EFFECTS OF OSMOTIC POTENTIAL, POTASSIUM CHLORIDE, AND SODIUM CHLORIDE ON GERMINATION OF GREASEWOOD (*SARCOBATUS VERMICULATUS*)[1]

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ABSTRACT.—Greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.) (Chenopodiaceae) typically grows on salt-affected soils where its germination requirements may reflect characteristics necessary for establishment in saline environments. The objective of this study was to determine the effect of osmotic potential and specific ions on the germination of seeds from three populations of greasewood. Seeds were germinated at 20 C in solutions of polyethylene glycol with water potentials ranging from −0.3 to −2.2 MPa that contained 0 to 68480 $\mu mol \cdot L^{-1}$ sodium chloride (NaCl) or 0 to 53640 $\mu mol \cdot L^{-1}$ potassium chloride (KCl). Germination of two populations was reduced by increasing salt concentration and decreasing osmotic potential; germination of one population was reduced by declining osmotic potential. No seeds germinated at an osmotic potential lower than −1.6 MPa. For all populations, days to 50% of final germination increased and abnormal germination decreased as osmotic potential declined. Comparison of our results with those from other studies suggests geographic ecotypic development in response to osmotic potential and NaCl and KCl concentrations during germination.

Greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.) grows in all states west of the 100th meridian, northern Mexico, and southern Alberta and Saskatchewan (Branson et al. 1967). Throughout its range, greasewood usually grows on fine-textured soils that are saline or alkaline, but occasionally it grows on nonsaline and coarse-textured soils (Shantz and Piemeisel 1940, Fireman and Hayward 1952, Gates et al. 1956, Rickard and Keough 1968). Because greasewood grows on a variety of soils, we hypothesized that populations from different sites would respond differently to osmotic potential and specific ions during germination.

Seed germination and seedling establishment may be the most critical stages in life cycles of plants in saline environments. The soil conditions to which seeds and seedlings will be exposed determine their success (Ungar 1982) and are a major source of attrition in the seedbank (Harper 1977). Salinity may affect germination and seedling growth through reduced osmotic potential, increased availability of a toxic ion, and reduced absorption of nutrients because of ion imbalance (Richards 1954, Hayward and Bernstein 1958). Generally germination is delayed and reduced when salt stress exceeds a critical level; the level of salinity at which germination is reduced varies with species, genotype, environmental conditions, osmotic potential, and specific ions (Ungar 1978).

Chapman (1974) concluded that a reduction in soil salinity is requisite for germination in saline environments. Reduction of soil salinity increases the osmotic potential and reduces ion concentrations (Richards 1954). Germination of some species is reduced more by osmotic potential than by specific ions (Choudhuri 1968, Ungar and Capilupo 1969, Ungar and Hogan 1970, Macke and Ungar 1971, Cluff et al. 1982); however, ions depress germination more than osmotic potential in other species (Choudhuri 1968, Hyder and Yasmin 1972, Redmann 1974, Wood et al. 1976, Young and Evans 1981). The effects of osmotic potential and ions also vary within species (Dewey 1960, Springfield 1966, Workman and West 1967, Clarke and West 1969, Clarke and West 1972), and differences may be related to genetics or environmental conditions.

The objective of this research was to ascertain the effects of osmotic potential and ions on the germination of greasewood. Seeds of three greasewood populations were incubated in a gradient of osmotic potentials and concentrations of KCl and NaCl.

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MATERIALS AND METHODS

Three sources of greasewood seeds were collected from sites located approximately 30 km south of Burns, Oregon. Elevation of all sites is approximately 1,255 m, and climatic conditions are similar. Soils of the North and South Harney sites were formed from alluvial materials and are moderately well drained, fine-loamy, mixed, mesic Xerollic Haplargids and fine-loamy, mixed, mesic Xerollic Camborthids, respectively. Soils at the Coyote Buttes site are moderately well drained, fine montmorillonitic, mesic Xerollic Haplargids, formed from alluvial materials.

