

TEMPERATURE AND HIGH SALINITY EFFECTS IN GERMINATING DIMORPHIC SEEDS OF *ATRIPLEX ROSEA*

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ABSTRACT.—*Atriplex rosea* L. (Chenopodiaceae; tumbling orach), an annual herb, is a widely established weedy species of disturbed sites in all counties of Utah. Seeds of *Atriplex rosea* were collected from a salt marsh in Faust, Utah, and are dimorphic, light brown, and 2–2.5 mm wide, or black and 1–2 mm wide. Seed germination responses of the black and brown seeds were studied over a range of salinity and temperature. Both brown and black seeds germinated at 1000 mM NaCl, and the optimal temperature for germination of both types was 20°–30°C. Variation in temperature, however, affected germination of black seeds more than brown seeds. At lower thermoperiod only 40%–50% black seeds germinated in nonsaline control, and germination was almost completely inhibited with the inclusion of salinity. However, all brown seeds germinated in control at temperatures above 5°–15°C, and inhibition caused by salinity was comparatively lower. Brown seeds had a higher germination rate than black seeds at all temperature and salinity treatments. The highest rate of germination of both seeds occurred at the temperature regime of 5°–15°C. Recovery of germination for black seeds when transferred to distilled water after being in various salinity treatments for 20 days was quite variable. Recovery decreased with increase in salinity at lower temperature regimes, increased with salinity at optimal thermoperiod, and had no effect at 20°–30°C. Brown seeds recovered poorly from salinity at all thermoperiods except 5°–15°C, where recovery decreased with an increase in salinity. Brown seeds are adapted to germination in the early part of the growing season, whereas black seeds are capable of surviving harsher conditions and can germinate in later time periods. Characteristics of the dimorphic seeds increase chances for survival in the harsh saline desert environment.

Key words: *Atriplex rosea*, halophyte, salinity, seed germination, temperature, dimorphic seeds.

Natural habitats where halophytes can grow are often subject to sudden changes in temperature and salinity regimes that could result in high mortality of seedlings (Ungar 1991). Severe environmental pressure may lead to the development of seed dimorphism in halophytes, which could provide different spatial and temporal dispersal potential by allocating their resources between smaller, more dormant, readily dispersed r-type units and larger, more readily germinable K-type units (Harper 1977, Khan and Ungar 1984a, 1984b, Khan et al. 2001a). Seed dimorphism and polymorphism have been reported in the genus *Atriplex* (Hall and Clements 1923, Beadle 1952, Frankton and Bassett 1968, Taschereau 1972, Drysdale 1973, Khan and Ungar 1984a, 1984b, Ungar 1984). However, the mechanism for production of large and small seeds is not clear for most species of *Atriplex* (Khan and Ungar 1984b). In *A. hortensis* large seeds are produced within bracteoles in earlier flowers that do not contain a perianth, while small seeds are produced later in the growing season by flowers containing a

perianth but no bracteoles (Ungar 1987). In *A. triangularis* both large and small seeds have bracteoles surrounding them when the fruit is mature (Ungar 1984). Germination polymorphism is extremely important to species growing in variable environments because it provides alternate temporal and spatial germination opportunities, preventing a single local hazard from eliminating an entire plant population (Khan et al. 2001a, 2001b). Seed dimorphism and polymorphism have also been reported for a number of halophytic taxa including *Arthrocnemum*, *Chenopodium*, *Cakile*, *Salicornia*, *Salsola*, *Spergularia*, *Suaeda*, and *Trianthema* (Ungar 1977, Khan and Ungar 1984a, 1984b, Galinato and van der Valk 1986, Mohammad and Sen 1988, Ungar 1988, Morgan and Myers 1989, Khan and Gul 1998) and may have resulted in plasticity in their germination responses to varying environments.

Atriplex species have been reported to vary considerably in their salinity tolerance at germination (Ungar 1995). *Atriplex patula* can germinate at 60 mM NaCl (Galinato and van

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der Valk 1986), *A. triangularis* at 280 mM NaCl (Khan and Ungar 1984a, 1984b), *A. rhagodooides* at 309 mM NaCl (Mahmood and Malik 1996), *A. griffithii* at 345 mM NaCl (Khan and Rizvi 1994), *A. nummularia* at 309 mM NaCl (Uchiyama 1981), *A. prostrata* at 600 mM NaCl (Bakker et al. 1985), and *A. halimus* at 856 mM NaCl (Zid and Boukhris 1977). *Atriplex* seeds can maintain viability after an extended exposure to salinity (Zid and Boukhris 1977, Uchiyama 1981, Keiffer and Ungar 1995), and the seeds recover completely when transferred to distilled water. This recovery of seed germination varies with species and changes in thermoperiod (Khan and Ungar 1997).

