Germination responses of desert saltgrass to temperature and osmotic potential

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Abstract

Desert saltgrass [*Distichlis spicata* var. *stricta* (Torr.) Beetle] is the dominant herbaceous forage on many saline rangelands. The ability to direct-seed this grass would permit revegetaton of disturbed saline soils. Seeding guidelines must be based on an understanding of germination requirements in relation to seedbed conditions. Germination responses to alternating temperatures in relation to sodium chloride (NaCl)-reduced osmotic potentials were studied in the laboratory and seedbed salinity and water potentials were measured in a typical saltgrass stand in Nevada. Optimum conditions for saltgrass germination were at -0.1 MPa osmotic potential and a 20° C differential in cold and warm period temperatures with warm period temperatures above 30° C. Decreasing osmotic potentials from 0 to -2 MPa decreased the rate of germination from 4.5 to 0.3 and total germination from 60 to 9% across all temperature regimes. Water potentials in the lower topographical positions of a typical saltgrass stand after an unusually wet winter were high enough for germination (>-2MPa) in June when temperatures were optimum for germination. In most years and on xeric sites, optimum temperature and moisture conditions would not overlap to result in high germination. Some germination occurs at cooler than optimum temperatures and low osmotic potentials. Some seeds may eventually germinate in saline seedbeds under these conditions but highest germination would be expected when unusually high precipitation or topographic position results in high seedbed water potentials during late spring and early summer when temperatures are optimum. Consequently, irrigation during late spring and summer should produce the best stands of saltgrass from direct seeding. Where irrigation is not possible, saltgrass should be seeded in the fall to permit germination during early spring when temperatures are suboptimum but the seedbed is still moist. Success of nonirrigated seedings will be highly dependent on seedbed salinity and moisture conditions in the spring.

Key Words: salinity, plant establishment, range revegetation, seedbed ecology

Desert saltgrass is an important forage species of many inland salt marshes of the western United States (Nielson 1956). Saltgrass is not considered to be as palatable as many other endemic grasses; however, it is relatively high in protein (Hanson et al. 1976), is grazing tolerant, and may provide the only available forage for cattle during the summer portion of the grazing season. Because it is salt tolerant and rhizomatous, saltgrass is considered a potential candidate for revegetation of mine spoils and roadsides (Butler et al. 1973, Pavlicek et al. 1977). Revegetation using saltgrass rhizomes is labor intensive, requires specialized equipment, and has limited success (Pavlicek et al. 1977, Caplan 1983). Revegetation by direct seeding could be more effective than planting rhizomes. An understanding of seed requirements for germination in relation to natural seedbed conditions is important in determining seeding constraints and guidelines.

In a previous study (Cluff et al. 1983), desert saltgrass seeds did not germinate at osmotic potentials as low as those measured during the growing season in saturated soils from 2 typical saltgrass stands in Nevada. It was hypothesized that germination and seedling establishment were episodic events, occurring only during seasons of higher than normal precipitation when enough salt could be leached from the soil to raise the osmotic potential to within the limits necessary for germination. This osmotic potential limit is around -1.5 MPa when the seeds are incubated for 1 month at an optimum temperature regime for germination. That temperature regime consisted of 16 hours at 5° C and 8 hours at 40° C. This temperature regime occurred in June or July in the seedbeds of 2 saltgrass stands in the cold desert in Nevada. Since the probability of receiving substantial precipitation during those months is very low (Houghton et al. 1975), optimum seedbed temperatures for germination would rarely overlap with high enough soil osmotic potentials for germination in more saline seedbeds.

Another hypothesis which could explain the germination of saltgrass in saline seedbeds is that seeds may germinate very slowly at cold temperatures in March and April. Suboptimum temperatures may affect the rate of germination more than the total germination. Numerous studies with different plant species have shown that low osmotic potentials may inhibit germination less at suboptimum than at optimum temperatures (Springfield 1966, Odegbaro and Smith 1969, Francois and Goodin 1972, and Sharma 1976). Eventually, some saltgrass seeds may germinate at suboptimum temperatures and low osmotic potentials.

The purpose of this study was to determine the long-term germination responses of desert saltgrass seeds under different temperature regimes to reduced osmotic potentials and interpret these responses with respect to seedbed conditions.

Methods

In October 1981, pistillate seedheads of desert saltgrass were collected by hand from a salt marsh area in the Stillwater National Wildlife Refuge, Churchill County, Nevada. The saltgrass at the site inhabits a 20 M-wide zone between an intermittent fresh-water lake and surrounding silt-dunes which are sparsely covered by greasewood [*Sarcobatus vermiculatus* (Hook.) Torr.] The seeds were cleaned using an air-screen and stored in the laboratory at room temperature at low humidity.

