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Establishment of Tall Wheatgrass [*Agropyron elongatum* (Host) Beav. 'Jose'] and Basin Wildrye (*Elymus cinereus* Scribn. & Merr. 'Magnar') in Relation to Soil Water and Salinity

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NEW

ESTABLISHMENT OF TALL WHEATGRASS [LAGROPYRON ELONGATUM (HOST) BEAV.
'JOSE'] AND BASIN WILD RYE (ELYMUS CINEREUS SCRIBN. & MERR.
'MAGNAR') IN RELATION TO SOIL WATER AND SALINITY

by
Bruce A. Roundy

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Range Science

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Tall Wheatgrass in Relation to Boron

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Bruce A. Roundy

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ABSTRACT

Establishment of Tall Wheatgrass [Agropyron elongatum (Host) Beauv.
'Jose'] and Basin Wildrye (Elymus cinereus Scribn. & Merr.
'Magnar') in Relation to Soil Water and Salinity

by

Bruce A. Roundy, Doctor of Philosophy

Utah State University, 1983

Major Professor: Dr. Cyrus M. McKell
Department: Range Science

The potential of basin wildrye (Elymus cinereus Scribn. & Merr. 'Magnar') and tall wheatgrass [Agropyron elongatum (Host) Beauv. 'Jose'] to establish on saline, arid rangelands in the Great Basin in relation to soil water and salinity was compared in field and laboratory experiments. Tall wheatgrass had higher emergence and establishment on a nonsaline and a saline soil (electrical conductivity of the saturation extract of $7 \text{ dS}\cdot\text{m}^{-1}$) over a range of spring precipitation as simulated by sprinkler irrigation. Basin wildrye will require supplemental irrigation to establish on soils of similar salinity. In the absence of precipitation, soil salinity increases and matric and osmotic potentials rapidly decrease as the surface soil dries in late spring. Germination and growth responses in relation to salinity and drought in laboratory experiments were consistent with emergence and establishment results in the field experiments. Tall wheatgrass had higher total germination,

rate of germination and radicle growth under decreasing osmotic potentials and higher emergence under decreasing matric potentials than basin wildrye. Tall wheatgrass had greater root and shoot yield than basin wildrye when osmotic potentials in sand cultures were decreased by solutions of NaCl, Na₂SO₄ and CaCl₂. Tall wheatgrass is more tolerant of salt and boron than basin wildrye, but basin wildrye is highly salt tolerant compared to most forage species. Tall wheatgrass had more rapid root elongation and more extensive root growth than basin wildrye seedlings grown in 60-cm soil columns filled with nonsaline and saline soil. Germination and growth of both species was reduced by ions in addition to the effects of water stress due to low osmotic potentials. Rate of germination and radicle growth of both species was less in salts than in isosmotic polyethylene glycol solutions. Seedlings exhibited less growth in saline than nonsaline soil even when plant water stress was minimal or when leaf water potentials were low but turgor was maintained by osmotic adjustment. Germination at low osmotic and matric potentials and root elongation in relation to salinity may be important plant responses to use in evaluating the potential for establishment of new plant materials on saline, arid rangelands.

(188 pages)

INTRODUCTION AND OBJECTIVES

Many flood plains and valley bottoms in the Great Basin were once dominated by the tall and robust grass, Great Basin wildrye (Elymus cinereus Scribn. and Merr.) (Young et al. 1975). These rangelands occur below the upper and higher precipitation sagebrush (Artemisia L.) zone and due to seasonally high water tables and saline soils. Billings (1945) considered the associated plant communities to be edaphic climaxes within the shadscale [Atriplex conerifolia (Torr. and Frem.) Wats.] zone. Because basin wildrye is sensitive to spring clipping (Perry and Chapman 1976) many native stands have been ^{degraded} decimated by mowing and continuous grazing, and are now dominated by the non-beneficial phreatophytes greasewood [Sarcobatus vermiculatus (Hook.) Torr.] and salt rabbitbrush [Chrysothamnus nauseosus (Palo) Britt. ssp. consimilis (Green) Hall and Clem.] (Lesperance et al. 1978). These shrubs can be controlled by repeated herbicide applications (Cluff et al. 1983), but recovery of the forage production of some of these rangelands requires seeding to species which can emerge and persist in the associated arid and saline soils. Basin wildrye is the most likely species for reseeding due to its known adaptability, but native collections of basin wildrye have had a reputation of low seed germination and low seedling vigor (Young and Evans 1981). Recently, the U.S. Department of Agriculture Soil Conservation Service and the Idaho Agricultural Experiment Station (1979) released a cultivar of wildrye called 'Magnar' which has high and viable seed production and high germination (Evans and Young, 1983).

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Another forage species most likely adapted to saline rangelands is

tall wheatgrass [Agropyron elongatum (Host) Beav.]. Tall wheatgrass is generally used as a standard for comparison of salt tolerance of forage grasses and its salt and sodium tolerances are well documented (Carter and Peterson 1962, Dewey 1960). 'Jose' tall wheatgrass has shown promise in seeding saline arid ranges in central Nevada (unpublished research, USDA Agricultural Research Service, Reno, Nevada).

The most important environmental variables limiting plant growth on these lowland rangelands are those associated with limited water. Precipitation is usually less than 30 cm annually, and mainly falls prior to, or early in the growing season in winter and early spring. Low soil matric potentials due to lack of precipitation and low soil osmotic potentials due to soil salinity also limit water availability to plants on these ranges. Specific ions may also occur in high enough concentrations to be toxic to plant growth.

Although mature plants may be able to persist in these conditions, successful seeding will only be possible if plants can initially germinate, emerge and survive with these limiting factors.

The purpose of this study was to compare field and laboratory responses of Jose tall wheatgrass and Magnar basin wildrye to soil water and salinity to determine which species is most suited to seeding saline, arid Great Basin soils. Determination of plant characteristics and responses best associated with successful seedling establishment will help in the future selection of adapted plant materials and help to avoid costly seeding failures.

Main objectives included:

- 1) To determine the effects of winter and spring precipitation and irrigation on salinity, penetrability, and matric and osmotic potentials of saline and nonsaline lowland soils known to support basin wildrye.

- 2) To determine the accuracy of osmotic and matric potential estimates from thermocouple psychrometer measurements of total soil water potential and soil saturation extract electrical conductivity measurements of salinity.
- 3) To determine the effects of winter and spring precipitation, irrigation, and soil salinity on seedling emergence and establishment.
- 4) To determine the effects of soil matric and osmotic potentials on seed germination, emergence and radicle growth.
- 5) To determine the effects of boron on germination and seedling growth and survival.
- 6) To determine the effects of salinity and drought on seedling shoot and root growth and osmotic adjustment.

The overall hypothesis is that because growing season precipitation is limited and erratic, seedbed water potentials decrease rapidly, therefore, to successfully establish on saline, arid soils, species must be able to germinate and grow under decreasing soil osmotic and matric potentials.

Detailed hypotheses include:

- I. Water potential components can be accurately estimated from psychrometer measurements of total water potential and electrical conductivity measurements.
 - A. Due to predominantly soluble salts, soil osmotic potential decreases linearly with soil water content.
 - B. Saturation extract electrical conductivity can be accurately estimated from electrical conductivity measurements of the saturated paste.

- C. Solution osmotic potential can be accurately estimated from electrical conductivity measurements.
 - D. Matric potentials estimated from total water potential measurements and osmotic potential estimates from electrical conductivity measurements are similar to those determined using a pressure plate.
- II. Precipitation, soil salinity and soil microtopography affect seedbed water potentials during the growing season.
- A. Precipitation maintains high seedbed total water potentials by increasing soil water content and leaching salts, thereby maintaining high soil matric and osmotic potentials.
 - B. Saline soils have lower total water potentials than nonsaline soils due to osmotic potential.
 - C. Shrub mound soils have similar water potential and salinity, but greater penetrability than interspace soils.
 - D. Precipitation increases penetrability of interspace soils.
- III. Precipitation, soil salinity, and soil microtopography affect seedling emergence and establishment.
- A. Precipitation increases seedling emergence and establishment.
 - B. Soil salinity decreases seedling emergence and establishment.
 - C. Seedling emergence is higher on mound than interspace soils.
 - D. Magnar basin wildrye and Jose tall wheatgrass differ in emergence and establishment in response to precipitation and soil salinity.
- IV. The ability to germinate under decreasing water potentials is important for successful emergence on saline, arid soils.
- A. The species that has the highest emergence in the field has

higher germination and germinates at lower matric and osmotic potentials than the other species.

- B. Germination under low osmotic potentials is similar to that at low matric potentials.
 - C. Salinity decreases germination by reducing the osmotic potential and not by ionic effects.
- V. The ability to osmotically adjust and grow at decreasing soil osmotic potentials is important to seedling survival in saline, arid soils.
- A. The species that has greater establishment and survival on a saline soil in the field also has greater root and shoot yield under decreasing soil osmotic potentials..
 - B. Osmotic adjustment maintains growth under low soil osmotic potentials.
 - C. Growth is decreased by decreasing osmotic potentials, not by specific ions. That is, growth is similar at isosmotic potentials decreased by different salts.
 - D. Osmotic adjustment is similar for both species and similar for plants water stressed by salination or drought.
- VI. The ability to rapidly elongate roots under decreasing soil osmotic and matric potentials is important to seedling survival in saline, arid soils.
- A. The species that has greater establishment and survival in the field also has more rapid root elongation and is able to grow at lower soil water potentials.
 - B. Osmotic adjustment and growth are similar for plants in non-saline and saline soil as matric potential decreases.

VII. Boron tolerance is important to seedling emergence and establishment on saline, arid soils.

A. Boron concentrations in the field are high enough to decrease germination and growth of seedlings.

B. The species with the higher emergence and survival in the field also has the greater germination and growth under high boron concentrations.

The objectives and hypotheses are addressed in a series of experiments reported in seven chapters which were prepared as separate manuscripts to be published in different scientific journals.

REVIEW OF LITERATURE

Environment and Limiting Factors

Precipitation

The environment of saline deserts has been characterized by Caldwell (1974) ^{and West (1983)} as having high seasonal temperature and precipitation fluctuations resulting in a short period of time when active growth is not limited by extreme temperatures and lack of moisture. In the northern valleys of the Great Basin, precipitation mainly falls in late fall, winter, and spring (Johnson 1980). Precipitation in March through June may be most critical to seedling establishment since during these months temperatures generally became high enough for germination and plant growth. Storms resulting in appreciable precipitation are generally infrequent in April and May and become even less frequent in June (Gifford et al. 1967). As temperatures increase, the lack of frequent precipitation may result in rapidly decreasing surface soil matric potentials which may limit seed germination in early spring and low root zone matric potentials which may limit seedling survival in the late spring.

Edaphic Factors

Physical and chemical characteristics of lowland Great Basin soils may limit seedling emergence and survival by their effect on soil water potential or by directly decreasing germination and growth. The internal drainage of the Great Basin has resulted in an accumulation of salts and fine sediments in the many closed basins created by basin and range faulting ^{beginning} in the Miocene (Papke 1976) ^{Branson et al 1983}. Although the associated fine-textured soils have high water holding capacity, they may limit soil

water availability due to low infiltration and low hydraulic conductivity resulting from high particle dispersion due to low organic matter (Blackburn 1975) or high sodicity (Hayward and Wadleigh 1949). The lack of organic matter additions and repeated wetting and drying (Miller 1971) may cause these fine-textured soils to form a platy to massive vesicular crust which decreases soil penetrability and may restrict seedling emergence in interspaces between shrub mounds. Unstable interspace soil may slake when saturated and completely fill deep furrows, burying seeds too deep for emergence (Eckert et al. 1978).

The accumulated salts of these lowland soils may limit germination and seedling growth by decreasing the soil solution osmotic potential or by entering the seed or plant and interfering with physiological processes (Hayward and Wadleigh 1949). The osmotic potential of the soil solution is a function of the concentration of specific ions in the soil solution. Sodium sulfate and chloride salts are dominant in these soils with little calcium (Ca) and magnesium (Mg) (Shantz and Piemeisel 1940, Kelley 1951, Gates ^{et al} 1956, Stuart et al. 1971). Since these sodium salts are highly soluble, the soil solution osmotic potential should decrease almost linearly with decreasing soil water content to fairly low osmotic potential. High boron (B) concentrations have also been reported for these lowland soils (Robinson 1970).

Surface soil salinity may vary with season and precipitation and capillary rise from the water table as related to soil morphology and texture (Jackson et al. 1956). High winter precipitation may increase surface salinity raising the water table so the capillary fringe is near the soil surface and salts are deposited on the surface as water evaporates (Richards 1954). If the water table is deep or evapotranspiration

breaks the capillary chain, surface salinization stops (Jackson et al. 1956). Lowland Great Basin soils vary in amount and vertical concentration of salts due to differences in depth to the water table as related to topographic position and drainage patterns. Spring precipitation may increase soil osmotic potential by leaching salts accumulated in the surface soil or by removing them in run off water and by diluting the soil solution. Teakle and Burvill (1938) found substantial leaching of salts in sandy and medium-textured soils but not on heavy-textured soils. In the Thar desert, India, rainy season precipitation leached salts and increased subsurface soil moisture, resulting in increased plant and soil osmotic potentials (Rajpurohit and Sen 1980). Zallar and Mitchell (1970) suggested that autumn rains leached salts on dry hard-pan sites in Australia, allowing germination and establishment of salt-tolerant grasses. Soil salinity and sodicity decreased after contour furrowing in southeastern Montana presumably due to increased infiltration and leaching (Soiseth et al. 1974). Spring rains could also decrease the osmotic potential of the subsurface soil solution by washing down salts that have precipitated out on the soil surface.

Spatial Variability

Soil matric and osmotic potentials and salinity may vary greatly spatially on lowland rangelands due to location of beach ridges, drainages and springs, resulting in large differences in site potential for plant establishment.

On a particular site, seedling establishment may vary greatly between mounds of soil and litter accumulations under shrubs and interspaces between mounds (Eckert et al. 1978, Rollins et al. 1968, Schlatterer and Hironaka 1972). These differences in seedling establishment associated

with microtopographical differences can be attributed to differences in physical and chemical properties of mound and interspace soils. Regular organic matter additions from shrub litter fall result in the friable, well aggregated and more fertile soil of mounds that have high infiltration rates (Blackburn 1975, Eckert et al. 1978). However, due to slightly higher microtopographical elevation and salt accumulation in the leaves of some shrubs such as greasewood and shadscale, mounds may have higher total salinity, sodicity and B concentrations than interspace soils (Roberts 1950, Fireman and Hayward 1952, Eckert and Kinsinger 1960, Rickard et al. 1973). Coarse-textured mound soils may be leached and therefore lower in salinity, sodicity and B than fine-textured interspace soils (Stuart et al. 1971, Rollins et al. 1968). Higher fertility of mound soils (Rickard et al. 1973, Charley and West 1975) may allow optimum shoot and root growth when soil moisture is available. Greater plant growth due to higher fertility of mound soils could result in faster moisture depletion and a shorter period when soil moisture is available for growth (Schatterer and Hironaka 1972).

Emergence and Survival of Seedlings

Seedling establishment in deserts may occur sporadically due to one or a culmination of favorable moisture events (Noy-Meir 1973). Years of high seedling establishment may be the product of weather conditions favoring high seed set, germination and seedling survival (Went 1955). ^{West 1980} Ries et al. (1976) have suggested that irrigation may be necessary to establish perennial species where precipitation during the establishment period may be highly variable. Seedling emergence may be high early in the spring due to winter and spring precipitation, but survival on arid and saline

soils is often very low during the first summer due to low and irregular rainfall, low humidity, high evaporation, soil salinity and high diurnal temperature fluctuations (Bleak et al. 1965, Wein and West 1971).