Atriplex rosea L. (Chenopodiaceae; tumbling orach), an annual herb, is a widely established weedy species of disturbed sites, often in riparian habitats, barnyards or annual bedding grounds, at elevations of 850–2560 m in all counties of Utah (Welsh et al. 1987). Native to Eurasia, it is widespread in North America. The species grows in the bottom of internally drained basins at the margins of the Great Basin salt playas (Billings 1945) where the majority of the salt in the soil is NaCl with concentrations up to 1027 mM (Hansen and Weber 1975). It is commonly found with *Triglochin maritime*, forbs *A. prostrata* and *Kochia scopari*, and the grass *Distichlis spicata*. *Atriplex rosea* produces seeds by autumn and most of the seeds are dispersed onto the saline soil around the parent plant. However, water upon which they readily float sometimes causes long-range dispersal of seeds. Seeds of *A. rosea* are dimorphic, light brown, and 2–2.5 mm wide, or black and 1–2 mm wide (Hall and Clements 1923, Welsh et al. 1987). The germination of halophyte seeds in temperate salt playas and salt marshes usually occurs in the spring when the temperatures are moderate (8°–18°C) and soil salinity is reduced by precipitation (Khan and Weber 1986, Gul and Weber 1999). The goal of this study was to examine effects of high salinity and thermoperiod on the germination and recovery of brown and black seeds of *A. rosea*.

MATERIALS AND METHODS

Seeds of *A. rosea* were collected during the autumn of 1996 from a salt marsh at Faust,

Utah, USA, 48 km south of the Great Salt Lake. Conductivity of the soils was determined using a Beckman RC16C meter. Seeds were separated from their inflorescence, air-dried, and then separated into groups of brown and black seeds. Seeds were stored at 4°C and were surface treated using the fungicide Phygon (2,3-dichloro-1,4-naphthoquinone). Germination was carried out in 50 × 9-mm tight-fitting plastic petri dishes (Gelman #7232) with 5 mL of test solution as described below. Each of these dishes was placed in a 10-cm-diameter plastic petri dish to further reduce the loss of water by evaporation. We used 4 replicates of 25 seeds for each treatment and considered seeds germinated with emergence of the radicle.

Effects of temperature on germination were determined using 12-hour alternating temperature regimes of 5°–15°C, 10°–20°C, 15°–25°C, 20°–30°C, and 25°–35°C. Both black and brown seeds were germinated in distilled water and 200, 400, 600, 800, and 1000 mM NaCl at each of the above-mentioned temperature regimes. Percentage germination was recorded every 2nd day for 20 days. After 20 days we transferred ungerminated seeds from the NaCl treatments to distilled water to study the recovery of germination, which was also recorded at 2-day intervals for 20 days. Recovery percentages were determined by the following formula: $(a - b) / (c - b) * 100$, where *a* is total number of seeds germinated after being transferred to distilled water, *b* is total number of seeds germinated in saline solution, and *c* is total number of seeds. The rate of germination was estimated using a modified Timson index of germination velocity = $\sum G/t$, where *G* is the percentage of seed germination at 2-day intervals and *t* is the total germination period (Khan and Ungar 1984a). The maximum value possible using this index with our data was 50 (i.e., 1000/20). The higher the percentage value, the more rapid the rate of germination. Germination data (20 days and rate of germination) were arcsine transformed before statistical analysis. Data were analyzed using a 3-way analysis of variance (SPSS, Inc. 2001) to determine the significance of main effects (salinity, thermoperiod, and seed type) and their interactions in affecting the rate and percentage of germination. If significant differences occurred, a Bonferroni analysis (multiple range test = modified LSD, *P* < 0.05) was

TABLE 1. Results of 3-way ANOVA of characteristics by seed color, salinity, and thermoperiod treatments. Numbers represent *F*-values.