Experimental procedures of Young et al. (1968) were used to determine the interactive effects of osmotic potential and temperature on saltgrass seed germination. Polyurethane foam was placed in polystyrene boxes, 11 by 11 by 4 cm in dimension, with moisture-tight lids and saturated with sodium chloride solutions with osmotic potentials of 0, -0.1, -0.5, -1.0, -1.5, and -2.0 MPa (Lang 1967). NaCl was used as the osmotic agent because it has been shown that it is not toxic to germinating saltgrass seeds (Cluff et al. 1983), produces relatively stable osmotic potentials in widely fluctuating temperatures, is easier to handle than other osmotic agents (Young et al. (1983), and is one of the dominant salts on western rangeland soils (Roundy 1984). Because the seeds were being tested in alternating temperatures and the osmotic potential of any solution varies slightly with temperature, the solutions were made for the means of the fluctuating temperature regime. In no cases did the actual osmotic potential differ by more than -0.05 MPa from the stated potential. Four replications of 25 seeds each were placed on top of the foam in each box. Replications were separated

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by placing them inside circles made from 2.5 cm length of 4.4 cm diameter polyvinyl chloride pipe. The seeds were incubated in dark germinators for 2 months, and germination counted every 2 to 3 days. In pilot experiments, seed germination did not respond to various light treatments. Seeds were considered germinated when the radicle had emerged at least 2 mm. The seeds were tested at 28 cool/warm period temperature regimes including 0/20, 25, 30, 35, 40, 45, and 50° C; 2 and 5/25, 30, 35, 40, 45, and 50° C; 10/30, 35, 40, 45, and 50° C; 20/40, 45, and 50° C; and 30/50° C. Seeds were exposed 8 hours to the cool temperatures and 16 hours to the warm temperatures in each 24-hour period. These temperature regimes were used because they were the only regimes that could be tested in standard germinators, which resulted in germination significantly higher (p=0.05) than zero in the previous study (Cluff et al. 1983). The seeds were tested at each of 6 osmotic potentials in each of the 28 temperature regimes. Since the experiment was conducted over a period of 1 year, germination was tested at the beginning and end of the experiment. Germination was tested after the method of Young and Evans (1979) using 4 replications of 25 seeds each placed on germination paper in petri dishes and kept moist with tap water. The seeds were incubated in dark germinators for 4 weeks at the temperature regime that was found to be optimum for germination in the previous study (Cluff et al. 1983): 16 hours at 5° C and 8 hours at 40° C.

The rate of germination was calculated for each temperature regime-osmotic potential treatment after Maguire (1962) where:

$$\text{Rate of Germination} = \Sigma_i[g_i - g_{(i-1)}/i]$$

in which g is the total germination percentage on an incubation day i minus the total germination percentage on the previous day $g_{(i-1)}$ divided by the incubation day i.

A response surface (Evans et al. 1982) using linear, quadratic, and interaction terms for cold and warm temperatures and osmotic potential was fit to germination percentage and rate data. Optimum temperature regimes were considered those for which mean germination responses at zero MPa osmotic potential were statistically similar (p>0.05) to that of the temperature regime with the highest germination responses. Suboptimum temperature regimes were those with significantly lower germination than maximum caused by what was believed to be a low warm period temperature. Slopes and intercepts of the regression of germination percentage and rate on osmotic potential were compared for optimum and suboptimum temperature regimes (Snedecor and Cochran 1971).

To relate germination responses to seedbed conditions, seedbed salinity and water potential of the saltgrass stand where seeds were collected were determined from samples collected on March and June 30, 1983. Seedbed temperatures would be expected to be suboptimum and optimum for germination at these dates, respectively. Samples were collected from 5 topographic positions with increasing distance from an intermittent fresh-water lake. The positions were edge of standing water, middle and edge of the marsh basin and saltgrass stand, and slopes and tops of adjacent upland silt dunes (Young et al. 1986). The top 3 cm of soil was sampled with a 2 cm-diameter auger at 4 locations for each topographic position and placed in a water-tight bottle. Approximately 2 g of the soil in each bottle were placed in psychrometer chambers described by Brown and Collins (1980). Total water potential of the samples was measured at 25° C before and after saturation with distilled water. The electrical conductivity of the saturated paste extract (ECe) of each sample was determined using methods and equipment described by Roundy (1984). An instant salinity meter was used to measure the electrical conductivity of the saturated paste (ECp) which was converted to the ECe using a linear regression of ECe on ECp calculated from 30 samples.

Results

There was no change in the germinability of saltgrass seeds over the 1-year period of testing. Seeds tested at the beginning and end of the experiment averaged 84 and 88% germination, respectively.