To establish on arid, saline soils, plants must be tolerant of drought and salinity. Although crested wheatgrass [Agropyron desertorum (Fisch. ex Link) Shutt] is known for its ability to establish under very dry conditions, it has failed to establish on saline soils (Haas et al. 1962, Shown et al. 1969). Tall wheatgrass has established well on some saline soils, but it may not persist on dry, saline soils (Forsberg 1953, Ludwig and McGinnies 1978, McGinnies and Ludwig 1978, and McPhie 1973) and is apparently more salt tolerant, but less drought tolerant than slender wheatgrass [A. trachycaulum (Link.)], Russian wildrye (Elymus junceus Fisch.) and crested wheatgrass. Young and Evans (1981) suggested that many of the sites where basin wildrye occurred naturally are too dry for tall wheatgrass and too saline for crested wheatgrass.

Tall wheatgrass and basin wildrye seeded on a saline/alkaline, greasewood/rabbitbrush [Chrysothamnus nauseosus (Pall.) Britton] site in central Nevada emerged, but did not survive without irrigation (Eckert et al. 1973, Rollins et al. 1968, Stuart et al. 1973). Higher establishment occurred with two irrigations per week than with one irrigation per week. Seedlings were successful and productive with irrigation on mound soils, but not on interspace soils due to high B, salinity, and sodicity. Surface electrical conductivity of the saturation extract (ECe) of the mounds ranged from 0.7 to 8.5 dS·m⁻¹ while that of the interspaces ranged from 3.4 to 103 dS·m⁻¹. Irrigation leached much of the B and soluble salts from the mound soils, but not from the interspace soils, due to the low infiltration rates of the associated vesicular soil crust. Stuart et al. (1973) reported that tall wheatgrass produced more seedlings and higher

yields than basin wildrye, and that yield and survival was greatly reduced when irrigation was terminated after 4 years. Apparently, the grass roots were unable to penetrate the duripan at 50 to 85 cm and tap water from the capillary fringe of the water table (Eckert et al. 1973).

Plant Responses to Salinity and Low Matric and Osmotic Potentials

To emerge and survive in lowland Great Basin soils, seeds and seedlings must either be able to avoid or tolerate high concentrations of certain ions and moisture stress due to low soil water potentials and high atmospheric moisture demands.

Germination

Seed germination is influenced by the direct effects of low water potentials on seed hydration as well as indirect effects associated with low soil matric and osmotic potentials. Seeds of different species may have different critical water potentials of hydration levels below which the physiological processes of germination are slowed or prevented (Hillel 1972, Hadas and Stibbe 1973). This direct effect of water potential on germination can be tested by determining germination responses in polyethylene glycols (PEG) of high molecular weight which do not enter the seed or by allowing seeds to imbibe to different water potentials and noting subsequent germination. Polyethylene glycol of molecular weight 6000 (PEG-6000) is generally preferred to that of molecular weight 20,000 (PEG-20,000) for testing seed germination. Hadas (1976) found no difference in water uptake between seeds soaked in PEG-6000 and in PEG-20,000, but the density and viscosity of PEG-20,000 caused stirring and aeration problems.

When seeds are incubated in solutions with osmotic potentials reduced by salts, ion entry into the seed may increase or decrease germination, depending on the toxicity of ions to the species. Entering ions lower the seed osmotic potential, which facilitates hydration of the seed (Sharma 1973) by allowing a higher seed matric potential than the osmotic potential of the solution surrounding the seed. The extent to which this favorable effect of increased hydration is equally or dominantly offset by interference of the ions with germination processes varies with the species and salts (Ungar 1978) and can be tested by comparing the germination in PEG versus germination in different salts at isosmotic potentials. Rauser and Crowle (1963) found tall wheatgrass and slender wheatgrass germination to be inhibited by the osmotic stress caused by sodium sulfate (Na_2SO_4), sodium chloride (NaCl), and calcium chloride (CaCl_2), rather than by toxicity to these salts. In that study, tall wheatgrass germination was reduced to 50% by an average osmotic potential of $-1250 \text{ J}\cdot\text{kg}^{-1}$ and germination was higher in NaCl and CaCl_2 than in PEG. Harradine (1982) also found tall wheatgrass had higher germination in NaCl (72.5%) than in PEG-6000 (37.5%) at an osmotic potential of $-1500 \text{ J}\cdot\text{kg}^{-1}$ and noted that the germination rate of tall wheatgrass decreased more than total germination with decreasing NaCl solution osmotic potential. A saline solution mixture of NaCl , CaCl_2 and magnesium chloride (MgCl_2) with a sodium absorption ratio (SAR) of 20 depressed germination rate and seedling radicle and plumule length more than total germination of tall wheatgrass at osmotic potentials of -435 to $-537 \text{ J}\cdot\text{kg}^{-1}$ (Moursi et al. 1977). Carter and Peterson (1962) found tall wheatgrass to germinate well at an exchangeable sodium percentage (ESP) of 60%, but germination time was increased by 1 to 2 days. Dewey (1960) found

three strains of tall wheatgrass germinated at 32, 33.1 and 53.6% at an ECe of $16.2 \text{ dS}\cdot\text{m}^{-1}$ and McElgunn and Lawrence (1973) found tall wheatgrass emergence was reduced by 50% at an ECe of 17 to $18 \text{ dS}\cdot\text{m}^{-1}$. Tall wheatgrass and basin wildrye emergence through wax crusts at osmotic potentials decreased by NaCl was compared by Frelich et al. (1973). Tall wheatgrass had greater emergence through the hard crust and at osmotic potentials of -670 and $-840 \text{ J}\cdot\text{kg}^{-1}$ than basin wildrye.

Choudhuri (1968) compared germination of a nonsaline and a saline soil seed source of basin wildrye in NaCl, sodium carbonate (Na_2CO_3) Na_2SO_4 , PEG-400, and pond water solutions at osmotic potentials from -51 to $-547 \text{ J}\cdot\text{kg}^{-1}$. The decreasing order of toxicity for both seed sources was pond water $< \text{NaCl} < \text{Na}_2\text{SO}_4 < \text{Na}_2\text{CO}_3 < \text{PEG-400}$. Germination of the saline collection was higher than that of the nonsaline collection only in solutions of Na_2CO_3 and Na_2SO_4 . Germination was greatly reduced at osmotic potentials of -253 to $456 \text{ J}\cdot\text{kg}^{-1}$. Young and Evans (1981) found germination of basin wildrye seeds at NaCl or PEG-6000 reduced osmotic potentials was negatively correlated with the ECe and SAR of the surface soils where the 20 different seed samples were collected. ~~In this study, NaCl reduced germination more than PEG and the greatest reduction in germination occurred at osmotic potentials from -400 to $-800 \text{ J}\cdot\text{kg}^{-1}$.~~ *to Results*

In addition to the direct effect of low water potentials on seed hydration, low soil matric potentials may reduce water entry into the seed by reduced seed-soil contact and lowered soil hydraulic conductivity (Sharma 1973, Hadas and Russo 1974a,b; Thill et al. 1979). Germination in soil can also be reduced due to seed microbial damage (Sharma 1973) or for some seeds the presence of an air gap between the seed coat and the pericarp (McWilliam and Phillips 1971). Germination of tall

wheatgrass and basin wildrye in soil at reduced matric potentials has not been studied. It has been suggested that species which can germinate and survive cool temperatures are more likely to establish on arid rangelands where soil water potential is high early in the spring when soil temperatures are low by growing sufficiently to withstand the summer drought (Young and Evans 1982).

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Growth and Survival

Since germination and seedling or mature plant tolerance of salinity and low soil osmotic potentials may not be correlated for a particular plant material (Manohar et al. 1968, McGinnies 1960, Sharma 1973) both germination and plant growth and survival studies are necessary in evaluating adaptability to saline, arid soils. Magnar basin wildrye has similar germination as Jose tall wheatgrass at moderate and colder than moderate temperature regimes considered representative of spring seedbed temperatures on sagebrush rangelands (Young and Evans 1982). Both ability of seeds to germinate at reduced matric potentials and ability of seedlings to tolerate or avoid low soil matric potentials are important in determining species establishment potential on arid rangelands.

The same characteristics of saline or saline/alkaline soils that depress seed germination also have a negative effect on plant growth and survival. Epstein (1972) Hayward and Wadleigh (1949), and Magistad (1945), have discussed these factors. Low osmotic potentials of saline solutions make it necessary that plants maintain intracellular osmotic potentials even lower than the substrate to prevent desiccation. To adjust osmotic potential downward, plants commonly absorb solutes or, less frequently, synthesize solutes.

Additional reviews of osmotic adjustment, turgor maintenance (Hsiao et al. 1976, Turner and Jones 1980) and salinity tolerance (Poljakoff-Mayber and Gale 1975) support the idea that plant growth under low soil osmotic potentials is dependent on osmotic adjustment to maintain turgor necessary for cell elongation and tolerance of high concentrations of specific ions taken up and possibly used in osmotic adjustment. Ions accumulated in plants:

"may disrupt the structure of enzymes of other macromolecules, may damage cellular organelles, may affect photosynthesis and respiration, may inhibit protein synthesis, and may cause ion deficiencies...". (Epstein 1972 p. 369-370).

The most common cause of specific ion toxicity is that of sodium and its tendency at high ESP's to induce calcium deficiencies (Hayward and Wadleigh 1949, Magistad 1945, Ratner 1935). Elzam and Epstein (1969) found that sharp decreases in root yield of tall wheatgrass associated with salination from 50 to 100 mM NaCl also coincided with a sharp decrease of Ca in the roots. They suggested that some salt damage may be due to lack of Ca to maintain the integrity of the cell membrane for the selective absorption of potassium (K) in the presence of sodium (Na). Pearson and Bernstein (1958) found little decrease in yield of tall wheatgrass with increasing ESP up to 50% even though Na increased and Ca decreased in leaf blades. They reported a 50% yield reduction in tall wheatgrass at an ESP of 64%. Carter and Peterson (1962) also reported that tall wheatgrass grew and produced well in the field at ESP's of 50 to 60%. Evidently, tall wheatgrass has high tolerance to sodium. However, Shannon (1978) found that the most salt tolerant lines of tall wheatgrass restricted accumulation of Na in the root and Na, Ca and Cl in the shoot and had higher soluble sugar contents than less tolerant lines. He suggested that ion uptake and proline and soluble sugar increases all

contributed to osmotic adjustment of tall wheatgrass lines. Sodium tolerance of basin wildrye has not been separated from effects of decreasing osmotic potential. Choudhuri (1968) reported 50% mortality of basin wildrye seedlings from nonsaline and saline soils at an average osmotic potential and sodium concentration of the saturation extract of $-1103 \text{ J}\cdot\text{kg}^{-1}$ and 4123 ppm, respectively.

Excessive Ca may also reduce plant growth by creating nutritional imbalances or by lowering the soil osmotic potential (Levitt 1980).

Tall wheatgrass is tolerant of high B concentration having a yield reduction of 50% at an average of 35 ppm of B in nutrient cultures and surviving at 150 ppm (Schuman 1969).

Numerous studies have quantified the yield responses of tall wheatgrass to increasing salinity and decreasing osmotic potentials. Although plant yield responses to salinity are influenced by stage of growth, soil fertility, soil solution ionic mix and specific ion toxicity, temperature and relative humidity and soil water content and aeration (Maas and Hoffman 1977), all studies agree that tall wheatgrass has very high salt tolerance. Salt tolerance indices (ECe where 50% reduction in yield occurs) of 13 (Moxley et al. 1978), 14 (Dewey 1960), and 18 (Berstein 1964) $\text{dS}\cdot\text{m}^{-1}$ have been reported for tall wheatgrass. Data of McElgunn and Lawrence (1973) indicate higher salt tolerance indices of 20 and 34 $\text{dS}\cdot\text{m}^{-1}$ for tall wheatgrass roots and shoots, respectively. Moxley et al. (1978) reported reduction in the yield of Jose tall wheatgrass did not occur below 6 $\text{dS}\cdot\text{m}^{-1}$ while yield reductions of 25, 70 and 83% occurred at ECe's of 10, 15, and 20 $\text{dS}\cdot\text{m}^{-1}$, respectively. Maas and Hoffman (1977) gave tall wheatgrass the highest qualitative salt tolerance rating and reported the maximum allowable ECe without yield reduction to be 7.5 $\text{dS}\cdot\text{m}^{-1}$ and listed a 4.2% reduction in yield of tall wheatgrass per unit increase

relevant here?

in salinity (E_{ce} in $dS \cdot m^{-1}$) above that threshold. Rauser and Crowle (1963) noted that tall wheatgrass, slender wheatgrass, and Russian wildrye established and persisted in soil with $-450 J \cdot kg^{-1}$ osmotic potential or an E_{ce} of $12 dS \cdot m^{-1}$, (~~Rauser and Crowle 1963~~). At high salt concentrations (8 to $16 dS \cdot m^{-1}$) slender wheatgrass yields were reduced, but tall wheatgrass and Russian wildrye yields were not reduced. Forsberg (1953) reported tall wheatgrass grew in saline soils at E_{ce} 's up to $15.3 dS \cdot m^{-1}$. Other than the data of Choudhuri (1968) reported above, little is known of the salt tolerance of basin wildrye.

Since growth is highly dependent on turgor pressure as the physical force which sustains cell enlargement (Hsiao et al. 1976), the ability to maintain turgor over a range of water stress may result in greater growth over that stress range (Johnson and Brown 1977) and possibly greater seedling survival. Turgor maintenance by osmotic adjustment is affected by the rate of development (Begg and Turner 1976) and degree of water stress, and the light and temperature environment (Turner and Jones 1980). Losses in turgor associated with large decreases in growth may indicate that the turgor pressure has fallen below some critical turgor necessary for cell elongation (Cleland 1971, Loescher et al. 1973) or that ionic imbalances or energy expenditures associated with osmotic adjustment are limiting growth (Bernstein 1963, Hsiao et al. 1976). A threshold turgor pressure may be necessary for biochemical modification of cell wall properties to take place and provide the force for cell wall extension (Cleland 1971). Decreases in cell osmotic potentials that maintain turgor may reduce growth by affecting enzymes that are sensitive to low osmotic potentials, high salt concentration, or specific ions (Bernstein 1963). These observations indicate that the ability of plants

to maintain turgor at reduced soil osmotic potentials may be indicative of their salinity tolerance. In fact, the discovery of Morgan (1977) that certain cultivars of wheat showed osmotic adjustment compared to no adjustment by other cultivars led him to suggest that breeding for osmotic adjustment might improve drought tolerance in wheat. Johnson and Brown (1977) initially found ability of Agropyron Gaertn. hybrids, Zea mays L. and Bromus inermis Leyss. to maintain positive turgor at reduced leaf water potential was correlated with field observations of resistance to plant water stress. In a later study, Johnson (1978) discovered that the ability of certain range grasses to maintain turgor at low leaf water potentials and associated species drought tolerance rankings varied with the temperature environment. In that study, basin wildrye had zero turgor at leaf water potentials of -1360, -1620, and -2200 J.kg⁻¹ for night/day temperatures of 15/25, 10/15 and 5/10°C, respectively.

Although the total water potential of the soil is generally considered to be the sum of the osmotic and matric components (Brown 1977) the effects of these two components on plant growth and development may not be equal (Goodin 1977).

Plants in wet, saline soils which can take up and tolerate ions may osmotically adjust to maintain positive turgor at lower soil osmotic potentials than they could at similar soil matric potentials. Greater water flow to the roots would be expected on wet, saline soils than in dry, nonsaline soils of the same total water potential due to the increased hydraulic conductivity (Hanks and Ashcroft 1980) and root penetrability (Greacen 1972) of wet soils. Sepaskha and Boersma (1979) found root elongation rates of wheat seedlings to be limited by low soil matric potential more than by low osmotic potential. Also, the

development of water stress may be more rapid in nonsaline, dry soils than saline, wet soils, due to the rapid decrease in soil matric potentials as water content decreases beyond a certain point as indicated by the logarithmic form of most moisture release curves (Hanks and Ashcroft 1980).

Interactions of salinity and drought on saline, arid soils may be complex (Goodin 1977). Caldwell (1974) has suggested availability of ions for uptake and accumulation may aid in osmotic adjustment to low soil water potentials. However, in soils with highly soluble salts, salt concentrations increase and soil solution osmotic potentials decrease almost linearly to a point with decreasing soil water content (Richards 1954). Thus, the decrease in matric and osmotic potentials of saline soils may result in very low total water potentials as soil water content decreases.