Independent variable	Seed color (SC)	Salinity (S)	Thermoperiod (T)	SC × S	SC × T	T × S	SC × T × S
Final germination	84***	346***	62***	5***	12***	7***	2**
Rate of germination	106***	417***	93***	10***	7***	10***	3**
Recovery rate of germination	100***	5***	12***	1.4 ^{n.s.}	31***	6***	2.6***
Percent recovery	20***	137***	21***	50***	6***	47***	10***

P* < 0.05*P* < 0.01****P* < 0.001

carried out to determine if significant differences occurred between individual treatments (SPSS, Inc. 2001).

RESULTS

A 3-way ANOVA indicated significant (*P* < 0.001) effects of salinity, temperature, and seed color on percent seed germination, rate of germination, recovery, and rate of recovery of *A. rosea* (Table 1).

Germination of both black and brown seeds was inhibited with the increase in salinity; few seeds of both germinated in 1000 mM NaCl (Figs. 1, 2). Both seed types germinated well at the optimal temperature regime of 20°–30°C, and any further increase or decrease in temperatures significantly decreased germination (Figs. 1, 2). However, the effect of temperature on seed germination was more pronounced in black seeds, which showed only 40% germination in nonsaline control at 5°–15°C and germination of only a few seeds at the lowest salinity treatment (100 mM; Fig. 1). Germination of brown seeds reached approximately 90% within about 2 days at the optimal temperature regime (20°–30°C) compared with 8 days in black seeds under similar conditions; however, about 18% of the seeds germinated with the 1000 mM NaCl treatment in both types of seeds (Figs. 1, 2).

A linear regression of final germination versus NaCl concentration explains a high proportion of the germination response, with *R*² values ranging from 0.54 to 0.86 for black seeds and from 0.58 to 0.89 for brown seeds in various temperature treatments (Fig. 3).

Rate of germination of both black and brown seeds progressively decreased with increases in salinity (Table 2). The fastest germination

rate of black seeds was obtained at 20°–30°C. Rates decreased with increase or decrease in temperature.

Black seeds showed varied response with change in temperature regime when transferred to distilled water after 20 days of salinity treatment (Fig. 4). At suboptimal temperature regimes, recovery decreased with an increase in salinity, while there was no change in recovery response with increase in salinity at 15°–25°C (Table 3). At optimal temperature regime (20°–30°C), however, recovery increased with salinity concentrations. In contrast, brown seeds showed a poor recovery at all temperatures except at lowest salinity treatment at 5°–15°C (Fig. 4). A linear regression explains a high proportion of the germination response with *R*² (coefficient of regression) values ranging from 0.04 to 0.73 for black seeds and from 0.09 to 0.27 for brown seeds in various temperature treatments (Fig. 4).

Rates of recovery of black seed germination were greatest at the warmest thermoperiod (25°–35°C) and progressively decreased with decreased temperature (Table 3). Recovery rate of germination was poor for brown seeds but remained unchanged with changes in thermoperiod (Table 3).

DISCUSSION

Seed dimorphism and polymorphism are reported in many *Atriplex* species growing under saline conditions (Koller 1957, Frankton and Bassett 1968, Drysdale 1973, Baker 1974, Khan and Ungar 1984a, 1984b, Ungar 1991). Gustafsson (1973) reported that the rate and percentage of germination of black and brown seeds of *A. triangularis* and *A. longipes* were scarcely different. Khan and Ungar (1984a,