Percent and rate of germination decreased with increasing cold period temperature, decreasing warm period temperature, and decreasing osmotic potential (Figs. 1 and 2). Maximum percent

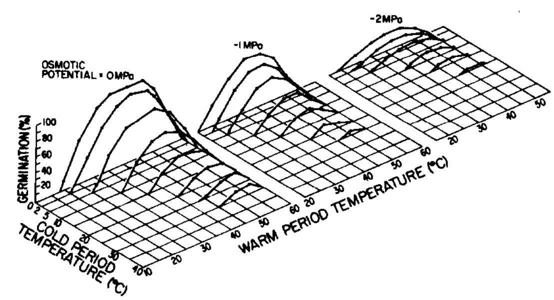

Fig. 1. *Quadratic response surface estimates of percent germination of desert saltgrass as a function of cold and warm period temperatures at 0, -1 and -2 MPa osmotic potential. The coefficient of determination (R^2) for the response surface was 0.75.*

and rate of germination was at the 0/40° C regime at each osmotic potential. No germination occurred unless there was at least a 20° C difference between cold and warm period temperatures.

Although there was a large reduction in percent germination as osmotic potential decreased, some seeds still germinated at −2 MPa

Table 1. Unsaturated and saturated soil water potential and saturation extract electrical conductivity (ECe) in the upper 3 cm of a saltgrass stand at Stillwater, Nevada in 1983.

	Topographic Position				
Sample date	Edge of lake	Middle of lake basin and saltgrass stand	Edge of lake basin and saltgrass stand	Slopes of silt dunes	Top of silt dunes
	ECe (dS m^{-1})				
March 20	0.7b[1]	2.5b	8.3b	19.6a	7.1a
June 30	2.6a	54.4a	85.9a	10.8b	11.4a
	Actual soil water potential (MPa)				
March 20	−1.05a	−0.67a	−0.95a	−5.55a	−6.23a
June 30	−0.43a	−1.59b	−7.0b	−7.0b	−7.0b
	Saturated soil water potential (MPa)				
March 20	−0.63a	−0.43a	−0.48a	−2.05b	−1.38b
June 30	−0.36a	−1.34a	−4.36b	−0.63a	0.66a

[1]Comparisons are made between dates for a given variable and topographic position. Means for dates followed by the same letter are not significantly different (p=0.05).

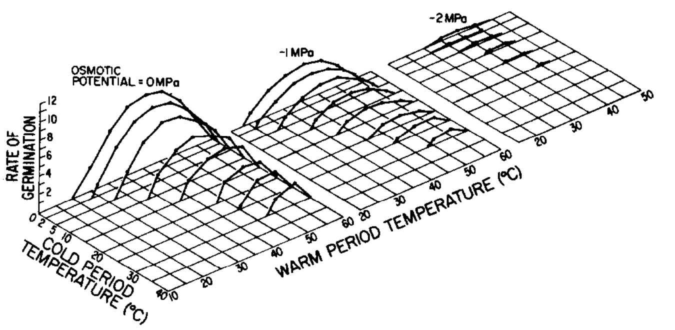

Fig. 2. *Quadratic response surface estimates of rate of germination of desert saltgrass as a function of cold and warm period temperatures at 0, -1 and -2 MPa osmotic potential. The coefficient of determination (R^2) for the response surface was 0.59.*

osmotic potential. The average reduction in total germination was from 60% at 0 MPa to 9% at -2 MPa osmotic potential. Percent germination was not reduced from 0 to -0.1 MPa. The rate of germination was reduced from 4.5 at 0 MPa to 0.3 at -2 MPa osmotic potential.

Optimum temperature regimes with average germination percentages and rates not significantly different from maximum were 0/35, 0/40, 0/45, and 2/40° C. Suboptimum regimes with lower germination responses than maximum were 0/25, 2/25, 5/25, and 5/30° C. These regimes all had at least a 20° C cold-warm period temperature differential, so reduced germination was considered to be due to suboptimum warm period temperatures.

As osmotic potential decreased, percent and rate of germination were reduced more at optimum than suboptimum temperature regimes (Fig. 3). The slope of percent and rate of germination as a

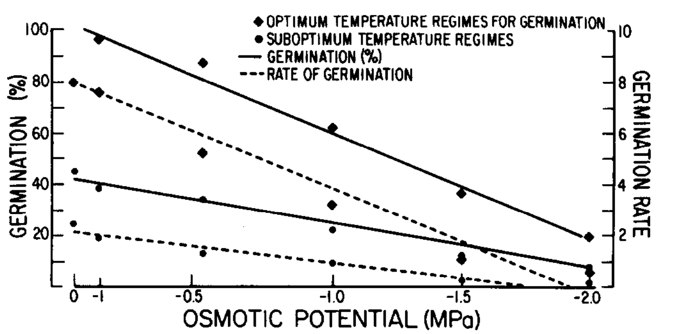

Fig. 3. *Linear regressions of percent and rate of germination of desert saltgrass seed on osmotic potential at optimal and suboptimal temperature regimes for germination. Simple correlation coefficients (R^2) were 0.97 and 0.73 for percent germination at optimum and suboptimum temperatures, and were 0.93 and 0.70 for rate of germination at optimum and suboptimum temperatures, respectively.*

function of osmotic potential (-MPa) was significantly lower for suboptimum than optimum temperature regimes (-16.7 and -41.7; -1.1 and -4.2, respectively for percent and rate of germination).