Seedling survival on arid, saline soils may be a function of tolerance to low soil osmotic potentials and avoidance of low soil matric potentials. Seedlings that can maintain growth under low osmotic, high matric potentials of saline soils recharged by winter precipitation may later avoid much lower matric and osmotic potentials by sending their roots below the upper soil-drying front. To test this hypothesis the correlation between seedling responses to decreasing osmotic and matric potentials in controlled experiments and field survival associated with measured soil osmotic and matric potentials would need to be determined.

Harris (1977) showed that elongation of roots at cool temperatures was important to establishment of grasses by keeping roots below the soil drying front and thereby avoiding severe drought. Elongation of roots at low osmotic potentials may be of similar importance to plant establishment on saline, arid soils.

Plants in the lower osmotic potentials of saline soils may have reduced growth and reduced transpiration resulting in decreased soil moisture depletion and a longer period of high matric potentials than plants in nonsaline soils (Stark and Jarrell 1980). Stark and Jarrell (1980) citing Gale (1975) and Maas and Nieman (1978) have listed the salinity-induced changes in plants that help maintain a favorable water balance by reducing plant water use. These include physiological adjustments such as osmotic adjustment and morphological adjustments such as smaller and fewer leaves, lower stomatal density,

"...increased leaf succulence, earlier lignification of roots, thickening of leaf cuticles and surface wax layers and reduced water conduction due to impaired development of vascular tissue" (Stark and Jarrell 1980, p. 745).

These authors found that maize with a salinity pretreatment had continued leaf elongation at lower predawn leaf water potentials as water stress increased than did unsalinized plants. Jensen (1982) found that salinization of barley before a drying cycle resulted in slower soil desiccation and an increased growth period, but no differences in yields, transpiration coefficients or wilting percentages compared to unsalinized plants. He speculated that the delay in water uptake due to salinity may be advantageous when the water supply is limited by intermittent periods of drought. Wright (1964) found drought tolerance rankings of seedlings as indicated by survival as a function of stress days (days that plants were unwatered and kept in a growth chamber programmed to represent field temperatures) was the same as field observation rankings. Seedling recovery after desiccation may be dependent on the period and environment of desiccation and, as Begg and Turner (1976) and Johnson (1980) have noted, could be greatly affected by the rate of stress development which is accelerated by restriction of roots in small containers.

Salinity may increase recovery after desiccation by reducing water use and thereby decreasing the period and rate of desiccation between moisture events.

ESTIMATION OF WATER POTENTIAL COMPONENTS OF
SALINE SOILS OF GREAT BASIN RANGELANDS

Introduction

Availability of water for seed germination and plant growth is of primary interest to scientists and managers of semiarid and arid rangelands. Soil water availability on these rangelands is the most important limiting factor to plant growth and survival and is also considered the most important determinant of vegetation distribution (Brown 1977). Because water moves through the soil and into, through, and out of plants along a potential energy gradient, it is most useful to quantify soil water in units of potential energy. The potential energy of soil water or the water potential can be described by:

$$\Psi_t = \Psi_m + \Psi_s + \Psi_g + \Psi_p.$$

Where Ψ_t is the total soil water potential, Ψ_m is the matric potential, Ψ_s is the solute or osmotic potential, Ψ_g is the gravitational potential, and Ψ_p is the pressure potential. The matric and solute water potential components are of most importance in considering availability of water to plants and represent the reduction in the free energy of water due to interactions with soil particles and soil solutes, respectively. Although in general, plants respond to the sum of the solute and matric potential (Maas and Hoffman 1977), some salt tolerant plants can osmotically adjust to low soil solute potentials by taking up and tolerating specific ions (Jefferies 1981). It may be possible that these plants can tolerate much lower soil solute than matric potentials.

Some drought tolerant plants may grow at or avoid low matric potentials, but may be very sensitive to specific ions associated with saline soils.

Quantification of the matric and solute components of the total soil water potential in relation to plant response on specific saline arid soils is important in assessing plant drought and salinity tolerance and is necessary to predict adaptability to other soils differing in salinity and soil water conditions. Numerous methods of quantifying soil matric and solute potentials have been described and are reviewed by Slavik (1974). Most commonly, the matric potential of saline soils at high matric potentials is measured directly by tensiometers, whereas the matric potential of drier saline soils is estimated from water content measurements after determining the moisture release curve with a pressure plate. However, due to hysteresis, estimates of matric potential from water content measurements may be very inaccurate (Taylor et al. 1961). Matric potential may also be calculated from measurements or estimates of the soil solute potential and the total soil water potential. Psychrometers are generally used to measure the total soil water potential of saline soils. The most accurate determinations of the solute potential of the soil solution are made after extracting the solution at actual water content or by using an in situ salinity sensor (Ingvalson et al. 1970) calibrated to solute potential. Soil solutions are extracted at actual water contents by a large heavy-duty press or by collecting the soil solution of a sample that has been displaced by adding water or some other liquid to the top of the sample (Adams 1974). These extraction techniques are limited to soils with high water contents as are salinity sensor measurements (Sands and Reid 1980). Oster et al. (1969) made very precise measurements of solute and matric

potentials by using a pressure chamber and a thermocouple psychrometer. A sensor developed by Scholl (1978) shows promise for relatively easy in situ determination of matric potentials and salinity. The sensor must be calibrated for a range of salinities and matric potentials.

Many of these methods of determining soil matric and solute potentials are time-consuming and impractical for rangeland applications, due to the need to make determinations for many samples from different locations, depths, and times in relation to precipitation to characterize soil water availability.

One method that can provide relatively rapid estimates of soil solute potential is that of linear dilution. Solute potential (ψ_s , in $J \cdot kg^{-1}$) is calculated from the electrical conductivity of the saturation extract (E_{ce} , in $dS \cdot m^{-1}$), the actual and saturation volumetric water contents (θ_{va} and θ_{vs} , respectively), and the coefficient of Richards (1954) which is based on the work of Campbell et al. (1948) relating E_{ce} to solution potential:

$$\psi_s = -\left(\frac{\theta_{vs}}{\theta_{va}}\right) \times E_{ce} \times 36.$$

Because the solute potential is a function of the moles of ions and salts in solution, this method assumes that the molality of the soil solution is directly proportional to the solution concentration and that the ionic composition of the saturation extract is the same as that of the soil solution at actual water content. Both of these assumptions are incorrect. Reitemeier (1946) showed that the soluble contents of Ca, Mg, Na, K, carbonate (CO_3), bicarbonate (HCO_3), and sulfate (SO_4) generally increase after soil dilution with water. These changes in ionic composition of the soil solution upon dilution are due to cation exchange reactions and changes in activity and solubility of salts (Oster and McNeal 1971, Adams 1974).

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Linear dilution has given reasonable estimates of solute potential in some soils (Sands and Reid 1980) but has underestimated (estimated too negative) the solute potential of other soils (Krahn and Fredlund 1972). Although precipitation of salts may result in solute potentials less negative than estimated by linear dilution, anion exclusion (Oster et al. 1969) would tend to result in solute potentials more negative than estimated by linear dilution. Linear dilution would be expected to give reasonable estimates of solute potential for saline-sodic soils in which soluble salts dominate. The purpose of this article is to report the use of psychrometric measurements and linear dilution calculations from ECE measurements to determine water potential components of a saline-sodic rangeland soil.

Methods

In conjunction with a seedling establishment study on basin wildrye and tall wheatgrass¹ over 400 soil samples each were taken from a saline and nonsaline rangeland soil in central Nevada from March to August of 1982. The saline soil is on the lake plain and the nonsaline soil is in a lagoon (Peterson 1981) of Pleistocene Lake Gilbert in Grass Valley, Nevada. The saline soil is a Gund silt-loam series identified as being a member of the fine-silty over clayey, mixed (calcareous), mesic family of Aquic Durorthidic Torriorthents (Appendix, Table 16) and the nonsaline soil is a member of the fine, montmorillonitic, mesic family of Typic Camborthids (Appendix, Table 17). Soil samples were taken with a 2-cm-diameter auger for depth intervals of 1-5, 5-10, 10-15, and 25-30 cm.

¹ Roundy, B.A. 1983. Emergence and establishment of tall wheatgrass and basin wildrye in relation to moisture and salinity. J. Range Manage. (submitted).

On each of eight dates four sets of samples were taken at each of four distances from a single sprinkler which was used to simulate a gradient in spring precipitation on the saline and nonsaline soil. Immediately after removal, the soil samples were placed in 3-cm diameter glass bottles which were 6 cm deep, and were covered with parafilm and capped. Bottles were stored at 5°C and allowed to warm to room temperature just before analysis to avoid condensation problems. Approximately 2 g of each soil sample were placed in psychrometer chambers described by Brown and Collins (1980). Total water potential of the subsamples was measured after a 4-hour equilibration period in a 25°C water bath held at constant temperature. The total water potential of the soil sample was calculated from psychrometer microvolt output after a 15-sec cool period by using the model of Brown and Bartos (1982) adjusted for individual psychrometer calibrations against NaCl solutions of known solute potential (Lang 1967).

Immediately after removing the 2-g subsample for total water potential determination, each soil sample was weighed, dried at 105°C for 24 hr, and reweighed to determine gravimetric water content. An average bulk density of $0.99 \text{ g}\cdot\text{cm}^{-3}$ was determined from twelve 0-30 cm soil samples and was used to calculate volumetric from gravimetric water content. Distilled water was then added to the oven-dried samples of the saline soil to make a saturated paste. The electrical conductivity of a small sample of the saturated paste (EC_p) was read with a GLA M33² instant salinity meter. This meter allows rapid determination of the electrical

² The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Dept. of Agriculture of any product or service to the exclusion of others that may be suitable.

conductivity (EC) of small samples of pastes and solutions and automatically corrects the readings from EC at actual temperature to EC at 25°C. The EC_p was converted to EC_e by using a linear regression of the two conductivities for 33 samples (Figure 1). Solute potential was calculated by linear dilution by using an average saturation volumetric water content of 0.51 as determined from twelve 0-30 cm soil samples. Matric potential of the saline soil was calculated as the difference between total and solute potential while that of the nonsaline soil was considered the same as the total soil water potential. Means of the four replications of each set of samples were calculated for total, solute and matric potential, volumetric water content, and EC_e. Means of matric potential were regressed on means of volumetric water content to obtain estimated moisture release curves for the saline and nonsaline soils.

Additionally, 10 large soil samples of each of the saline and nonsaline soils were taken from the 0-30 cm depth interval in the same area in which the smaller samples were taken. The samples were passed through a 2-mm screen and thoroughly mixed, and the relationship of matric potential to water content was determined by measuring gravimetric water contents at pressures of 100, 600, and 1500 J·kg⁻¹ in a pressure plate. Matric potential was regressed on volumetric water content to obtain moisture release curves as produced by the pressure plate method. Confidence intervals for the matric potential estimates of moisture release curve regressions from both psychrometer and pressure plate measurements were calculated according to Ott (1977).

The relationship of EC to solute potential was determined by measuring the EC and solute potential of saturation extracts of five of the large 0-30 cm samples of the saline soil after different periods of evaporation (Figure 2).

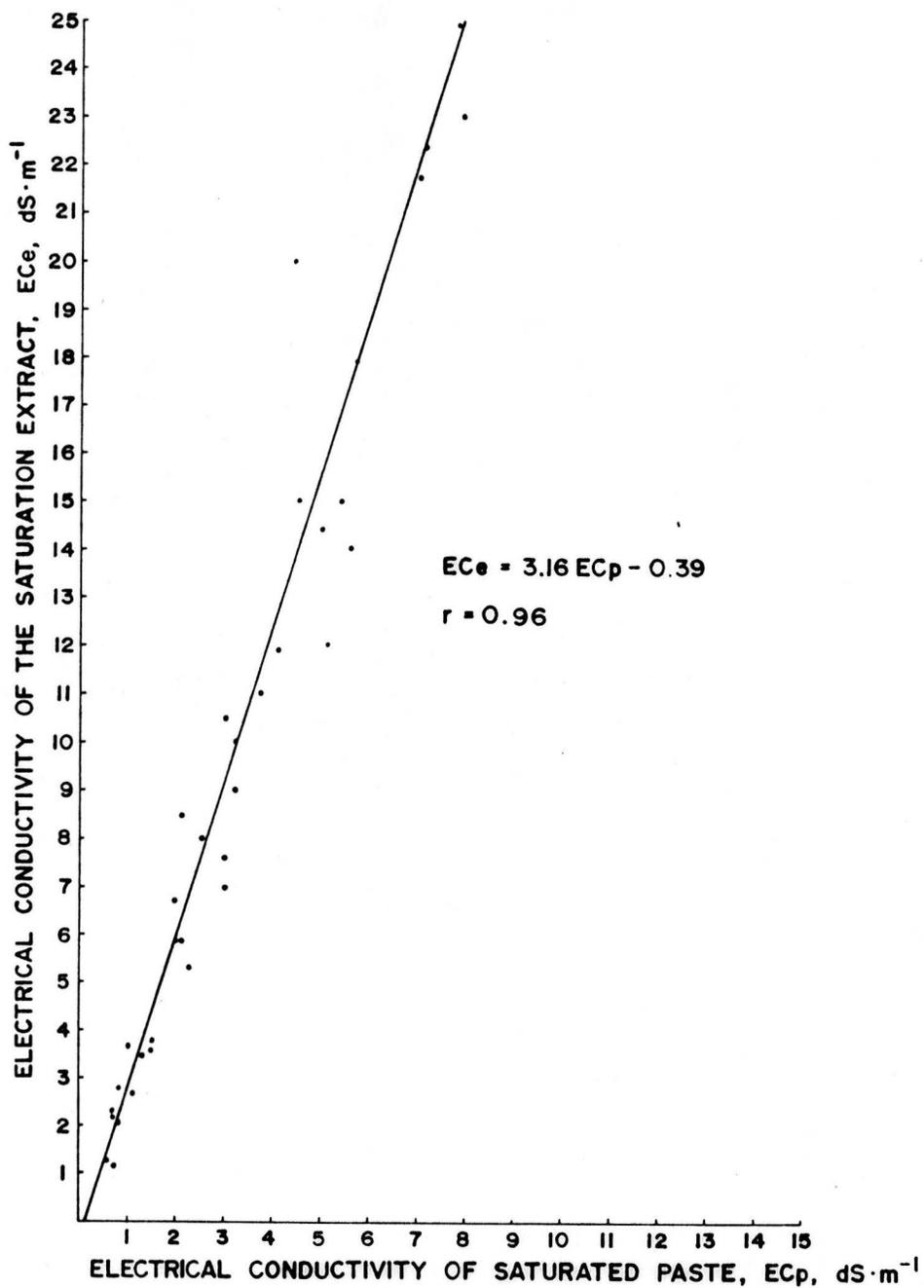


Figure 1. Linear regression of electrical conductivity of Gund silt-loam saturated paste on that of the saturation extract as measured by an instant salinity meter.