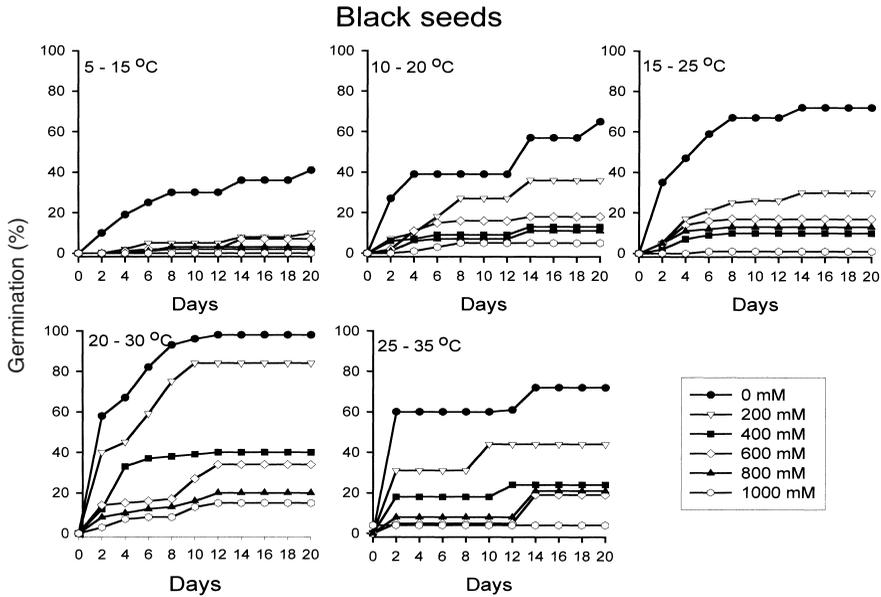


Fig. 1. Percentage germination (mean \pm $s_{\bar{x}}$) of black seeds of *Atriplex rosea* in 0, 200, 400, 600, 800, and 1000 mM NaCl at thermoperiods of 5°–15°C, 10°–20°C, 15°–25°C, 20°–30°C, and 25°–35°C.

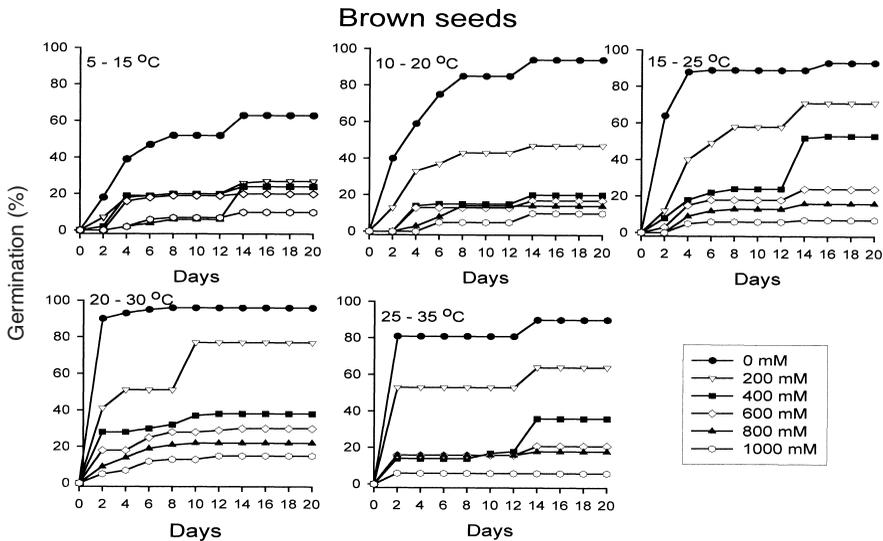


Fig. 2. Percentage germination (mean \pm $s_{\bar{x}}$) of brown seeds of *Atriplex rosea* in 0, 200, 400, 600, 800, and 1000 mM NaCl at thermoperiods of 5°–15°C, 10°–20°C, 15°–25°C, 20°–30°C, and 25°–35°C.

1984b) reported that black seeds of *A. triangularis* were both morphologically and physiologically different from brown seeds. Small black seeds have hard seed coats, more ions and phenolic contents, and dormancy with lower

salt tolerance while large brown seeds have soft seed coat, lower ionic and phenolic acid contents, higher salt tolerance, and ready germinability (Khan and Ungar 1984a, 1984b, 1986a, 1986b).