Seeds (utricles) were collected from several plants at each site in October 1982. After collection, seeds were dried at room temperature and stored in paper envelopes. Bracts were removed with a flail, and seeds were sorted with air to reduce variation in size; the heavier one-half of each seedlot was used for germination trials. Seeds were approximately eight months old when tested.

Five osmotic solutions were prepared by adding polyethylene glycol (M.W. 20000) to distilled water. Solutions were buffered to pH 8.0 with (Tris-[Hydroxylmethyl] Amino-Methane) buffer. Each solution was divided into 9 aliquots, and 2 M sodium chloride (NaCl) or potassium chloride (KCl) was added to bring solutions to 0, 8560, 17120, 34240, and 68480 $\mu mol \cdot L^{-1}$ for NaCl and 0, 6705, 13410, 26820, and 53640 $\mu mol \cdot L^{-1}$ for KCl. Salt concentrations were selected to bracket K^+ and Na^+ concentrations determined for saturation extracts (Richards 1954) from soils collected from the top 5 cm of the solum in four greasewood communities. Sodium and potassium concentrations ranged from 27000 to 75000 and 11278 to 26739 $\mu mol \cdot L^{-1}$ of saturation extract, respectively. Concentrations ranged from 2750 to 5500 $\mu mol \cdot L^{-1}$ for calcium and 1200 to 3250 $\mu mol \cdot L^{-1}$ for magnesium.

Osmotic potentials of germination solutions, determined on the fourth and eighth days of incubation, were -0.3, -0.7, -1.2, -1.6, and -2.2 MPa for both NaCl-PEG and KCl-PEG solutions. Although the addition of NaCl and KCl may have reduced osmotic potentials, no differences were found between the various concentrations. Osmotic potentials were determined from filter paper discs, 5 mm in diameter, placed in petri dishes when incubation was initiated. Osmotic potentials of these discs were determined with a Wescor[4] HR-33T microvoltometer and a Wescor[4] C-52 sample chamber psychrometer after calibration with standard NaCl solutions.

Before commencing germination tests, lots of 50 seeds were counted and stored in paper envelopes. Ten envelopes of each collection were randomly selected and used for determining seed weights. Another set of envelopes was randomly selected, and seeds were placed in petri dishes on a #4 Whatman[4] filter paper disc that was underlaid by germination blotter. Twenty-five ml of osmoticum were added to each dish, and the dishes were covered and sealed in plastic bags to prevent desiccation. Seeds were incubated in darkness at 20 C for 14 days and exposed to light only briefly when germination was recorded at two-day intervals. Seeds were considered germinated when the embryo had uncoiled and cotyledons were reflexed. Seeds that initiated germination but failed to meet the germination criteria were recorded as abnormal germination. At the end of the incubation period, ungerminated seeds were dissected to determine seed fill. The number of days to 50% of final germination was used as a measure of germination rate.

Within salts, treatments were applied factorially in a randomized complete block design with four replications. Factors were salt concentrations and osmotic potential. Time was used as blocks because replications were started at approximately two-week intervals.

Data were initially analyzed within seed sources with a factorial analysis of variance after transforming counts with arc sin $\sqrt{\hat{p}}$ (Snedecor and Cochran 1980). Polynomial response curves or multiple linear regression response surfaces were then developed using untransformed data (Neter and Wasserman 1974). Tukey's W-procedure was used for testing differences between means (Snedecor and Cochran 1980). All statistical tests were conducted at $p = 0.05$ probability level.

[4]Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by U.S. Department of Agriculture or Oregon State University and does not imply approval to the exclusion of other products that may also be suitable.

TABLE 1. Seed weights and seed fill for three seed collections of greasewood from southeastern Oregon.

	Collection source		
	North Harney	South Harney	Coyote Buttes
Mean weight (mg/50 seeds)	79.6[1]	97.5[1]	81.3[1]
Mean percent seed fill	96.4[2]	96.6[2]	96.0[2]

[1]HSD = 12.6
[2]$S_{\bar{x}}$ = .70

TABLE 2. Analysis of variance for total germination, days to 50% of final germination, and abnormal germination for greasewood seeds incubated 14 days in NaCl-PEG and KCl-PEG solutions.