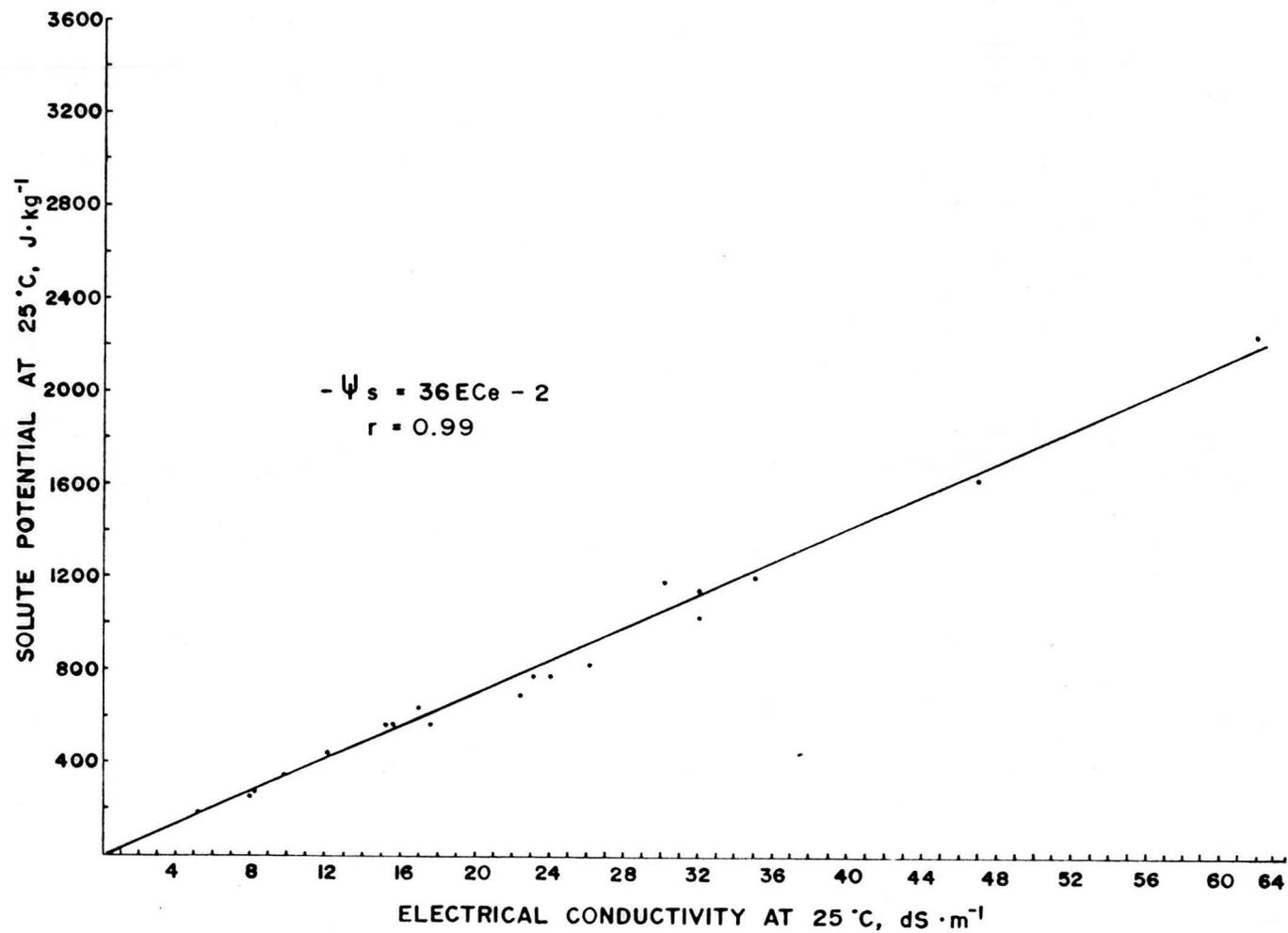


Figure 2. Linear regression of electrical conductivity on solute potential for saturation extracts of Gund silt-loam.

To further compare the effect of salt concentration on linear dilution and psychrometric estimation of matric potential, water potential components were determined in relation to volumetric water content for subsamples of seven of the large, 0-30 cm samples of saline soil. These samples ranged in E_c from 22.4 to 1.3 dS·m⁻¹. Four replications of approximately 2 g subsamples of each of the seven large samples were placed in psychrometer chambers. The subsamples were brought to approximately field capacity water content and the samples were weighed and the total water potential was measured after eight different evaporation periods. For each water content measurement the solute potential was calculated by linear dilution and the matric potential was calculated from total and solute potential. Matric potential was regressed on volumetric water content and regression coefficients, and intercepts for the samples with different salinities were compared according to the slope and elevation tests of Snedecor and Cochran (1971).

The soil and saturation extracts of an additional twelve 0-30 cm deep soil samples from the saline and nonsaline soils were analyzed for chemical properties. Means of the chemical data of samples of low, high, and moderate salinity (Table 1) for the saline soil were input in a model (Robbins 1979, Tillotson et al. 1980) that uses chemical equilibrium equations to calculate EC of the soil solution at actual water contents. The model takes into account ionic activity, formation of ion pairs, the solution ionic strength, salt solubility and cation exchange reactions involving Ca, Mg, Na, and K. The model EC predictions have been verified by actual salinity measurements (Robbins 1979, Tillotson et al. 1980).

Table 1. Chemical properties of saline and nonsaline soils sampled in Grass Valley, Nevada and other saline soils in the Great Basin.

| Location & Reference | Vegetation | Depth (cm) | E _{ce} (dS·m ⁻¹) | Cation Exch. Capac. (meq/100 g) | Gypsum (%) | Lime (%) | Na | K meq/L | Ca in the saturation extract | Mg | Cl | SO ₄ | CO ₃ | HCO ₃ |
|--|-----------------------------|------------|---------------------------------------|---------------------------------|------------|----------|-------|---------|------------------------------|-----|------|-----------------|-----------------|------------------|
| Grass Valley, Nevada (Present study, saline soil) | Greasewood/salt rabbitbrush | 0-30 | 2.2 | 23.2 | 0 | 1.7 | 13.0 | 5.1 | 1.9 | 0.6 | 4.4 | 17.8 | -- | -- |
| | | 0-30 | 7.3 | 23.2 | 0 | 2.4 | 61.6 | 16.1 | 2.1 | 1.5 | 21.0 | 41.4 | -- | -- |
| | | 0-30 | 17.9 | 23.2 | 0 | 2.3 | 150.8 | 46.9 | 4.5 | 3.7 | 72.3 | 102.3 | -- | -- |
| Grass Valley, Nevada (Present study, nonsaline soil) | Greasewood/salt rabbitbrush | 0-30 | 0.4 | 23.4 | 0 | <1.0 | 1.7 | 0.7 | 1.6 | 0.6 | 1.5 | <1.0 | -- | -- |
| Curlew & Rush Valley, Utah (Gates et al. 1956) | Greasewood | 0-15 | 2.2 | 19.3 | -- | 13 | 25.2 | 4.0 | 3.1 | 1.6 | 22.2 | 2.9 | 0 | 9.6 |
| | | 15-45 | 6.1 | 20.5 | -- | 19 | 81.1 | 3.0 | 4.4 | 3.9 | 68.4 | 27.6 | 0 | 11.4 |
| | Shadscale | 0-15 | 1.0 | 17.0 | -- | 18 | 8.2 | 4.0 | 2.4 | 1.0 | 5.4 | 1.7 | 0 | 8.8 |
| Humboldt sink north of Fallon, Nevada (Ando 1980) | Greasewood/Shadscale | 15 | 0.9 | -- | -- | -- | 6.9 | -- | 0.9 | -- | 2.3 | 2.6 | 0.4 | 2.1 |
| | | 90 | 23.3 | -- | -- | -- | 164 | -- | 1.6 | -- | 67.3 | 223 | 4.0 | 3.2 |
| Ca + Mg | | | | | | | | | | | | | | |
| parts per 100,000 parts of dry soil | | | | | | | | | | | | | | |
| Escalante Valley, Utah (Shantz & Piemeisel 1940) | Saltgrass | crust | -- | -- | -- | -- | 8504 | 703 | 57 | 62 | 4870 | 6200 | 2650 | 2420 |
| | | 0-30 | -- | -- | -- | -- | 529 | -- | 49 | T | 510 | 350 | 202 | 10 |
| | Greasewood/Saltgrass | crust | -- | -- | -- | -- | 20926 | 444 | 286 | 43 | 5850 | 36830 | 26 | 272 |
| | | Shadscale | 0-50 | -- | -- | -- | -- | 69 | -- | T | 0 | 22 | 36 | 0 |

Miller et al
JRM 35: 462-468.

Results and Discussion

The saline soil sampled in this study and other saline-sodic soils of the Great Basin tend to contain more soluble than insoluble salts (Table 1, also see Stuart et al. 1971 and Vest 1962). In these soils where Na, SO_4 and Cl are the dominant ions, the main soluble salts would be NaCl and Na_2SO_4 rather than the less soluble salts of $\text{CaSO}_4 \cdot 2\text{H}_2\text{O}$, CaCO_3 and $\text{CaMg}(\text{CO}_3)_2$.

Instant salinity measurements of EC of the saturated paste and of the ECe were highly correlated for these soils (Figure 1). This method of determining ECe is much easier and faster and uses a much smaller sample than the method of extracting the saturated soil solution with a Baroid press and measuring the ECe with a wheatstone bridge and conductivity cell. Once the EC of the saturated paste is calibrated against the ECe for a particular soil this method can provide ECe estimates of numerous soil samples which would better characterize the soil salinity than taking fewer samples and determining ECe by conventional methods.

Saturation extract solute potential for the saline soil was found to be related to ECe similarly to the relationship stated by Richards (1954) where an ECe of $1 \text{ dS} \cdot \text{m}^{-1}$ is equal to a solute potential of $-36 \text{ J} \cdot \text{kg}^{-1}$ (Figure 2).

Electrical conductivity of the soil solution calculated by the chemical model of Robbins (1979) and Tillotson et al. (1980) and that calculated by linear dilution was very similar down to a volumetric water content of 0.1 (Figure 3). With the chemical model estimates as a standard, linear dilution overestimated the soil solution electrical conductivity at a volumetric water content of 0.05 by 2.7, 8.8, and $36.8 \text{ dS} \cdot \text{m}^{-1}$ for soils having an ECe of 2.2, 7.3, and $17.9 \text{ dS} \cdot \text{m}^{-1}$, respectively.

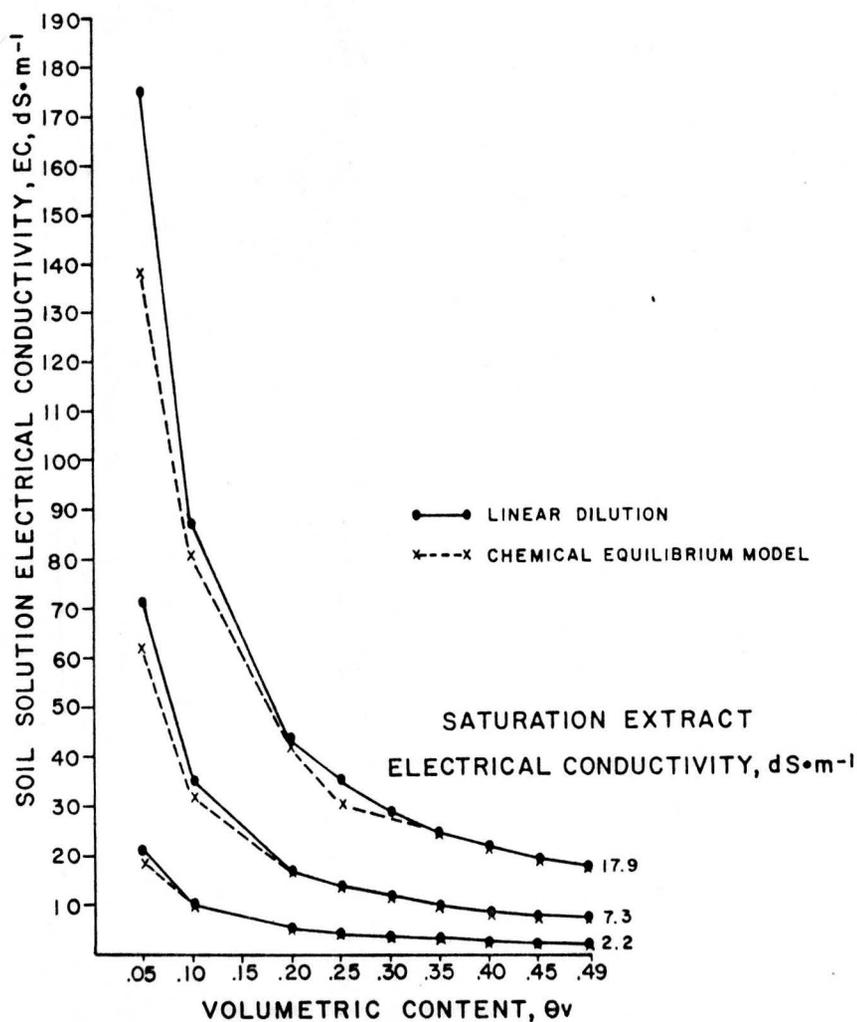


Figure 3. Soil solution electrical conductivity at different volumetric water contents as calculated by linear dilution and by the chemical equilibrium model of Robbins (1979) and Tillotson et al. (1980) for Gund silt-loam soils with different saturation extract electrical conductivities.

Indications are that even for soils where soluble salts predominate, accurate calculations of actual soil solution EC by linear dilution is limited to certain ranges of water content depending on the salinity of the saturation extract. Accurate calculations of the actual soil solution EC and solute potential of highly saline soils is possible only at higher volumetric water contents.

Moisture release curve data determined from psychrometer measurements and from pressure plate measurements described a log-log function (Figures 4 and 5) as has been shown to be the case for other soils (Campbell 1974). Matric potential estimates from psychrometer measurements and linear dilution calculations where the volumetric water content was greater than 0.09 were 100 to 300 $\text{J}\cdot\text{kg}^{-1}$ less negative than those from the pressure plate for the saline soil at a given water content (Figure 4). Psychrometer measurements of matric potential were somewhat less negative at lower water contents and more negative at high water contents than those determined by the pressure plate for the nonsaline soil (Figure 5). Given the great variation that can occur in the relationship of matric potential to water content, the moisture release curves determined by the two different methods were very similar for both of these soils. The more negative moisture release curve from the psychrometer and linear dilution method may indicate that the solute potential of the saline soil was slightly underestimated (estimated too negative), resulting in overestimation of matric potential.

Regression statistics of matric potential on water content from the psychrometer and linear dilution method were generally not different for the seven soil samples of different ECes up to $14.4 \text{ dS}\cdot\text{m}^{-1}$ (Table 2). The intercept of the soil with an ECe of $22.4 \text{ dS}\cdot\text{m}^{-1}$ was significantly higher (less negative) than those of three other soil samples with lower

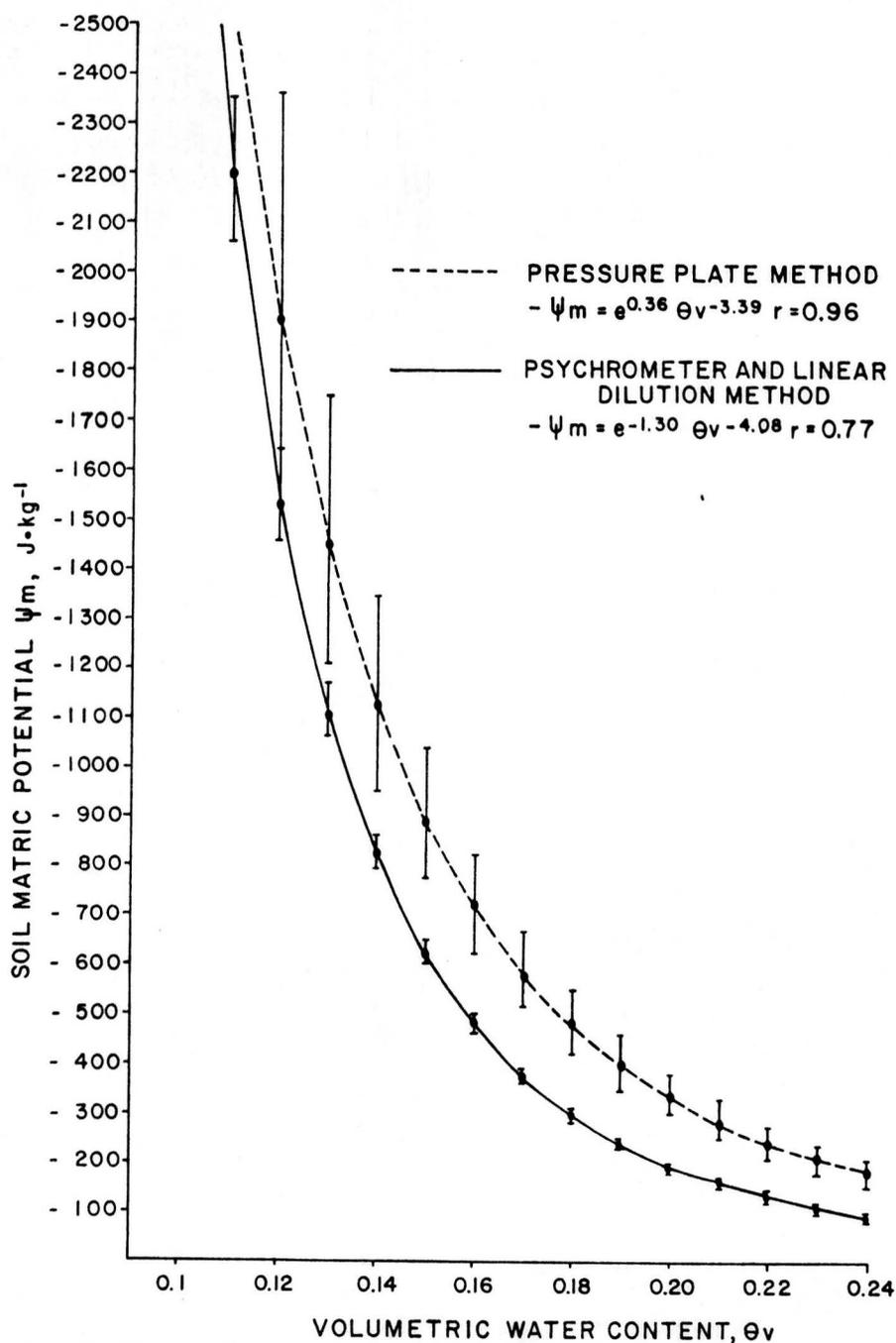


Figure 4. Soil matric potential as a function of volumetric water content for saline Gund silt-loam soil estimated by linear dilution estimates of solute potential and psychrometric measurement of total potential and as determined by a pressure plate. Vertical bars are 95% confidence intervals for the regression lines calculated according to Ott (1977).

