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Variation in germination response to temperature and salinity in shrubby *Atriplex* species

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Germination response to temperature and salinity was measured for 13 seed accessions of shrubby *Atriplex* belonging to five species. Optimum germination temperature varied both among and within species, as did maximum germination expressed as percentage of filled seed. All accessions showed depressed germination with increasing salinity at high temperature, while germination percentages at low salt levels frequently exceeded the water control values at intermediate or low temperatures. Within-species variation was not clearly correlated with any habitat attribute. The high degree of variation emphasises that between-species comparisons can only be meaningful if an adequate evaluation of within-species variation is available.

Introduction

Shrubby species of the genus *Atriplex* (Chenopodiaceae) are landscape dominants in many arid and semi-arid regions of the world, particularly in habitats that combine relatively high soil salinity with aridity (McArthur & Sanderson, 1984). Established on all continents and many islands (Osmond *et al.*, 1980), this important genus provides forage for domestic livestock and wildlife and is effective in erosion control and stabilisation of severely disturbed lands (Beadle, 1952; Springfield, 1970; Ansley & Abernethy, 1984; Booth, 1985). Efforts to utilise these valuable plants in artificial revegetation have met with mixed success (Chatterton & McKell, 1969; Olivares & Johnston, 1978; Tiedemann *et al.*, 1984) due in part to a lack of knowledge about specific germination requirements of the seed source.

In *Atriplex* species, several germination control mechanisms have been reported (Beadle, 1952; Koller, 1957; Nord & Van Atta, 1960; Springfield, 1970; Sharma, 1976; Fernández, 1978; Johnston & Fernández, 1978; Khan & Ungar, 1984; Warren & Kay, 1984; Ansley & Abernethy, 1985). Most, if not all, species possess two or more mechanisms that probably act in concert to regulate the temporal spread of germination both seasonally within a year and among years. Complex multiple dormancy mechanisms may hamper the effectiveness of artificial revegetation from seed (Lailhacar-Kind & Laude, 1975; Warren & Kay, 1984).

A further consideration in revegetation success is the degree to which within-species variation contributes to the overall variation in germination response. Ecotypic variation in the germination response of *Atriplex* species has not yet been evaluated. Most germination studies to date are based on one seed source per species. Understanding the environmental cues that trigger germination under laboratory conditions and the variation

in germination response between species and species accessions should make it possible to improve species and ecotype selection, seed treatments, and planting techniques for artificial revegetation using these species.

In our study, seed collections from a variety of Mojave Desert species and ecotypes were compared under a common set of treatment conditions. This permits direct evaluation of both interspecific and intraspecific variation in germination response. We looked at response to temperature using regimes representative of winter, summer, and spring/fall in the Mojave region. We also examined germination response to salinity (NaCl) over a range commonly encountered in *Atriplex*-dominated soils. The two variables were combined factorially so that temperature–salinity interactions could be evaluated.

Materials and methods

Thirteen seed accessions representing five species of shrubby *Atriplex* were collected from Mojave Desert locations in Nevada and California, mostly in April 1989 (Table 1). At least two accessions were collected for each species. Seeds mature in autumn or early winter, so that at the time of collection the seeds had already after-ripened 4 to 6 months on the bushes. The seed collections were cleaned by screening, hand-rubbing, and blowing, which resulted in removal of bract wings but left the structure of the bracts intact around the one-seeded fruits. Seed collections were stored at the Shrub Sciences Laboratory, unsealed at room temperature (21°C) until use.

Bracted fruits (hereafter referred to as seeds) of each accession were germinated under three temperature regimes and at four salinity levels in a completely randomised factorial design with four replicates of 25 seeds each. Temperatures were 5/15, 10/20 and 20/30°C (12 h at each temperature). Salinity levels were 0 (control), 0·05 M, 0·20 M and 0·40 M sodium chloride. Actual salinity levels may have varied somewhat from those listed above due to salts present in both the bracts and the germination blotters (Morgan & Booth, 1990). Seeds were germinated in 9 cm plastic petri-dishes containing two standard blue germination blotters moistened with 10 ml of distilled water or other test solution. The petri-dishes were stacked and sealed in plastic bags to prevent moisture loss during the 3-week incubation. A 12-h photoperiod (cool-white fluorescent lights) coincided with the higher temperature in each alternating temperature regime. Radicle protrusion was the criterion for germination, which was recorded twice weekly. The experiment took place in May 1989.

Fruit fill percentage was determined for each accession by cutting 100 dry seeds. In addition, ungerminated seeds from the water control treatment at each temperature were also cut to determine fill percentage. Total germination within each treatment was adjusted based on fill percentage of 400 seeds for that accession. Fill percentage provides a liberal estimate of total viable seed percentage, so that germination percentages based on fill tend to be conservative.