Source	Source of variation	Degrees of freedom	Osmotica NaCl-PEG	Osmotica KCl-PEG
			Total germination (%)	
North Harney	Osmotic potential (P)	3	14326.2*†	14694.9*
	Salt concentration (S)	4	40.3NS‡	55.8NS
	PXS	12	26.2NS	35.1NS
	Error	57	25.7	31.8
South Harney	P	2	23128.3*	21567.2*
	S	4	157.3*	291.6*
	PXS	8	48.2NS	54.6NS
	Error	42	57.9	45.5
Coyote Buttes	P	2	16519.4*	15247.3*
	S	4	389.7*	172.2*
	PXS	8	100.1*	50.5NS
	Error	42	39.1	36.7
			Days to 50% of final germination	
North Harney	P	3	189.3*	240.7*
	S	4	2.1NS	3.4NS
	PXS	12	2.5NS	2.5NS
	Error	57	2.9	2.2
South Harney	P	2	101.4*	134.3*
	S	4	3.6*	2.4*
	PXS	8	2.3NS	2.2NS
	Error	42	1.9	1.3
Coyote Buttes	P	2	130.1*	173.5*
	S	4	2.2NS	3.1NS
	PXS	8	1.6NS	1.9NS
	Error	42	3.2	1.3
			Abnormal germination (%)	
North Harney	P	4	36.8*	26.5*
	S	4	3.6NS	6.2NS
	PXS	16	6.1NS	7.4NS
	Error	72	6.7	5.1
South Harney	P	4	15.5*	32.7*
	S	4	2.0NS	3.2NS
	PXS	16	3.1NS	4.0NS
	Error	72	3.8	4.5
Coyote Buttes	P	4	37.7*	80.5*
	S	4	9.3NS	8.7NS
	PXS	16	8.1NS	7.2NS
	Error	72	6.7	5.7

†* = F significant at the 0.05 level.
‡NS = Not significant at the 0.05 level.

TABLE 3. Regression equations and coefficients of determination for total germination, days to 50% of final germination, and abnormal germination for greasewood seeds incubated 14 days in NaCl-PEG and KCl-PEG solutions.

Seed source	Osmotica: NaCl-PEG Regression equation	R^2	Osmotica: KCl-PEG Regression equation	R^2
	Total germination (%)			
North Harney	$Y=91.97+114.64X_1^{\dagger}+36.67X_1^2$	0.94	$Y=93.56+116.77X_1+37.64X_1^2$	0.93
South Harney	$Y=117.91+205.48X_1+89.36X_1^2-0.0001X_2^{\ddagger}$	0.92	$Y=115.52+198.52X_1+85.22X_1^2-0.0002X_2$	0.94
Coyote Buttes	$Y=105.69+161.41X_1+61.42X_1^2-0.0004X_2-0.0003X_1X_2$	0.94	$Y=91.89+127.97X_1+44.7X_1^2-0.0002X_2$	0.92
	Days to 50% of final germination			
North Harney	$Y=2.4-5.5X_1$	0.65	$Y=2.7-4.9X_1$	0.73
South Harney	$Y=3.5-4.9X_1$	0.78	$Y=3.2-5.1X_1$	0.81
Coyote Buttes	$Y=3.7-5.0X_1$	0.80	$Y=3.7-4.9X_1$	0.80
	Abnormal germination (%)			
North Harney	$Y=4.94+1.30X_1$	0.31	$Y=4.48+0.86X_1$	0.21
South Harney	$Y=2.99+1.23X_1+0.05X_1^2$	0.37	$Y=3.96+1.68X_1$	0.47
Coyote Buttes	$Y=4.93+1.79X_1$	0.42	$Y=6.06+2.61X_1$	0.58

†X_1 = Osmotic potential (−MPa).
‡X_2 = Salt concentration ($\mu mol \cdot L^{-1}$).