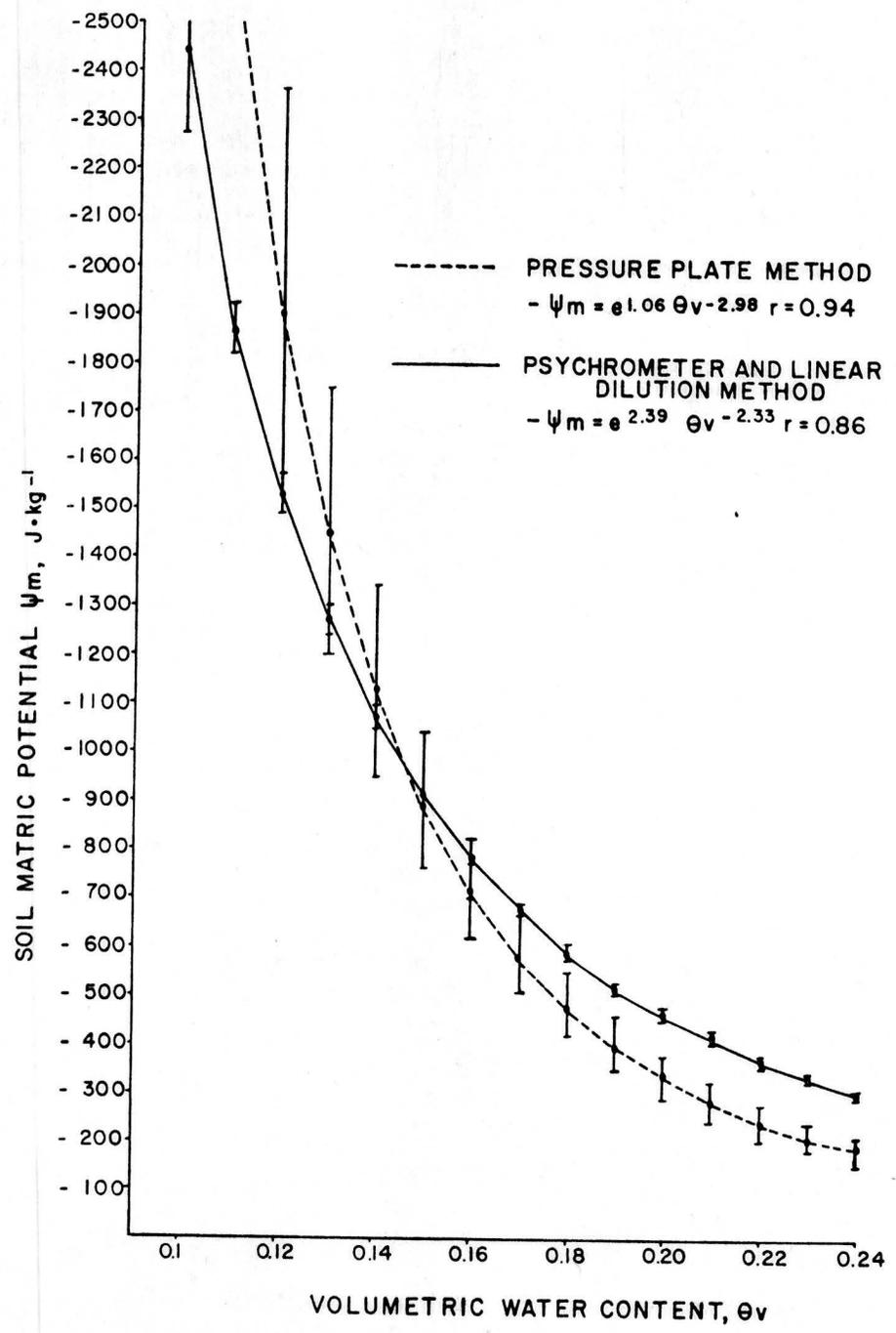


Figure 5. Soil matric potential as a function of volumetric water content for nonsaline silty-clay as measured by psychrometers and by a pressure plate. Vertical bars are 95% confidence intervals calculated according to Ott (1977).

Table 2. Intercepts (a), regression coefficients (b) and correlation coefficients (r) for moisture release curves of Gund silt-loam soils with different saturation extract electrical conductivities of the form: $\ln \Psi_m = a + b \times \ln \Theta_v$, where Ψ_m is soil matric potential ($-J \cdot kg^{-1}$) and Θ_v is volumetric water content.

| Saturation Extract Electrical Conductivity ($dS \cdot m^{-1}$) | Regression Statistics* | | |
|--|------------------------|----------|-----------------------|
| | <u>a</u> | <u>b</u> | <u>r</u> ⁺ |
| 22.4 | 1.94b | -2.07ab | 0.60 |
| 14.4 | 3.05a | -1.76ab | 0.87 |
| 5.9 | 2.35ab | -2.13a | 0.96 |
| 3.5 | 2.75ab | -1.91ab | 0.88 |
| 2.7 | 2.45ab | -2.01ab | 0.63 |
| 2.1 | 3.43a | -1.59b | 0.87 |
| 1.3 | 3.30a | -1.72ab | 0.90 |

* Intercepts and regression coefficients followed by the same letter are not significantly different ($p = 0.05$) according to the elevation and slope tests of Snedecor and Cochran (1971).

+ All r values are significant at the 0.01 level.

ECes. This indicates again that for soils with high ECes, linear dilution may underestimate solute potentials which, when subtracted from total potential measurements by psychrometers results in overestimation of matric potentials.

For the saline soil sampled in this study, it appears that reasonable estimation of water potential components by the psychrometer and linear dilution method is possible at a water content greater than 0.09 and at an ECe up to at least 14 to 15 $\text{dS}\cdot\text{m}^{-1}$.

Soluble salts greatly reduce the total soil water potential as soil water content and matric potential decreases (Figure 6). This reduction suggests that for plants to establish in saline, semiarid soils, they must be able to adjust osmotically to maintain rapid root growth when soil water contents and matric potentials are high, but solute potentials may be comparatively low.

Results of this study indicate that measurements of ECe and linear dilution calculations can be used to obtain reasonable estimates of the solute potential at certain water contents of saline-sodic rangeland soils in which the dominant salts are highly soluble. These measurements can be done rapidly and easily on numerous small samples by using the instant salinity meter. Psychrometer measurement of total soil water potentials coupled with ECe measurements for determination of solute potential allow fairly easy determination of water potential components for numerous samples. This method may be useful in relating plant responses to water availability on semiarid saline rangeland soil where numerous samples must be taken to characterize water availability due to high vertical and horizontal variability in soil salinity.

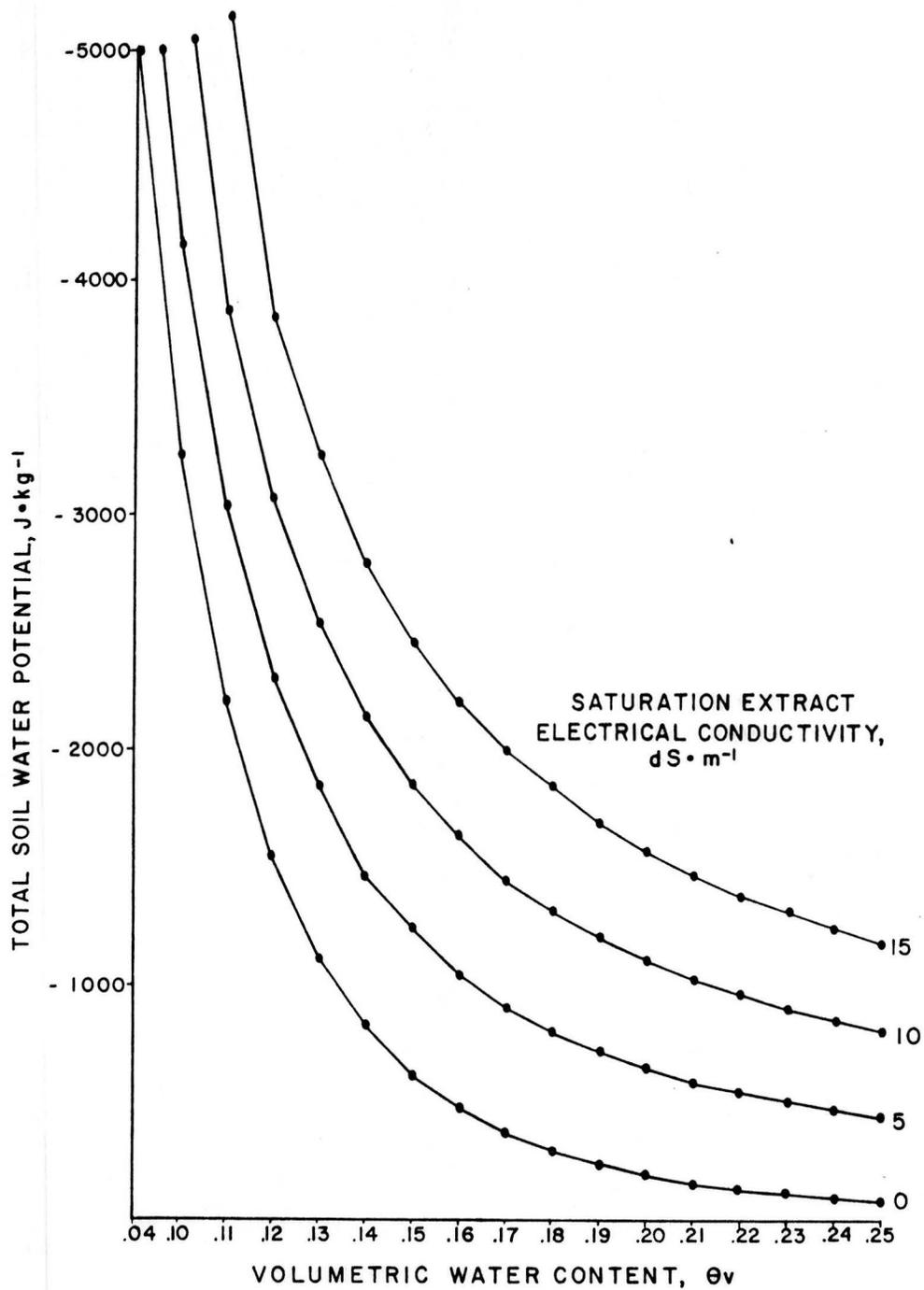


Figure 6. Total soil water potential as a function of volumetric water content for saline Gund silt-loam soils with different saturation extract electrical conductivities.

results of the tests of
In conclusion, the hypotheses can be reported as follows:

- I. A. Osmotic potential did decrease linearly; probably because the predominant salts were NaCl and Na₂SO₄, which are highly soluble.
- B. and C. Solution osmotic potential was accurately estimated from electrical conductivity measurements and saturation extract electrical conductivity was accurately estimated from saturated paste electrical conductivity.
- D. Soil water characteristic curves generated from psychrometer and salinity measurements to estimate matric potential were very similar to those determined with a pressure plate.

Water potential components can be accurately estimated from psychrometer and salinity measurements for water contents greater than 0.09 and E_{Ce}'s less than 15 dS·m⁻¹ for the saline soil in this study.

SURFACE SOIL AND SEEDBED ECOLOGY IN SALT
DESERT PLANT COMMUNITIES

Introduction

Salt desert shrub vegetation, composed dominantly of chenopods (West 1983), has been estimated to occupy 15 (Branson et al. 1967) to 17 (Küchler 1964) million hectares in the western United States. Caldwell (1974) and West (1983) have characterized the environment of saline deserts as having high seasonal temperature and precipitation fluctuations resulting in a short period of time when active growth is not limited by extreme temperatures and lack of moisture. Precipitation in the Great Basin mainly occurs in fall, winter and spring. Storms resulting in effective precipitation become less frequent but possibly more critical to seedling establishment from March through June or July as temperatures become more favorable for germination and growth (Figure 7).

Chemical and physical properties of salt desert soils may affect soil water availability to plants during this critical spring period or may have a direct affect on germination, emergence and growth. An understanding of these characteristics of salt desert soils is not only necessary to understand natural plant distribution, but is also necessary in determining range improvement and management practices. This paper will discuss some of the properties of salt desert soils that affect plant distribution, growth and establishment, and present water potential, salinity and soil penetrability data for a salt desert soil in central Nevada.