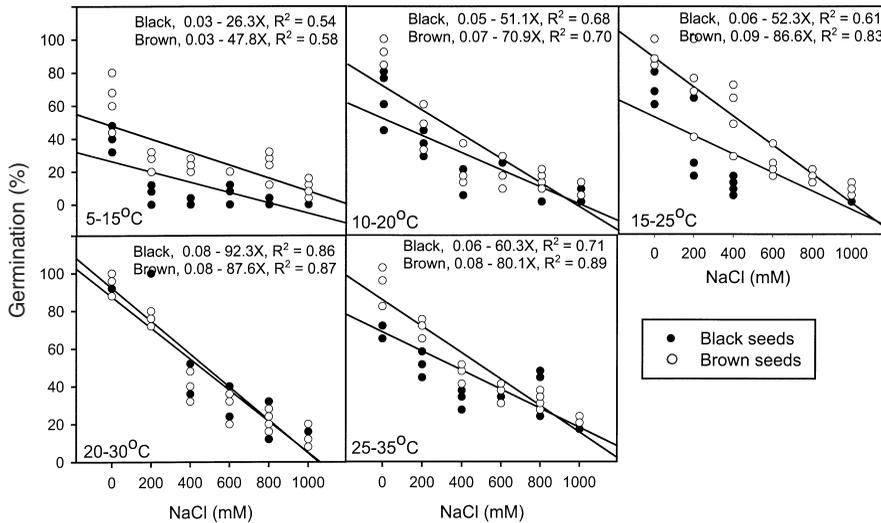


Fig. 3. Regression lines of germination (%) of black and brown seeds of *Atriplex rosea* after being in 0, 200, 400, 600, 800, and 1000 mM NaCl at thermoperiods of 5°–15°C, 10°–20°C, 15°–25°C, 20°–30°C, and 25°–35°C for a 20-day period.

Atriplex rosea seeds have distinct morphology and are physiologically different to some extent. Great Basin desert halophytes are a group of plants that are more salt tolerant than any other group of plants that have been reported. These halophytes, *Kochia americana* (Clarke and West 1969), *Salicornia pacifica* var. *utahensis* (Khan and Weber 1986), *Allenrolfea occidentalis* (Gul and Weber 1999), *Salicornia rubra* (Khan et al. 2000), *Suaeda moquinii* (Khan et al. 2001a), *Kochia scoparia* (Khan et al. 2001b), *Sarcobatus vermiculatus* (Khan et al. 2002a), and *Salsola iberica* (Khan et al. 2002b), germinate at salinity concentrations higher than 800 mM NaCl. All of them except *Allenrolfea occidentalis* have some germination at 1000 mM NaCl. Both brown and black seeds of *A. rosea* showed 15% germination at 1000 mM NaCl. This pattern is consistent with the other Great Basin species. However, when comparison of seed germination responses with salinity was made among *Atriplex* species, *A. rosea* appeared to be more salt tolerant during germination. Species like *A. nummularia*, *A. patula*, *A. triangularis*, and *A. rhagoides* could germinate in up to 300 mM NaCl (Uchiyama 1981, Galinato and van der Valk 1986, Khan and Ungar 1984a, 1984b, 1986a, 1986b, Mahmood and Malik 1996), *A. griffithii* at 345 mM NaCl (Khan and Rizvi 1994), and *A. prostrata* and *A. halimus* at concentrations

higher than seawater (Bakker et al. 1985, Zid and Boukharis 1977). *Atriplex rosea* seeds were collected from a population found in the salt marshes of Faust, Utah, along with other halophytes such as *A. patula*, *Distichlis spicata*, *Scirpus maritimus*, *Suaeda moquinii*, and *Triglochin maritima*, with soil electroconductivity (EC) ranging from 850 mM to 1031 mM NaCl in the *A. rosea* zone. Plants surviving in such a high saline environment require a higher degree of salt tolerance during seed germination.

Variations in temperature regime under both saline and nonsaline conditions have different effects on brown and black seeds of *A. rosea*. Black seed germination was more sensitive to changes in temperature regimes. Both types of seeds have optimal germination at 20°–30°C, but black seed germination was inhibited substantially with a decrease in temperature. Temperature and salinity interact to affect germination of halophytes (Khan and Ungar 1984a, 1984b, Khan and Weber 1986, Khan and Rizvi 1994, Khan and Ungar 1996, 1997, Khan and Gul 1998, Khan and Ungar 1998, 1999). Some species are more sensitive to change in temperature (*Cressa cretica*, *Triglochin maritima*, *Polygonum aviculare*, and *Zygophyllum simplex*) than others (*Arthrocnemum indicum*, *Haloxylon recurvum*, and *Suaeda fruticosa*; Sheikh and Mahmood 1986, Khan 1991, Khan

TABLE 2. Rate of germination (mean \pm $s_{\bar{x}}$) of *Atriplex rosea* black and brown seeds in various salinities and thermoperiods. Different letters in superscript represent significant ($P < 0.05$) differences between salinity treatments at each temperature regime. ANOVA, Bonferroni test.