RESULTS

Percent seed fill was similar between collections (Table 1). Weights of sorted seeds were different, however, between collections, with the South Harney collection significantly ($p = 0.05$) heavier than the North Harney and Coyote Buttes collections.

Percent germination of the North Harney collection was related to osmotic potential in NaCl-PEG and KCl-PEG solutions, but salt concentration was not significant ($p = 0.05$) (Tables 2, 3). Seeds germinated at all osmotic potentials tested except −2.2 MPa (Table 4). Days to 50% of final germination were related to osmotic potential in both NaCl-PEG and KCl-PEG solutions (Tables 2, 3), increasing as osmotic potential decreased (Table 5). Some abnormal germination occurred at all osmotic potentials tested, and it decreased as osmotic potential declined (Tables 2, 3, 6).

Germination of the South Harney collection was reduced by declining osmotic potential and increasing NaCl and KCl concentrations (Tables 2, 3). Seeds germinated at −0.3 and −0.7 MPa, but no germination was observed at the lower osmotic potentials tested (Table 4). Osmotic potential was the only factor that affected days to 50% of final germination as osmotic potential declined (Table 5). Some seeds germinated abnormally at all osmotic potentials tested, but germination was not significantly ($p = 0.05$) affected by salt concentration (Tables 2, 3); abnormal germination declined as osmotic potential decreased (Table 6).

In NaCl-PEG and KCl-PEG solutions, total germination of the Coyote Buttes collection was significantly ($p = 0.05$) affected by osmotic potential and salt concentration (Tables 2, 3), with osmotic potential causing the greatest reduction (Table 4). Some seeds germinated at all osmotic potentials tested except −1.6 and −2.2 MPa (Table 4). Days to 50% of final germination and abnormal germination were related only to osmotic potential (Tables 2, 3); days to 50% of final germination increased and abnormal germination decreased

TABLE 4. Estimates of total germination for greasewood seeds after 14 days of incubation in NaCl-PEG and KCl-PEG solutions. Regression equations used to predict values are presented in Table 3.

Seed source	Osmotica	Salt concentration ($\mu mol \cdot L^{-1}$)	Osmotic potential (−MPa)			
			0.3	0.7	1.2	1.6
			%			
North Harney	NaCl	0-68480	60.9	29.7	7.2	2.4
	KCl	0-53640	61.9	30.3	7.6	3.1
South Harney	NaCl	0	64.3	17.9	0.0	0.0
		8560	63.4	17.0	0.0	0.0
		17120	62.6	16.1	0.0	0.0
		34240	60.9	14.4	0.0	0.0
		68480	57.4	11.0	0.0	0.0
	KCl	0	63.6	18.3	0.0	0.0
		6705	62.3	17.0	0.0	0.0
		13410	60.9	15.6	0.0	0.0
		26820	58.3	12.9	0.0	0.0
		53640	52.4	7.0	0.0	0.0
Coyote Buttes	NaCl	0	62.8	22.8	0.4	0.0
		8560	60.2	21.2	0.1	0.0
		17120	57.5	19.6	0.0	0.0
		34240	52.2	16.3	0.0	0.0
		68480	41.6	9.8	0.0	0.0
	KCl	0	56.8	23.4	1.9	0.0
		6705	55.4	22.1	0.6	0.0
		13410	54.1	20.8	0.6	0.0
		26820	51.4	18.1	0.0	0.0
		53640	46.0	12.7	0.0	0.0

TABLE 5. Estimates of days to 50% of final germination for greasewood seeds incubated for 14 days in NaCl-PEG and KCl-PEG solutions. Regression equations used to predict values are presented in Table 3.