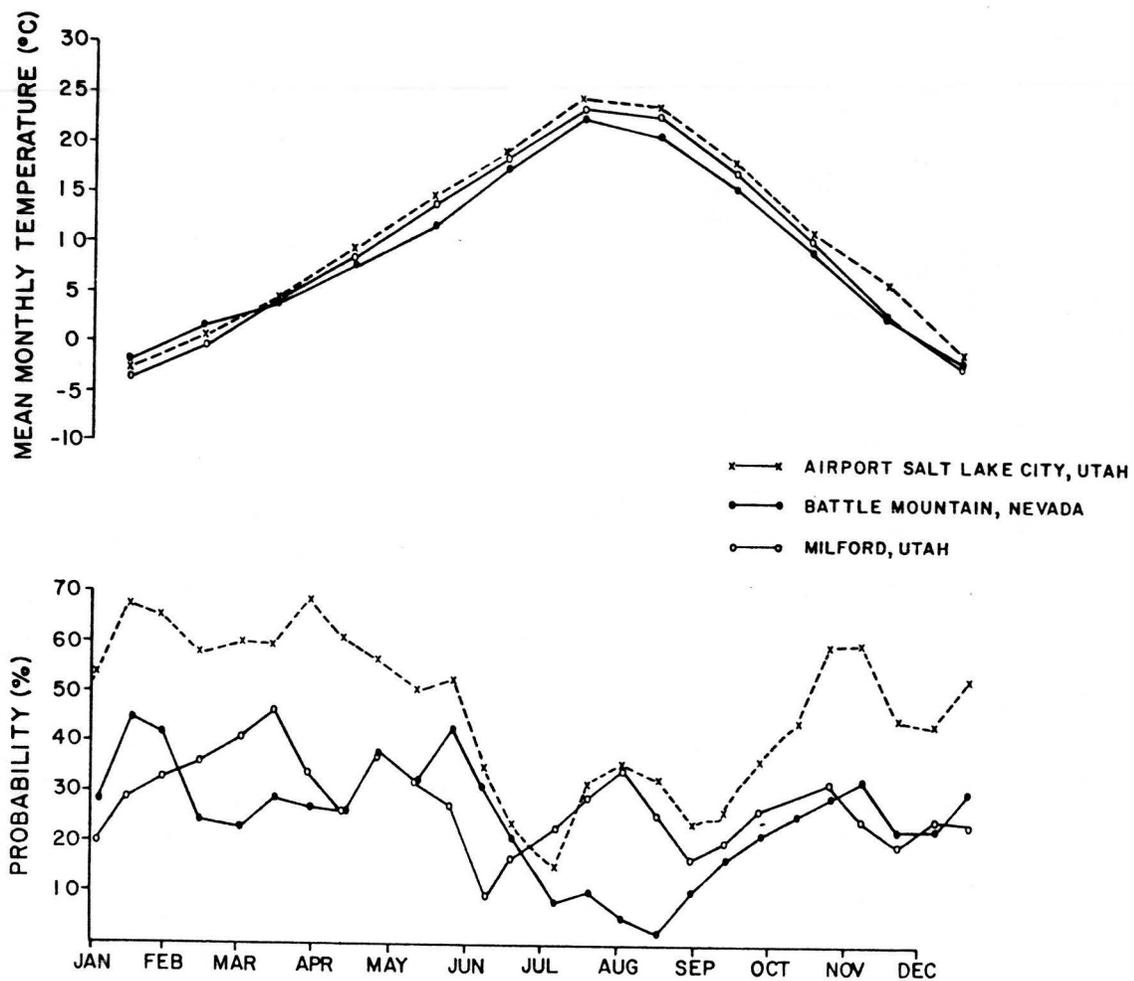


Figure 7. Mean monthly temperatures (above, U.S. Dept. Comm. 1979, 1982) and probabilities of receiving 1 cm of precipitation in a two-week period (below, Gifford et al. 1967) for three salt desert weather stations in the Great Basin.

Review of Literature

Much research has been devoted to the description and classification of salt desert communities and soils in an effort to relate plant distribution to site characteristics (Kearney et al. 1914, Shantz and Piemeisel 1924 and 1940, Flowers 1934, Billings 1945, Fautin 1946, Gates et al. 1956, Vest 1962, Mitchell et al. 1966, Branson et al. 1967, West and Ibrahim 1968, Goodman 1973, Miller et al. 1982). Distribution and growth of salt desert species have been related to numerous edaphic factors and interactions of the factors. Some important factors are 1) tolerance of plants to total salt content of the soil (Billings 1945, Bolen 1964, Daubenmire 1970, Dodd and Coupland 1966, Flowers 1934, Hunt and Durrel 1966, Kearney et al. 1914, Keith 1958, Ungar 1962, 1966, Ungar et al. 1966), 2) tolerance to relative amounts of specific ions in the soil solution (Flowers 1934, Heimann 1966, Naphan 1966, Tiku 1975), 3) depth of soil salinity (Billings 1945, Fautin 1946, Shantz and Zon 1924), 4) tolerance to flooding and poor soil aeration (Daubenmire 1970, Dodd and Coupland 1966, Evans 1953, Flowers 1934, Shantz and Piemeisel 1940), and 5) water table depth and quality of ground water (Billings 1951, Bolen 1964, Daubenmire 1970, Fautin 1946, Flowers 1934, Harris et al. 1924, Hunt and Durrel 1966, Jackson et al. 1956, Robinson 1958, Shantz and Zon 1924, Shantz and Piemeisel 1924, 1940, White 1932, 6) soil texture as related to geology and erosion patterns (West and Ibrahim 1968). Other important considerations in relating growth and distribution of halophytes to soil conditions include: 1) total soil moisture potential and the proportionality of its components, osmotic and matric potential (Branson et al. 1967, Goodin 1975, Miller et al. 1982), 2) seasonal variability of such factors as salinity and moisture

as related to germination and growth (Evans 1953, Jackson et al. 1956, Goodin 1975), 3) ecotypic adaptation to specific soil conditions (Clark and West 1971, Goodin 1975, Goodman and Caldwell 1971, Goodman 1973, Workman and West 1967, 1969), and 4) the synecological context in which the plant occurs as related to its ability to compete and reproduce (Billings 1952, West and Tueller 1971).

The internal drainage of the Great Basin has resulted in an accumulation of salts and fine sediments in the many closed basins created by basin and range faulting^{beginning} in the Miocene (Papke 1976). The predominant ions accumulated in surface soils of many valleys of the Great Basin are Na, Cl and SO₄ with comparatively little Ca and Mg (Shantz and Piemeisel 1940, Gates et al. 1956, Vest 1962, Stuart et al. 1971, Ando 1980, Roundy 1983¹ (Table 1). These sodium salts are highly soluble and reduce the total soil water potential by reducing the soil solution osmotic potential linearly with decreasing water content¹. The high sodicity of these fine-textured soils also reduces infiltration (Hayward and Wadleigh 1949). Soil salts may also reduce germination and growth by entering the seed or plant and creating nutritional imbalances or interfering with physiological processes (Bresler et al. 1982). In addition to Na, high B concentrations have been reported on salt desert soils (Robinson 1970) and may be limiting to growth of some plants.

Surface soil salinity may vary with season and precipitation and capillary rise from the water table as related to soil morphology and texture (Jackson et al. 1956). High winter precipitation may increase surface salinity by raising the water table so the capillary fringe is

¹ Roundy, B.A. 1983. Estimation of water potential components of saline soils of Great Basin rangelands, Soil Sci. Soc. Am. J. (submitted).

near the soil surface and salts are deposited on the surface as water evaporates (Richards 1954). If the water table is deep or evapotranspiration breaks the capillary chain, surface salinization stops (Jackson et al. 1956). Lowland Great Basin soils vary in amount and vertical concentration of salts due to differences in depth to the water table as related to topographic position and drainage patterns. Spring precipitation may increase soil osmotic potential by leaching salts accumulated in the surface soil or by removing them in run off water and by diluting the soil solution. Teakle and Burvill (1938) found substantial leaching of salts in sandy and medium-textured soils of western Australia but not on heavy-textured soils. In the Thar desert, India, rainy season precipitation leached salts and increased subsurface soil moisture, resulting in increased plant and soil osmotic potentials (Rajpurohit and Sen 1980). Zallar and Mitchell (1970) suggested that Autumn rains leached salts on dry hard-pan sites in Australia, allowing germination and establishment of salt-tolerant grasses. Soil salinity and sodicity decreased after contour furrowing in southeastern Montana presumably due to increased infiltration and leaching (Soiseth et al. 1974). Spring rains could also decrease the osmotic potential of the subsurface soil solution by washing down salts that have precipitated out on the soil surface.

Salt desert chenopods accumulate high amounts of Na, K and Cl, (Eckert and Kinsinger 1960, Rickard 1965, Chatterton et al. 1970, Wiebe and Walter 1972). These salts may allow salt desert shrubs to osmotically adjust to low soil water potentials (Caldwell 1974), but they also increase the salinity and sodicity of the soil surface through litter fall and leaching of plant parts (Roberts 1950, Fireman and

Hayward 1952, Eckert and Kinsinger 1960, Rickard et al. 1973, Sharma and Tongway 1973). Although the accumulations of salts under shrubs may reduce infiltration and result in ion concentrations toxic to some plants, the litter fall of shrubs is also associated with higher soil fertility than the interspaces (Rickard et al. 1973, Charley and West 1973). Also, coarse-textured shrub mounds associated with windblown soil accumulation may be more readily leached and lower in salinity, sodicity and B than interspace soils (Rollins et al. 1968, Stuart et al. 1971).

The fine-textured soils generally associated with the salt desert have high water holding capacity, but they may limit soil water availability due to low infiltration and hydraulic conductivity resulting from high particle dispersion due to low organic matter (Blackburn 1975) in addition to high sodicity. Eckert et al. (1978) have described the surface soil morphology associated with shrub mounds and interspaces of aridisols in Nevada. Regular organic matter additions from shrub litter fall result in friable, well-aggregated mound soils which have high infiltration rates. In the interspaces, the lack of organic matter additions and repeated wetting and drying (Miller 1971) may cause silty soils to form a platy to massive vesicular crust which decreases soil penetrability and may restrict seedling emergence. Stephens (1980) found that slightly crusted pinnacled soil surfaces or crusted polygonal units separated by cracks were important microsites for seedling emergence in vesicular crusted soils in Nevada. Duba (1976) observed [Halogeton glomeratus (Bieb.) C.A. Mey] seedlings to emerge mainly from cracks between polygonal soil surface peds. These cracks are undoubtedly safe sites (Harper 1977) for seedling emergence. They catch seeds and

allow unrestricted emergence compared to the hard crusts of the soil polygons.

Seedling establishment in deserts may occur sporadically due to one or a culmination of favorable moisture events (Noy-Meir 1973). It has been hypothesized that years of high seedling establishment may be the product of weather conditions favoring high seed set, germination and seedling survival (Went 1955, West 1979).¹⁹⁸²

Methods

To determine the effects of high spring precipitation on salinity, water potential components and crust penetrability, a nonsaline and a moderately saline salt desert soil were sampled in the spring and summer of 1982 in central Nevada. The saline soil is a Gund silt-loam series identified as of the fine-silty over clayey, mixed (calcareous), mesic family of Aquic Durorthidic Torriorthents (Appendix, Table 16) and the nonsaline soil is of the fine, montmorillontic, mesic family of Typic Camborthids (Appendix, Table 17). Both soils supported a greasewood/salt rabbitbrush/basin wildrye community. The shrubs were eliminated by spraying with $3.4 \text{ kg} \cdot \text{ha}^{-1}$ of 2,4-D [(2,4-dichlorophenoxy) acetic acid] in the spring of 1980 and by rotobating later in the summer. Soils were seeded to Jose tall wheatgrass and Magnar basin wildrye in the fall of 1981. Natural winter precipitation between November 1981 through March of 1982 was average for the site at 13.9 cm, but spring precipitation from April through June was 4.6 cm, about 5 cm below average. Thus 1981-1982 was a relatively wet winter and dry spring and a good year to measure the effects of supplemental precipitation simulated by irrigation on soil salinity and water potential. A gradient in spring precipitation was created by irrigating the soils with a single sprinkler on four dates

in May and June of 1982. Water applied decreases almost linearly with the distance from the sprinkler (Appendix, Figure 28) (Hanks et al. 1976). Soils were sampled at depth intervals of 0-1, 1-5, 5-10, 10-15 and 25-30 cm at approximately 2-week intervals from later April through mid-August. Soils were generally sampled 2 weeks after each of the four irrigations. At each sample date, two mound and two interspace soils were sampled at distances of 2.5, 6.5, 10.5 and 16 m (no irrigation) from the sprinkler. The highest irrigation (2.5 m from the sprinkler) added a total of 10 cm to the 4.6 cm of natural rain that fell in April through June. Total water potential of the samples was determined in psychrometer chambers and soil osmotic potentials were estimated from measurements of volumetric water content and E_c was described in detail by Roundy (1983)¹. Matric potential was estimated by subtracting osmotic from total water potential. Crust penetrability was measured in relation to precipitation and irrigation by recording the pressure necessary to push a 2-cm diameter by 4-cm long penetrometer cone with a 30-degree angle into the surface soil so the top of the cone was flush with the soil surface.

Results

Salinity

The saline soil had an average E_c of 7.0 dS·m⁻¹ and an average SAR of 44 in the upper 30 cm. The water table in the saline soil was 2.1 m deep and fluctuated less than 0.3 m during the year. Except for the surface 0-1 cm of soil, salinity generally increased with depth (Figure 8a). Excavations indicated a zone of dry soil and therefore, no capillary chain between the water table and the surface soil so that changes in salinity in the surface were a function of initial salinity conditions, precipitation and evapotranspiration.

Salinity of the surface cm was lowest in early spring following winter precipitation, then increased greatly in mid-spring as the soil began drying and salts accumulated in the surface (Figure 8a). Salinity of the upper cm then decreased over summer possibly due to wind erosion. Subsurface salinity (1-15 cm) increased gradually from early spring through summer probably due to upward movement of water and salts from lower depths as the upper soil dried (Figure 8a). Spring irrigation decreased this upward movement of salts, probably by continued leaching. Important implications for plants are that the very surface seedbed may be very high in salinity as the soil dries in response to warming spring temperatures and that increased spring precipitation may keep the salinity of the root zone low. The salinity of mounds and interspaces was very similar in these soils. From April through August the upper 1-15 cm of mounds and interspaces had an average E_c of 5.0 and 5.7 dS·m⁻¹, respectively.

Water Potential Components

Total water potential of the surface cm of soil increased and decreased rapidly in response to precipitation and drying periods (Figure 8b). In the absence of frequent storms, seeds would either have to germinate very rapidly from the surface soil, or be able to emerge from lower depths which have much higher and less fluctuating water potentials than the surface. Seeds germinating in cracks would be expected to avoid the high salinity and lower water potential fluctuations of the surface soil.

Total soil water potential began decreasing in early June and continued to decrease sharply over the summer (Figure 8b). Moore and Caldwell (1972) and Everett et al. (1977) have reported similar seasonal

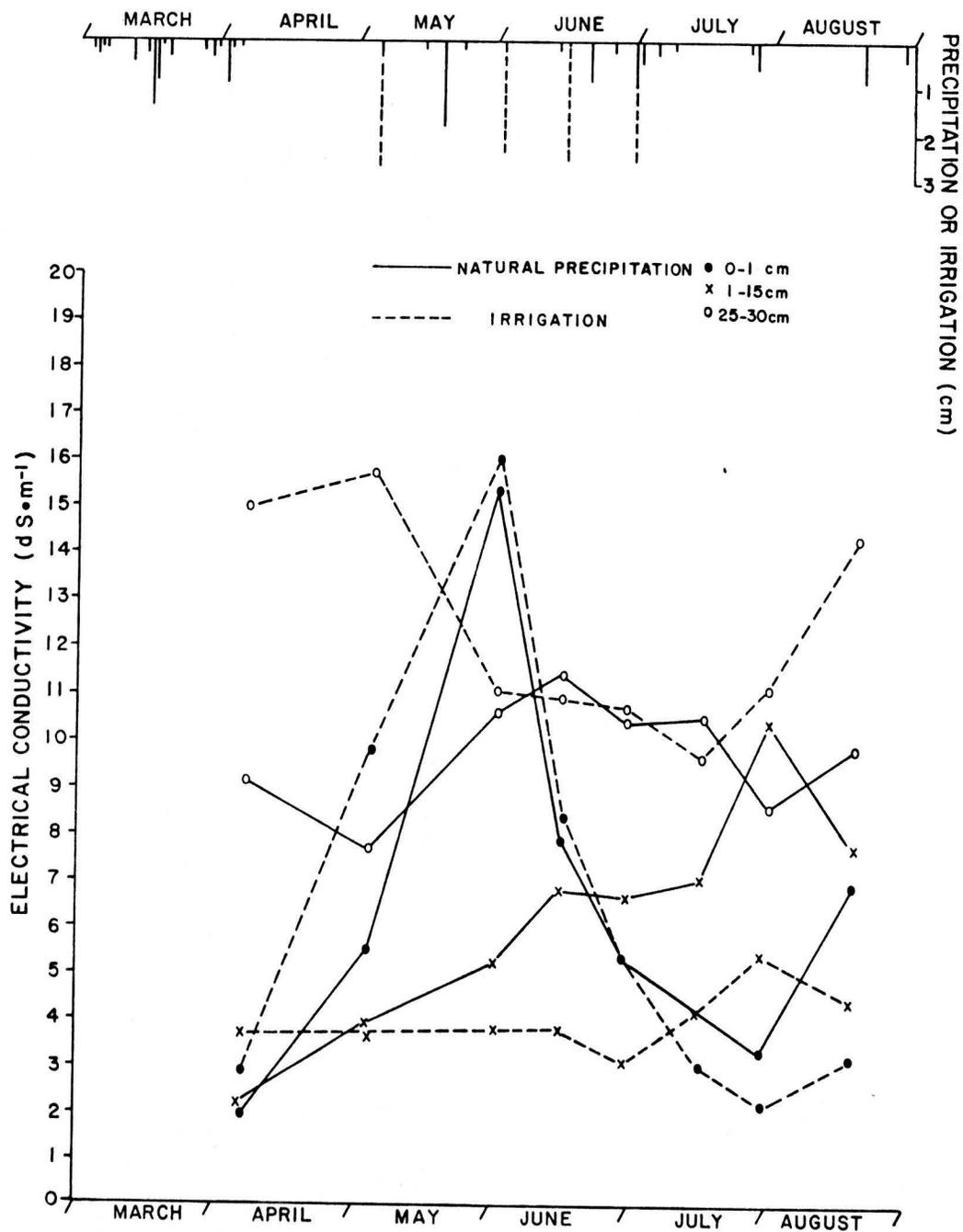


Figure 8. Electrical conductivity of the saturation extract (a) and total (b), osmotic (c) and matric (d) soil water potentials for saline soils in Grass Valley, Nevada receiving natural precipitation and irrigation in the spring and summer of 1982.