NaCl (mM)	5°–15°C		10°–20°C		15°–25°C		20°–30°C		25°–35°C	
	Black	Brown	Black	Brown	Black	Brown	Black	Brown	Black	Brown
0	15 ± 3 ^a	26 ± 6 ^a	53 ± 3 ^a	40 ± 1 ^a	32 ± 1 ^a	44 ± 3 ^a	44 ± 2 ^a	48 ± 2 ^a	33 ± 5 ^a	42 ± 4 ^a
200	3 ± 1 ^b	10 ± 1 ^b	13 ± 1 ^b	20 ± 2 ^b	12 ± 4 ^b	28 ± 3 ^b	36 ± 2 ^b	33 ± 1 ^b	19 ± 2 ^b	29 ± 1 ^b
400	1 ± 1 ^c	10 ± 1 ^b	5 ± 1 ^c	8 ± 2 ^c	9 ± 1 ^b	17 ± 3 ^c	18 ± 3 ^b	18 ± 2 ^c	11 ± 2 ^c	12 ± 2 ^c
600	2 ± 0.7 ^c	9 ± 0.3 ^c	7 ± 1.1 ^c	7 ± 1.7 ^c	8 ± 0.6 ^c	9 ± 1 ^d	13 ± 2 ^b	13 ± 1 ^c	5 ± 1 ^d	9 ± 1 ^c
800	1 ± 0.4 ^c	6 ± 0.8 ^c	4 ± 1.5 ^d	5 ± 1.0 ^c	6 ± 0.6 ^c	6 ± 1 ^d	8 ± 2 ^c	10 ± 1 ^c	7 ± 2 ^e	8 ± 1 ^c
1000	0 ± 0 ^d	4 ± 0.6 ^d	2 ± 0.8 ^e	3 ± 0.5 ^d	0 ± 0 ^d	3 ± 1 ^e	6 ± 1 ^d	6 ± 1 ^d	2 ± 1 ^f	3 ± 1 ^d

TABLE 3. Rate of recovery of germination (mean \pm $s_{\bar{x}}$) of *Atriplex rosea* black and brown seeds in various salinities and thermoperiods. Different letters in superscript represent significant ($P < 0.05$) differences between salinity treatments at each temperature regime. ANOVA, Bonferroni test.

NaCl (mM)	5°–15°C		10°–20°C		15°–25°C		20°–30°C		25°–35°C	
	Black	Brown	Black	Brown	Black	Brown	Black	Brown	Black	Brown
0	10 ± 2.2 ^a	10 ± 3.0 ^a	16 ± 7 ^a	0 ± 0	4 ± 1.2 ^a	0 ± 0	0 ± 0	0 ± 0	26 ± 9 ^a	0 ± 0
200	2 ± 2.1 ^b	31 ± 2.5 ^b	18 ± 3 ^b	18 ± 2 ^b	27 ± 8 ^b	0 ± 0	9 ± 4 ^a	0 ± 0	31 ± 4.9 ^b	8 ± 4.4 ^b
400	9 ± 0.9 ^a	17 ± 0.7 ^a	8 ± 1.7 ^c	11 ± 3.5 ^c	27 ± 2 ^b	4 ± 2.2 ^c	28 ± 5 ^b	22 ± 4.2 ^b	17 ± 2 ^c	10 ± 3.3 ^c
600	10 ± 1 ^c	9 ± 0.7 ^c	3 ± 1.1 ^c	10 ± 3 ^c	27 ± 5 ^c	7 ± 4.5 ^c	31 ± 6 ^b	10 ± 4 ^c	27 ± 3.7 ^d	9 ± 0.9 ^e
800	2 ± 0.4 ^c	7 ± 0.8 ^c	5 ± 2.5 ^d	7 ± 2.5 ^c	22 ± 3 ^c	7 ± 2.4 ^c	32 ± 2 ^b	5 ± 1.8 ^c	24 ± 5 ^{e1}	13 ± 2 ^c
1000	0 ± 0 ^d	9 ± 1.0 ^d	7 ± 0.8 ^e	6 ± 0.5 ^d	16 ± 2.0 ^d	1 ± 0.3 ^d	36 ± 2 ^c	8 ± 3.1 ^d	15 ± 4.8 ^f	7 ± 0.6 ^d