Fill-adjusted germination percentage data were arc-sine transformed prior to analysis of variance. Differences between means were evaluated using the Student Newman–Keuls means comparison test. To evaluate within-species vs. among-species variation, the seed source term was divided into species and accession terms, with accession used as the error term for species. Also, because of the marked differences in response among accessions and the objective of comparing responses among accessions in the temperature and salinity experiment, analysis of variance was performed on each seed accession separately and on the data set as a whole.

Results

The effect of temperature, salinity level and seed accession were all highly significant, as were all the second-order and higher-level interactions, indicating strong interdependence

Table 1. *Collection information for Atriplex seed collections used in germination experiments*

Code	Species/subspecies	Probable ploidy	Elevation (m)	Habitat	Collection date
ATCACA 1	A. canescens canescens (Pursh) Nutt.	4x	1419	Valley bottom	12/88
ATCACA 2	A. canescens canescens	4x	1032	Sand and gravel	04/89
ATCALA 1	A. canescens laciniata Parish.	12x	183	Playa	04/89
ATCALA 2	A. canescens laciniata	12x	30	Valley bottom	04/89
ATCO 1	A. confertifolia (Torr. & Fremont) Wats.	4x	1116	Sand and gravel	04/89
ATCO 2	A. confertifolia	8x	265	Playa	04/89
ATLELE	A. lentiformis lentiformis (Torr.) Wats.	2x	−6	Valley bottom	04/89
ATLETO 1	A. lentiformis torreyi (Wats.) McMinn.	2x	708	Low spots, valley	04/89
ATLETO 2	A. lentiformis torreyi	2x	1098	Low spots, valley	04/89
ATLI 1	A. linearis Wats.	2x	110	Playa	04/89
ATLI 2	A. linearis	2x	−55	Barren	04/89
ATPO 1	A. polycarpa (Torr.) Wats.	4x	610	Hillside	04/89
ATPO 2	A. polycarpa	4x	−38	Lake sediments	04/89

among the three variables under study (Table 2). In general, germination decreased with increasing temperature (Table 3). The highest germination over all salinity levels and accessions was obtained at the lowest temperature (5/15°C), with a slight but significant decrease at 10/20°C. A marked decrease occurred at the highest temperature (20/30°C).

Germination also decreased with increasing salt concentration (Table 3). The highest germination averaged over all temperatures and accessions was obtained in the distilled water control, although germination was only slightly lower at the 0·05 M sodium chloride concentration. A much greater depression in germination percentage was observed at the 0·20 M and especially at the 0·40 M levels.

Table 3 shows the strong interaction between temperature and salinity level, with temperature and salinity acting synergistically to suppress germination disproportionately at the highest temperature and salinity levels. In the water control, overall germination was only slightly depressed at the highest temperature, whereas at 0·40 M sodium chloride, germination at the lowest temperature was over four times that at the highest temperature. Temperature also affected germination suppression at given salinities. At the lowest temperature, germination at 0·40 M was approximately one-quarter that of the water control, whereas at the highest temperature, 0·40 M germination was less than 1/17 that of the water control. At low and intermediate temperatures, germination percentages at 0·05 M were not significantly different from the water control, but at the highest temperature there was a significant drop in germination percentage even at 0·05 M.

Different seed accessions showed marked differences in overall germination response and in response to temperature and salinity levels (Table 4). Mean germination percentage varied from 1 (ATCO 2) to 67 (ATPO 1), while germination percentage in the best treatment varied from 7 (ATCO 2) to 94 (ATPO 1). Seed accessions with relatively low levels of dormancy tended to be less sensitive to variation in temperature and salinity (e.g. ATPO 1, ATLELE, ATCACA 2). There were no clear trends by species except for *A. confertifolia*, which was consistently highly dormant. Other species showed a broad range

Table 2. *Summary of analysis of variance for germination*

Source of variation	df	SS	MS	F	Significance
Temperature regime	2	2·00	1·00	109·94	0·0001
Source of seed	12	35·39	2·95	324·85	0·0001
Temperature × source	24	3·65	0·15	16·77	0·0001
Salt concentration	3	23·01	7·67	845·00	0·0001
Temperature × salt	6	0·80	0·13	14·76	0·0001
Source × salt	36	6·77	0·19	20·73	0·0001
Temperature × source × salt	72	5·01	0·07	7·66	0·0001

Table 3. *Temperature main effect, salinity main effect, and temperature × salinity interaction mean germination percentages (averaged across all seed accessions). Main effects means followed by different letters are significantly different at the $p < 0.05$ level*

Salinity level	Temperature regime (°C)			Mean
	5–15	10–20	20–30	
0·00 M	34·3	36·7	30·0	33·7a
0·05 M	36·0	34·1	23·2	31·1b
0·20 M	20·3	20·6	9·3	16·7c
0·40 M	7·8	3·0	1·7	4·2d
Mean	24·6a	23·6b	16·1c	

Table 4. *Mean germination percentages for temperature and salinity main effects by accession*