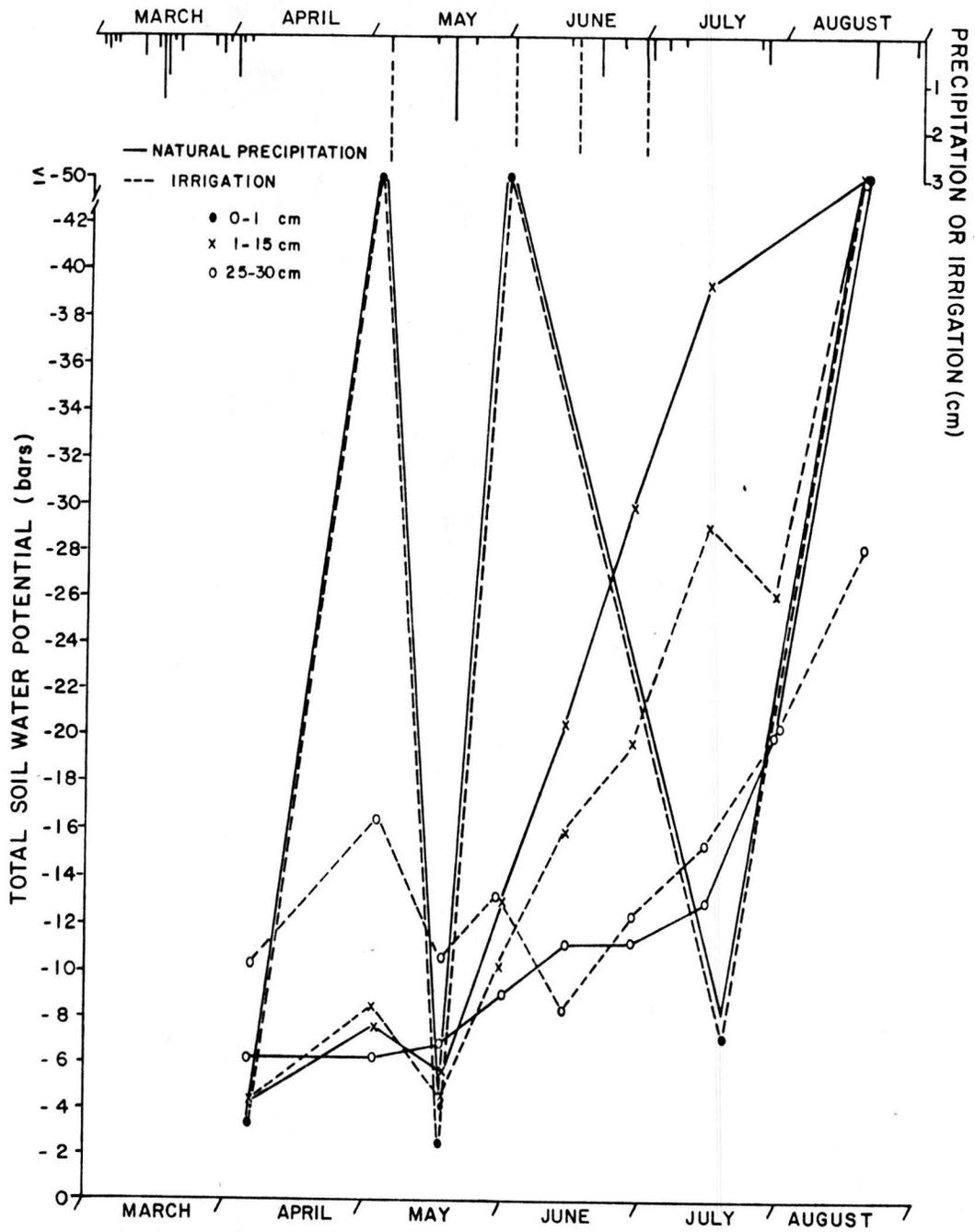


Figure 8b.

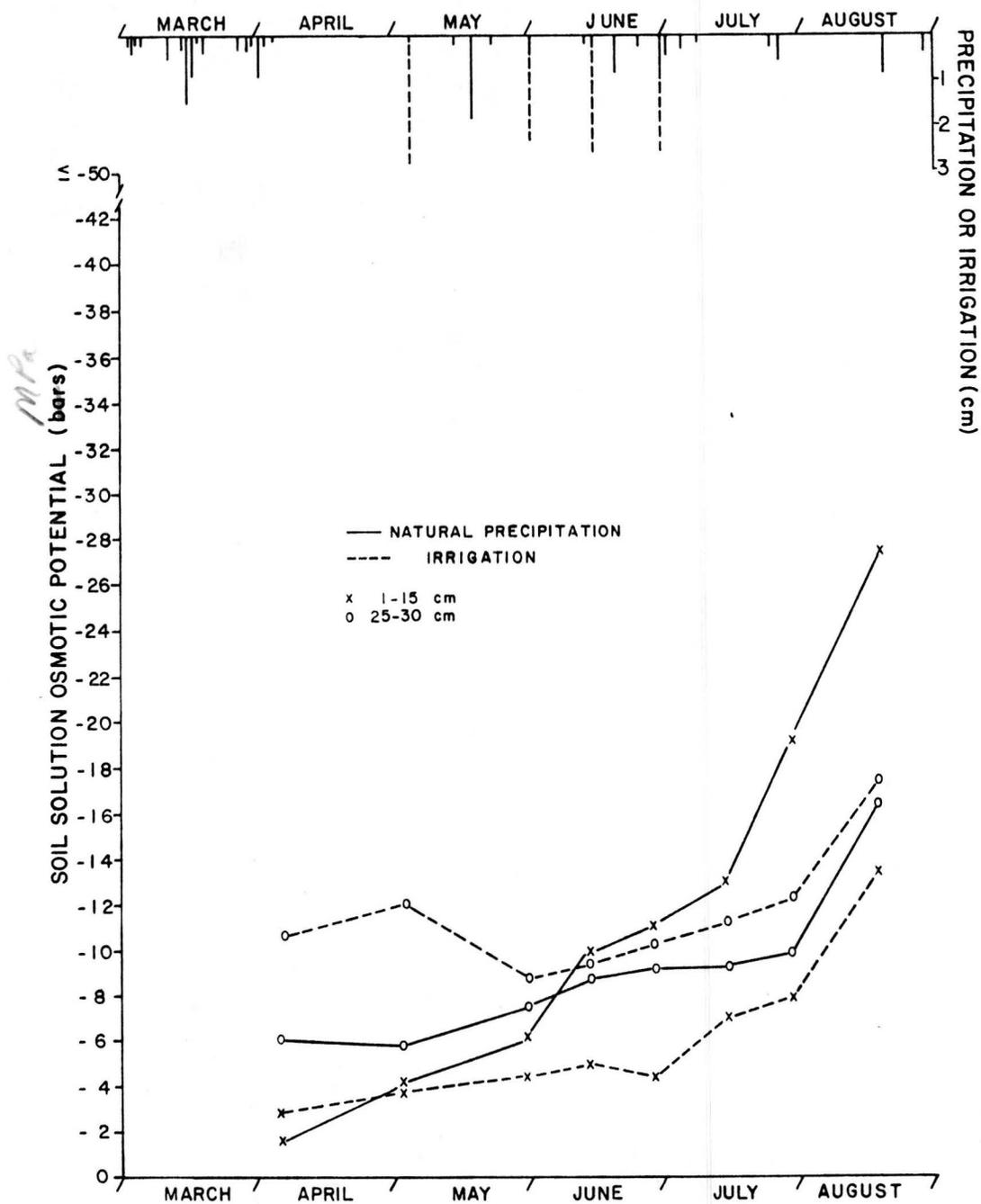


Figure 8c.

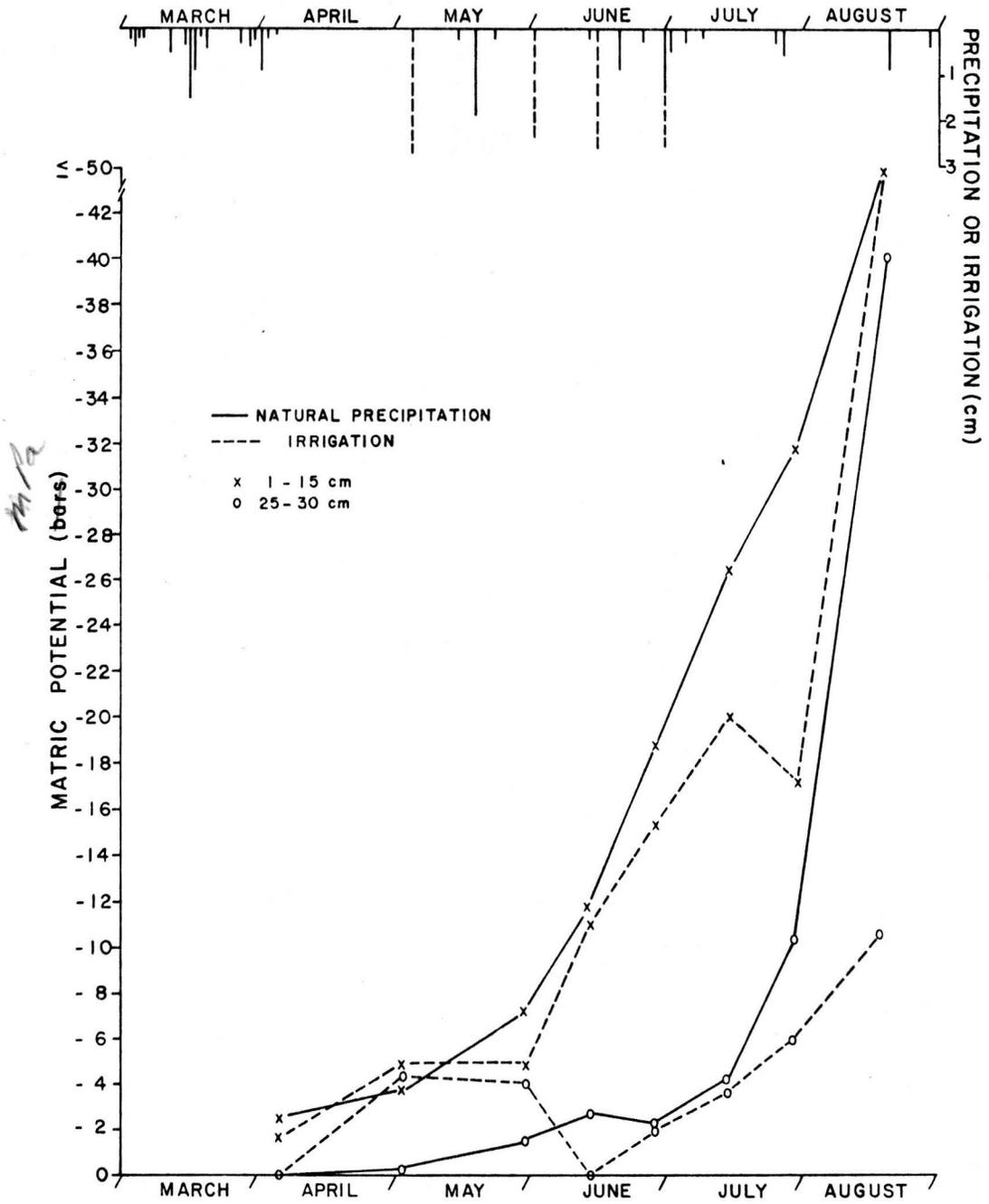


Figure 8d.

decreases in the soil water potential of shadscale communities. Irrigation maintained higher total water potentials of the subsurface soil than nonirrigated subsurface soil by decreasing salinity by leaching and by increasing soil water content, thereby increasing soil osmotic and matric potentials (Figure 8). Total soil water potential of the saline soil receiving the highest irrigation (3 - 2.5 cm irrigations in June) still decreased rapidly from June through the summer (Figure 8b). Irrigation or storms are less effective in maintaining high soil water potentials in late spring and early summer than in early spring due to increased evapotranspiration associated with warming temperatures. Osmotic potential of the irrigated soil at 25-30 cm was more negative than that of the nonirrigated soil due to higher salinity. This difference in salinity was probably due to horizontal variations in salinity concentrations. The irrigated soil maintained higher matric potentials at 25-30 cm than the nonirrigated soil after mid-summer.

The nonsaline soil generally had higher total water potentials than the saline soil (Figures 9 and 10). The lower total water potential of the saline soil can be attributed to its osmotic potential where the matric potentials of the two soils were similar (Figure 9). The osmotic and matric potentials were each about 50% of the total water potential of the saline soil in the spring when soil water content was comparatively high. In April and May, soil osmotic potential decreased with depth due to increasing soil salinity and matric potential increased with depth due to increasing soil water content (Figure 8c, 8d). As water content decreased in summer, the matric potential decreased more rapidly than osmotic potential and thereby became the dominant component of the total soil water potential. As soil water content decreases

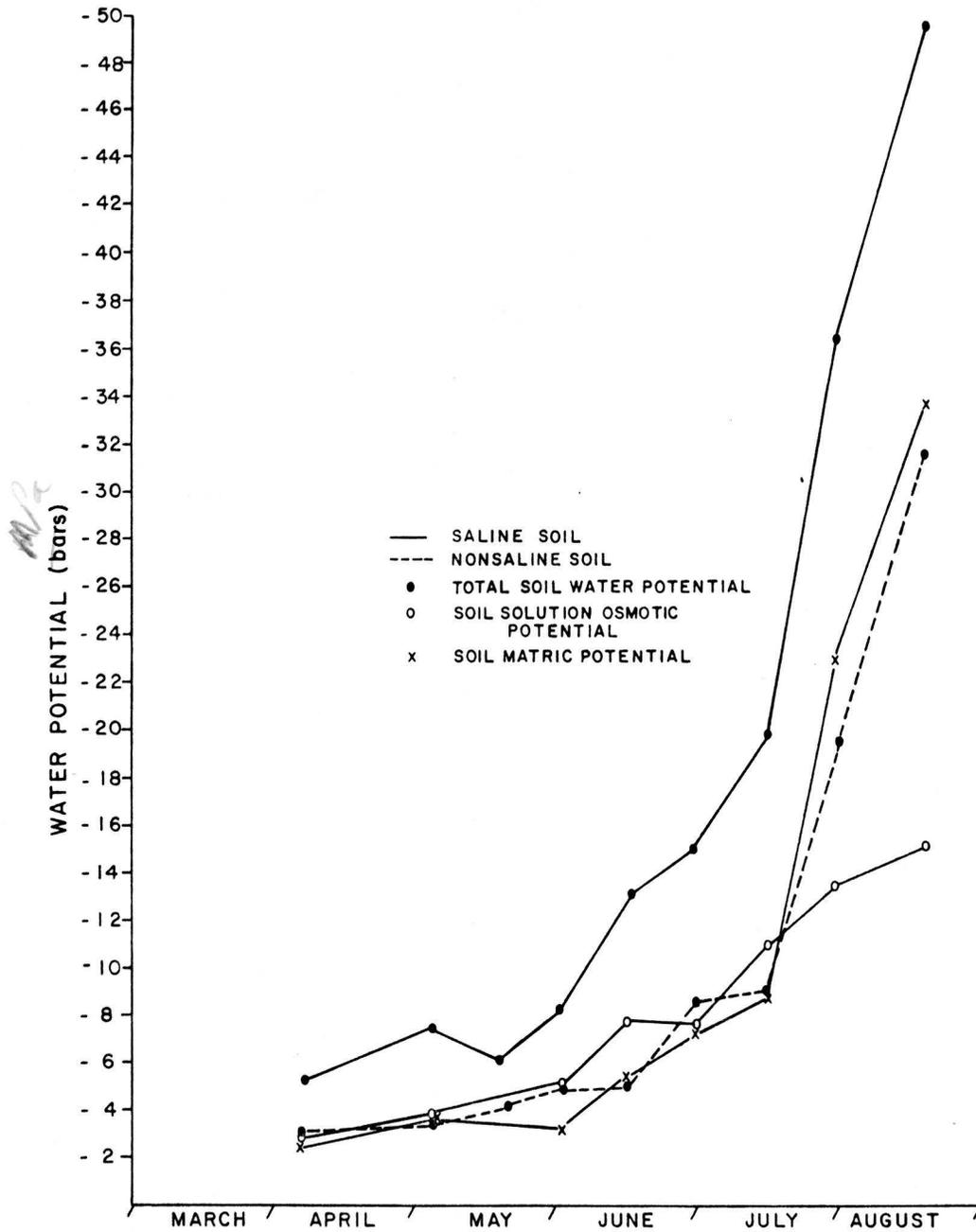


Figure 9. Total, osmotic and matric soil water potentials for a saline soil and total soil water potential of a nonsaline soil for the 10-15 cm depth interval in the spring and summer of 1982 in Grass Valley, Nevada.