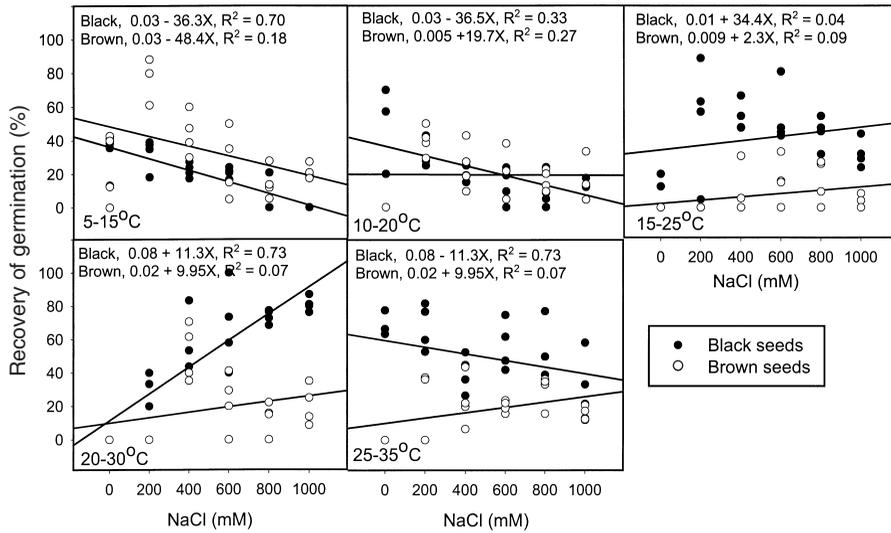


Fig. 4. Regression lines of the recovery of germination (%) of black and brown seeds of *Atriplex rosea* after being in 0, 200, 400, 600, 800, and 1000 mM NaCl at thermoperiods of 5°–15°C, 10°–20°C, 15°–25°C, 20°–30°C, and 25°–35°C for a 20-day period.

and Rizvi 1994, Khan and Ungar 1996, Khan and Gul 1998). Germination percentage of several *Atriplex* species was greater in the range of 12°–25°C at various salinity concentrations but declined beyond this range; i.e., the tolerance of salinity stress was greater at the optimum temperature (Beadle 1952, Springfield 1966, Ignaciuk and Lee 1980, Khan and Ungar 1984a, 1984b, Khan and Rizvi 1994). Khan and Ungar (1984a) found that alternating temperatures of 25°C and 5°C enhanced seed germination of *A. triangularis* and that increases in salinity (86–285 mM) decreased both the rate of and total seed germination. Khan and Rizvi (1994), reporting the effect of temperature regimes on seed germination of *A. griffithii* var. *stocksii* (*Atriplex stocksii*), found that a relatively cooler temperature regime (10°–20°C) promoted seed germination in both saline and nonsaline conditions.

Brown seeds of *A. rosea*, when exposed to salinity for 20 days and then returned to distilled water, showed a substantial recovery at lower temperature regimes, which decreased with increase in salinity. However, at optimal temperature regimes, recovery percentages increased with increase in salinity. Brown seeds showed a poor recovery response. Zid and Boukharis (1977) found that a high percentage of ungerminated seeds of *A. halimus* recov-

ered completely after they were transferred to distilled water. Similar recovery responses have been reported from a number of halophytic species (Khan and Ungar 1996, 1997, 1998), while species like *Z. simplex* had little recovery at any NaCl concentration in all thermoperiods. Nondormant seeds of glycophytes normally die when exposed to salinity (Partridge and Wilson 1987).

Atriplex rosea produces brown and black seeds on the same plant. It has been demonstrated that seed dimorphism provides an adaptive advantage in saline habitats through production of multiple germination periods that increase chances of survival for at least some seedling cohorts (Ungar 1995). *Atriplex rosea* usually grows as one of the salt marsh species of Great Basin playas where soil salinity is extremely high (100 dS m⁻¹). These plants recruit through seeds, leaving no evidence of vegetative propagation (personal observation), and grow in areas characterized by great fluctuations in soil salinity and ambient temperature. The present study has determined that dimorphic seeds produced by this plant also differ physiologically in their response to temperature and salinity during germination. Black seeds are more sensitive to change in temperature, and lower temperature regimes decreased seed germination in both saline and

nonsaline conditions. However, brown seeds are more tolerant of both temperature and salinity at cooler conditions. It appears that brown seeds could germinate early in the growing season to preempt the site and have an early start. This could result in a plant with more vigor and a higher reproductive effort later in the growing season as reported for *A. triangularis* (Khan and Ungar 1996). Saline desert habitats are subjected to rapid change in environmental conditions. Delay in rainfall could cause salinity concentration of the soil solution to increase manyfold, which could result in high mortality of young plants. Under these conditions new plants could be recruited through black seeds, thereby ensuring continuity of the species. So both seed morphs have the potential for complementary establishment syndromes.

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