Accession	Overall	Temperature (°C)					Salinity (M)				
		Best	5–15	10–20	20–30	OSL*	0·00	0·05	0·20	0·40	OSL*
ATCACA 1	20	48	22	21	17	NS	38	32	9	1	0·0001
ATCACA 2	31	72	29	25	40	0·0001	50	42	26	7	0·0001
ATCALA 1	15	46	20	21	4	0·0001	30	20	10	0	0·0001
ATCALA 2	12	27	18	13	6	0·0001	19	17	7	6	0·0001
ATCO 1	2	12	0	0	5	0·0001	4	3	0	0	0·0001
ATCO 2	1	7	2	1	0	0·0025	3	0	0	0	0·0006
ATLELE	40	76	41	47	32	0·0003	63	66	31	1	0·0001
ATLETO 1	29	71	41	35	9	0·0001	53	42	20	0	0·0001
ATLETO 2	15	38	22	17	7	0·0001	28	24	9	1	0·0001
ATLI 1	9	22	9	13	6	0·0001	14	16	6	0	0·0001
ATLI 2	27	63	35	29	17	0·0001	44	45	18	2	0·0001
ATPO 1	67	94	71	70	60	0·0128	79	80	76	33	0·0001
ATPO 2	9	21	8	14	6	0·0001	14	17	4	2	0·0001

* Observed significance level (*F* ratio probability value).

of variation in overall dormancy level. In fact, when the variation due to seed source (Table 1) was partitioned into species and accession components, over half of the mean squares was due to differences between accessions. The accession term in the analysis remained significant ($p = 0.009$), but the species term did not ($p = 0.2024$).

Some accessions were relatively insensitive to temperature (e.g. ATCACA 1, ATLELE). Others showed sharply decreased germination at higher temperatures (e.g. ATCALA 1, ATCALA 2, ATCO 2, ATLETO 1, ATLETO 2). Several accessions showed highest germination percentages at intermediate (ATLELE, ATLI 1, ATPO 2) or high (ATCACA 2, ATCO 1) temperatures. In ATPO 1, an increasing temperature response for water controls was completely reversed at higher salt concentrations (Table 5). There was no clear pattern by species in temperature response, with considerable variation present among species accessions. Even the two highly dormant accessions of *A. confertifolia* showed contrasting responses to temperature.

Similar contrasts can be seen in seed accession responses to salinity (Table 4). Reduction in germination due to increasing salinity was least marked in ATPO 1, which showed a reduction of less than two-thirds relative to the water control even at 0·40 M. Other accessions (e.g. ATCALA 1, ATCO 2, ATLETO 1) showed significant reduction at 0·05 M relative to the water control and complete germination suppression at 0·40 M. In the remaining accessions, salinity-induced germination suppression was intermediate, with no significant suppression at salt levels below 0·20 M. No clear pattern by species was discernible.

The salinity by temperature interaction was highly significant ($p < 0.01$) for 10 of the 13 accessions (Table 5). The suppressive effect at intermediate salinity was generally least marked in the optimum temperature regime, although there were exceptions (e.g. ATCACA 2, ATPO 1). All accessions showed generally decreased germination with increasing salinity at the highest temperature, if they germinated at all. However, several accessions showed enhanced germination in the presence of low to moderate amounts of salt at low (ATCALA 2, ATLI 2, ATPO 2 = 0·05 M optimum; ATPO 1 = 0·20 M optimum) or intermediate temperatures (ATCACA 2, ATLELE = 0·05 M optimum). Several accessions that showed their highest water control germination at intermediate or high temperatures also showed decreased germination with increasing temperature in the presence of 0·20 M or greater salt (ATCALA 1, ATCALA 2, ATLETO 1). Again, there were no clear trends by species in patterns of interaction.

Discussion

In general, the salinity response results obtained here are in agreement with those obtained for many other halophyte species (Ungar, 1978). Salt concentration had the greatest effect on seed germination of any of the factors examined in this study. Germination was highest in water or at low salinities with increasing suppression as salinity increases. The rate of suppression varied among species and among accessions within species but was not related in any obvious way to habitat characteristics. Differential effects from bracteole leaching may have contributed somewhat to the observed variation in salinity response. Soaking or leaching of *Atriplex* fruits often results in enhanced germination, and several workers have attributed this enhancement to the removal of osmotically active solutes, especially sodium chloride (Beadle, 1952; Koller, 1957; Twitchell, 1955; Cornelius & Hylton, 1969; Young *et al.*, 1980).

In this study, we obtained additional data to support the previously observed synergistic relationship between germination suppression at high temperatures and increasing salinity (Springfield, 1966; Sharma, 1976; Khan & Ungar, 1984; El-Sharkawi & Farghali, 1985; Potter *et al.*, 1986; El-Sharkawi *et al.*, 1989; Hampson & Simpson, 1990). Although the mechanisms for salt–temperature interactions is poorly understood (Hampson & Simpson, 1990), this relationship may have the field effect of reducing germination at a