. BARBOUR. 1972. Autecology of *Atriplex polycarpa* from California. *Ecology* 53: 1155-1162.
- SHARMA, M. L. 1976. Soil water regimes and water extraction patterns under two semiarid shrub (*Atriplex* spp.) communities. *Aust. J. Ecol.* 1: 249-258.
- SPRINGFIELD, H. W. 1966. Germination of fourwing saltbush seeds at different levels of moisture stress. *Agron. J.* 58: 149-150.
- TAYLORSON, R. B., AND S. B. HENDRICKS. 1977. Dormancy in seeds. *Annu. Rev. Plant Physiol.* 28: 331-354.
- TIMSON, J. 1965. New methods of recording germination data. *Nature* 207: 216-217.



- UCHIYAMA, Y. 1981. Studies on germination of salt-bushes: 1. The relationship between temperature and germination of *Atriplex nummularia* Lindl. Jpn. J. Trop. Agric. 25: 62-67.
- UNGAR, I. A. 1962. Influence of salinity on seed germination in succulent halophytes. Ecology 43: 763-764.
- . 1971. *Atriplex patula* var. *hastata* (L.) Gray seed dimorphism. Rhodora 73: 548-551.
- . 1974. Inland halophytes of the United States. In R. Reimold and W. Queen [eds.], Ecology of halophytes, pp. 235-305. Academic Press, New York.
- . 1977. The relationship between soil water potential and plant water potential in two inland halophytes under field conditions. Bot. Gaz. 138: 498-591.
- . 1978. Halophyte seed germination. Bot. Rev. 44: 233-264.
- . 1982. Germination ecology of halophytes. In D. N. Sen and K. S. Rajpurohit [eds.], Contributions to the ecology of halophytes, pp. 143-154. Dr. W. Junk Publishers, The Hague.
- , AND W. HOGAN. 1970. Seed germination in *Iva annua* L. Ecology 51: 150-154.
- WARD, J. M. 1967. Studies in ecology of a shell barrier beach. III. Chemical factors of the environment. Vegetatio 15: 77-112.
- WERTIS, B. A. 1982. Aspects of the population biology of halophytes *Atriplex triangularis*. M.S. thesis, Ohio University, Athens.
- YOUNG, J. A., B. L. KAY, H. GEORGE, AND R. A. EVANS. 1980. Germination of three species of *Atriplex*. Agron. J. 72: 705-709.