Seed source	Osmotica	Salt concentration ($\mu mol \cdot L^{-1}$)	Osmotic potential (−MPa)			
			0.3	0.7	1.2	1.6
			%			
North Harney	NaCl	0-68480	4.1	6.3	9.0	11.2
	KCl	0-53640	4.2	6.1	8.6	10.5
South Harney	NaCl	0-68480	5.0	6.9	9.4	–†
	KCl	0-53640	4.7	6.8	9.3	–
Coyote Buttes	NaCl	0-68480	5.2	7.2	9.7	–
	KCl	0-53640	5.2	7.1	9.6	–

†No seeds germinated at this osmotic potential.

TABLE 6. Estimates of abnormal germination for greasewood seeds incubated for 14 days in NaCl-PEG and KCl-PEG solutions. Regression equations used to predict values are presented in Table 3.

Seed source	Osmotica	Salt concentration ($\mu mol \cdot L^{-1}$)	Osmotic potential (−MPa)				
			0.3	0.7	1.2	1.6	2.2
			%				
North Harney	NaCl	0-68480	4.6	4.0	3.4	2.9	2.1
	KCl	0-53640	4.2	3.9	3.4	3.1	2.6
South Harney	NaCl	0-68480	2.6	2.2	1.6	1.2	0.5
	KCl	0-53640	3.5	2.8	1.9	1.3	0.3
Coyote Buttes	NaCl	0-68480	4.4	3.7	2.8	2.1	1.0
	KCl	0-53640	5.3	4.2	2.9	1.9	0.3

as osmotic potential declined (Tables 5, 6).

DISCUSSION

The differences in germination observed in this study may be attributed to genetics of the populations, environmental conditions, or both. It was not possible to separate their effects in this study. Regardless of which factor influenced germination, there were inter- and intrapopulation differences in responses to osmotic potential and concentrations of NaCl and KCl.

Germination of all populations was primarily reduced by osmotic potential, but germination in a portion of the South Harney and Coyote Buttes collections was reduced by increasing NaCl and KCl concentrations. Sensitivity to osmotic potential, rather than specific ions, may be important for survival since seeds are exposed to myriad combinations of ions under field conditions (Ungar 1982). Sensitivity to osmotic potential may be an adaptation that limits most germination to periods when salts are diluted or leached and conditions are favorable for seedling growth. In the Great Basin, soil water potentials are highest and salinity is lowest in the spring because salts are diluted or leached by winter precipitation (Roundy 1984).

On sites where seeds were collected for this germination study, greasewood seedlings were observed only during spring. Because Glenn and O'Leary (1984) found that growth of young greasewood plants decreased directly in response to increasing salinity, and because we found that water stress reduced and slowed germination, we hypothesize that most seeds of greasewood germinate when soil moisture is high for extended periods. This adaptation may maximize the time for growth of seedlings. Similar regeneration adaptations have also been suggested for other species in the Great Basin (Wood et al. 1976, Young and Evans 1981, Cluff et al. 1983, Roundy 1985).

Comparison of results in this study with previously published studies on greasewood germination suggests the possibility of geographical ecotypic differentiation. Sabo et al. (1979) reported a New Mexico collection of greasewood germinated 80% or more at osmotic potentials ranging from 0 to −1.6 MPa. Seeds collected in eastern Montana germinated at osmotic potentials as low as −3.6 MPa (Romo and Eddleman 1985). Furthermore, Romo and Eddleman (1985) reported that Na_2SO_4 and NaCl stimulated germination rate and total germination in greasewood, but germination of these collections from Oregon was either unaffected or reduced by NaCl and KCl. These southeastern Oregon collections germinated only at osmotic potentials of −1.6 MPa or higher, and germination was less than 30% at osmotic potentials lower than −0.3 MPa. Failure to germinate at low osmotic potentials and high salt concentrations may act to preserve a portion of the seed population and condition them for germination over a wider range of ensuing environmental conditions (Hegarty 1978, Ungar 1978).

Responses to osmotic potential and specific ions are only two factors to consider when characterizing the germination ecology of greasewood. Germination of these southeastern Oregon collections of greasewood was primarily limited by availability of water and, to a lesser degree, by specific ions. Germination under field conditions is, however, probably quite different from laboratory results because of interacting effects of climatic and edaphic factors.

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