In a typical saltgrass stand, seedbed salinity and water potential varied with season and topographic position (Table 1). Generally, salinity increased and soil water potential decreased with distance and increasing elevation from standing water at the edge of the lake to the silt dunes above the lake basin. Water potential was lowest at the tops of the dunes where saltgrass was absent and highest in the middle of the stand and the edge of the lake where saltgrass was very dense. Salinity was highest at the margin of the saltgrass stand and, at the end of June, in the middle of the stand.

Salinity increased and soil water potential decreased from March to June. Soil water potentials at the edge of the saltgrass stand decreased from potentials high enough for germination to potentials far too low for germination. Soil water potentials were not significantly lower at the end of June than in March in the middle of the saltgrass stand even though salinity was higher. This was probably because the middle of the lake basin and saltgrass stand was flooded by runoff water by the end of June. At the end of June, soil water potentials averaged -1.5 MPa in the middle of the saltgrass stand. Winter precipitation for this area during the sampling year (1983) was 190% of normal (U.S. Department of Commerce 1983).

Discussion

Optimum conditions for germination of saltgrass are high water potentials and a 20° C differential in cold and warm period temperatures with warm period temperatures above 30 but less than 60° C (Cluff et al. 1983). These temperature-moisture conditions would rarely occur in saline seedbeds in the cold desert of the western United States. Surface soil water potentials decrease rapidly in the spring in the salt desert as temperatures increase and soil water from winter or spring storms evaporates (Roundy et al. 1984). Optimum temperatures for saltgrass germination occurred from May through the summer in 2 saltgrass stands measured by Cluff et al. (1983). One of these stands was that where seeds were collected and salinity and water potentials were measured in this study. In 1980, water potentials of the seedbed of this stand were never greater than -2 MPa when temperatures were optimum for germination. However, in 1983, unusually high winter precipitation resulted in flooding of the stand and high enough water potentials for germination in lower topographic positions of the stand when temperatures were optimum in June. High germination of saltgrass could occur when topographic position or weather conditions result in high seedbed water potentials in late spring and summer. Seeds in moist areas such as near the edge of a marsh or lake or depressions where water collects could have high germination. We have observed natural germination of saltgrass seeds in the summer on the beach of Pyramid Lake in the salt desert in western Nevada. Natural saltgrass stands are most dense on these moist sites and the grass apparently spreads onto more xeric or saline sites by rhizomes. High germination on xeric sites would only be expected during years of unusually high and frequent spring and summer precipitation. Due to the possibility of poor seedling survival, it may be nonadaptive for saltgrass or other halophytes to have high germination at low osmotic potentials (Roundy 1987). Chapman (1974) suggested that natural leaching of surface salts may be necessary for halophyte germination in saline soils.

The present study confirms the possibility of another way that saltgrass seeds may germinate in saline seedbeds. Some germination occurs after long incubation periods at optimum and suboptimum temperatures and low osmotic potentials. A percentage of seeds in the seed bank could eventually germinate when day and night temperatures differ by 20° C and water potentials are at least greater than -2 MPa. These conditions and saltgrass germination would most likely occur on less saline but more xeric sites in early spring and on more saline but move mesic sites in spring and early summer. Other possible mechanisms for germination of saltgrass and other halophyte seeds might be by natural stratification or osmoconditioning (Young and Evans 1981). Osmoconditioning is the soaking of seeds at controlled osmotic potentials and temperatures to allow germination processes to begin but not to allow radical emergence (Koller and Hadas 1982). Increased rate, percentage, and uniformity of germination and seedling growth are reported responses to artificial osmoconditioning (Khan et al. 1980/81). Moist, saline seedbeds in winter may naturally stratify or osmocondition saltgrass or other halophyte seeds resulting in rapid germination when temperatures increase in spring. The biological responses to natural stratification and osmoconditioning and their ecological significance in the establishment of halophytes are important subjects for future research (Roundy 1987).

The above observations suggest some recommendations for revegetation by direct seeding with saltgrass. In areas without dependable summer rain, best stands of saltgrass will be obtained by irrigation in the spring and summer when seedbed temperatures are optimum. Where irrigation is not possible, fall seeding should result in emergence of some saltgrass during early spring when temperatures are suboptimum for germination but seedbeds are still moist. The success of such nonirrigated seedings will be highly dependent on soil salinity and spring moisture conditions.

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