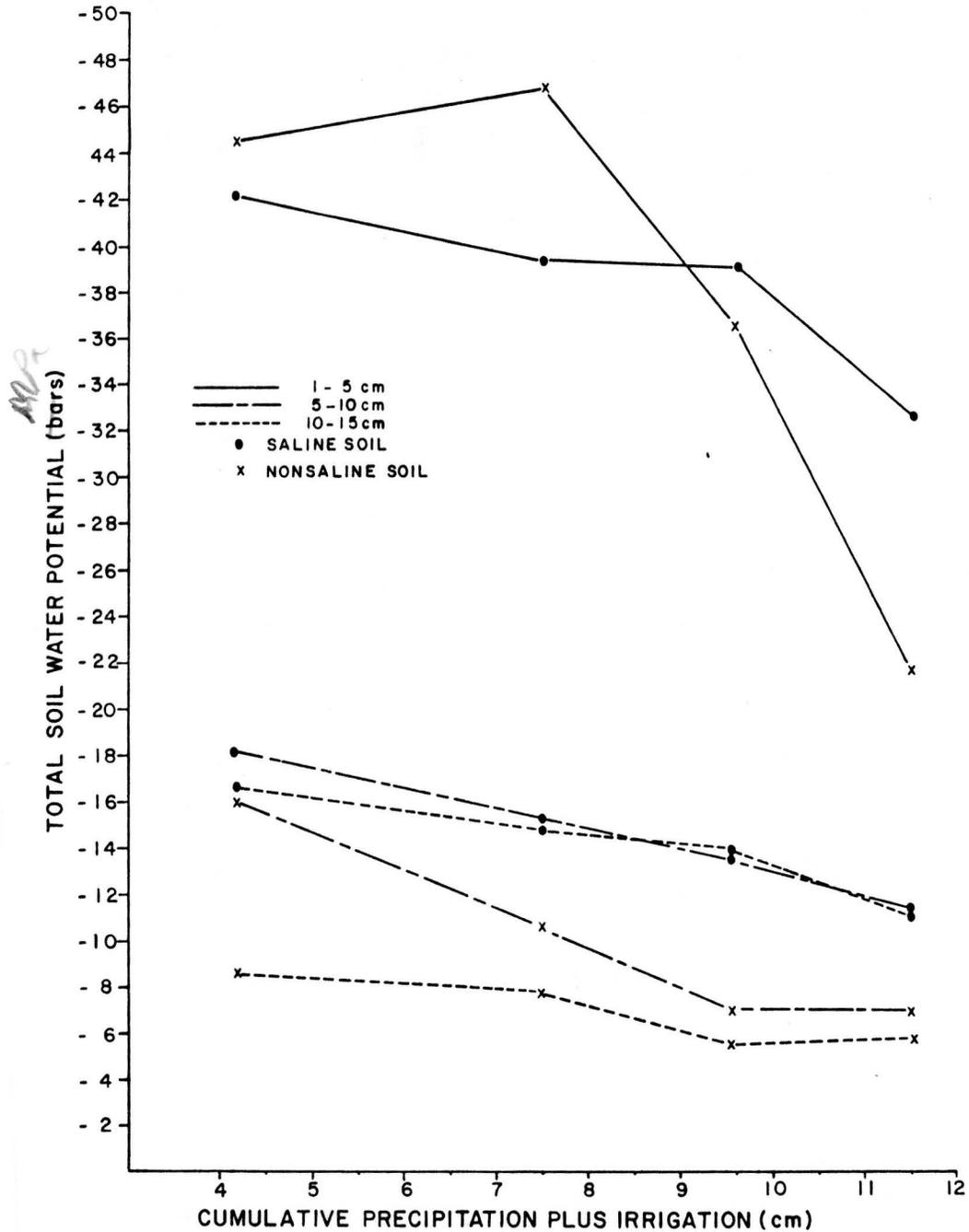


Figure 10. Average total soil water potential of a saline and of a nonsaline soil between May 18 and July 8, 1982 as a function of cumulative precipitation plus irrigation for the same time period in Grass Valley, Nevada.

to a point, matric potential decreases logarithmically, whereas osmotic potential in soils with highly soluble salts decreases linearly with decreasing water content. This linear decrease in soil osmotic potential with decreasing water content and the gradual increase in soil salinity as the soil dried resulted in increasingly more negative total water potentials of the saline than the nonsaline soil through the summer. Plants in these environments which can adjust osmotically may avoid the soil osmotic component of total soil water potential. These plants may grow similarly in saline as in nonsaline soils, if they are tolerant to low cell osmotic potentials and accumulated ions. Differences in ability of salt desert plants to accumulate ions and osmotically adjust may be related to adaptability to soils of different salinities and osmotic and matric proportions of the total water potential.

The effects of increasing irrigation amounts on total soil water potential of the saline and nonsaline soils from 2 weeks after the first irrigation to 2 weeks after the last irrigation are shown in Figure 10. Irrigation amount had a greater effect in increasing the total potential of the 1-5 cm interval of the saline soil and the 5-10 cm interval of the nonsaline soil than it had on other depth intervals of these soils. A smaller effect of irrigation amount on the water potential of deeper intervals of the saline soil may have been due to low infiltration due to the high SAR. Since soil samples were taken 2 weeks after irrigations, the differences in water potential due to irrigation amount were probably minimized due to evapotranspirational water losses. These data underscore the importance of frequent spring rains in maintaining favorable water potentials of saline surface soils, especially for seeds that require warm temperatures for germination.

On the saline soil, mounds had total water potentials an average of 3 bars lower than interspace soils in the upper 1-15 cm between April and the end of June. Since salinity of the mounds and interspace soils was similar, the difference in total potential would be due to differences in matric potential rather than osmotic potential. A graph of the moisture release curves as determined by a pressure plate showed that at given water contents, mound soil had more negative matric potentials than interspace soils even though the particle size distribution of both soils was similar.

Soil Penetrability

Shrub mound soils were much more penetrable than interspace crusts (Figure 11) and would offer little mechanical resistance to emerging seedlings. The penetrability of interspace soils increased with the amount of irrigation, but decreased again rapidly the first day after irrigation as the soil dried.

Discussion

Total water potentials are at a maximum in early spring following the winter period of high precipitation and low evapotranspiration. During this time, matric potentials are high due to high soil water content and soil solution osmotic potentials are maximum due to leaching of salts and high soil water content. With increasing temperatures and the absence of frequent spring rains, salinity may increase and water potential decrease greatly in the surface cm as the soil dries. The vesicular crust of interspaces between shrubs may soften after spring rains, but rapidly hardens as the soil dries. Cracks separating the polygons of vesicular crusts are important safe sites for seed germination

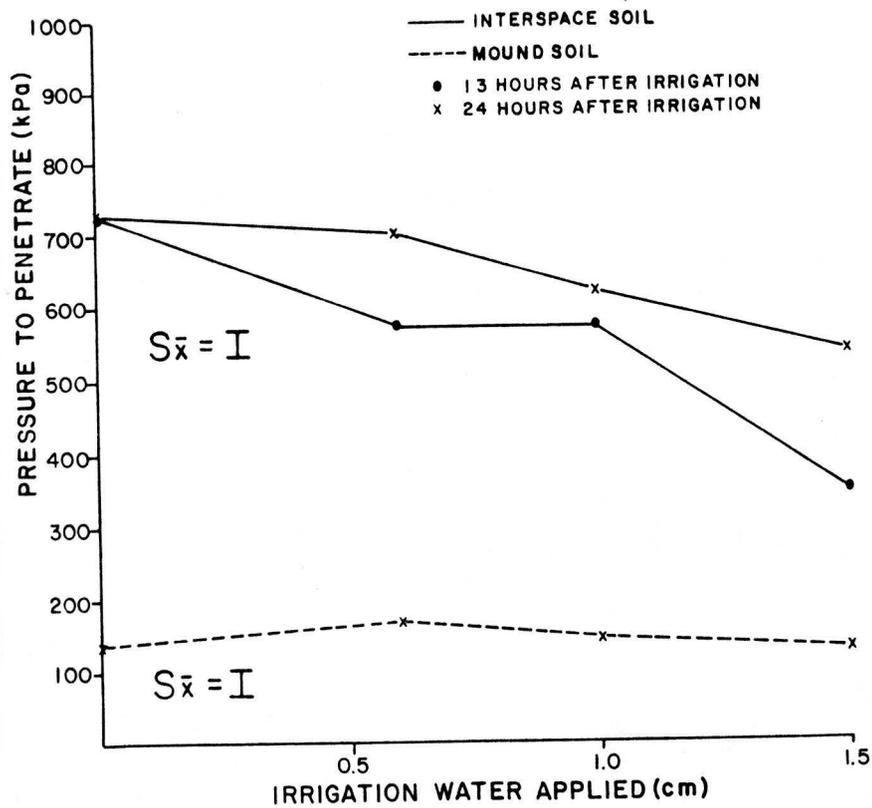


Figure 11. Pressure required to penetrate mound and interspace salt desert soils in Grass Valley, Nevada in relation to amount of irrigation and time after irrigation.

and emergence. They catch the seeds which then are able to emerge unrestricted by the vesicular crust from lower soil depths where the soil water potential is much higher and fluctuates less than in the surface cm. Natural seedling emergence of halogeton, wedgescale [Atriplex truncata (Torr.) Gray] and basin wildrye was observed only in crevices and cracks in the salt desert soil in this study. High spring precipitation favors seedling establishment on saline soils by maintaining higher total soil water potentials. As the soil surface dries in late spring and early summer, salinity of the seedbed increases as salt-bearing water from lower depths rises in response to the more negative hydraulic potential of the drier surface soil. Frequent spring precipitation slows the accumulation of salts in the surface 1-15 cm of the soil by continued leaching and results in higher soil solution osmotic potentials. In the absence of frequent rains, seedbed osmotic and matric potentials decrease rapidly in the spring and early summer. During years of minimal spring precipitation seedling establishment on salt desert soils, where salinity increases with depth, may be dependent on rapid and early root growth and the ability to osmotically adjust to maintain root growth in the wetter, but increasingly saline subsurface soil. Although mound soils may be higher in fertility, aggregate stability and penetrability, they may have the same salinity and osmotic potentials, but have lower matric potentials for a given water content than interspace soils. The results of this study underscore the importance of cracks between the soil polygons as safe sites and high spring precipitation to seedling establishment in salt desert soils.

results of test, the
In conclusion, the hypotheses can be reported as follows:

- II. A. Precipitation simulated by irrigation did result in low soil salinity and higher soil water contents, and therefore higher total, matric and osmotic potentials than nonirrigated soil.
- B. The nonsaline soil did generally have higher total water potentials than the saline soil. Generally, the difference in total water potential was equal to the osmotic potential of the saline soil.
- C. Shrub mound soils averaged lower water potentials, similar salinity and greater penetrability than interspace soils.
- D. Precipitation or irrigation increased the penetrability of interspace soils, but the surface crust rapidly rehardened as it dried out.

Precipitation and soil salinity affected seedbed water potentials as was hypothesized, but microtopography effects were different than those expected.

EMERGENCE AND ESTABLISHMENT OF BASIN WILDRYE AND TALL
WHEATGRASS IN RELATION TO MOISTURE AND SALINITY

Introduction

Valley bottoms and flood plains of the Great Basin historically were important grazing lands for the livestock of early ranchers (Lesperance et al. 1978). In the late 19th century, many of the cattle grazing sagebrush/grasslands were wintered on the extensive basin wildrye stands dominating many of these lowlands (Hazelton et al. 1961, Lesperance et al. 1978, Young and Evans 1981). Because basin wildrye is sensitive to spring clipping and frequent herbage removal during the growing season (Krall et al. 1971, Perry and Chapman 1974, 1975, 1976), many stands were decimated by excessive grazing (Young et al. 1975). *degraded means reduced by 10, see dictionary*

Recovering the forage production of these lowland ranges is desirable because they are extensive and in close proximity to many ranch base properties. Many areas have the potential for high forage production due to the subsurface and overland drainage water they receive and the high water holding capacity of the associated fine-textured soils. Extensive lowlands now dominated by greasewood and salt rabbitbrush and lacking an understory of basin wildrye could be productive after chemical brush control (Cluff et al. 1983) and establishment of forage species adapted to the saline/alkaline and arid soils (Roundy et al. 1983).

Seedling establishment on these soils may be limited by low water potential due to infrequent precipitation, low soil matric potentials and high soil salinity. Salts lower the osmotic potential of the soil

solution and specific ions may be toxic to germinating seeds and seedlings. Precipitation in the Great Basin mainly occurs in fall, winter, and spring (Figure 7). As storms resulting in effective precipitation become less frequent from March through June, soil water content decreases so that the soil matric and osmotic potentials are decreased and soil water may be unavailable for seed germination or seedling growth (Roundy et al. 1984). Successful seedling establishment is dependent on frequency and amount of winter and spring precipitation and the ability of the seeded species to germinate and grow as soil matric and osmotic potentials decrease. Forage species most recommended for seeding saline, dry soils include Russian wildrye, tall wheatgrass, and basin wildrye (Plummer et al. 1955, 1968). Russian wildrye is difficult to establish due to poor seedling vigor (Hafenrichter et al. 1968, Vallentine 1961). Tall wheatgrass is well known for its salt and sodium tolerance (Carter and Peterson 1962, Dewey 1960, Moxley et al. 1978, Shannon 1978, Rauser and Crowle 1963) and has established well on wet saline soils, but may not persist on dry saline soils (Forsberg 1953, Ludwig and McGinnies 1978, McGinnies and Ludwig 1978, McPhie 1973). Rollins et al. (1968) and Eckert et al. (1973) reported difficulty in establishing tall wheatgrass and basin wildrye on a greasewood/rabbitbrush site in central Nevada due to high salinity, sodicity and high boron concentrations. Young and Evans (1981) suggested that many of the sites where basin wildrye occurred naturally are too dry for tall wheatgrass and too saline for crested wheatgrass. Although basin wildrye has had a reputation for low seed germination and poor seedling vigor (Young and Evans 1981), a selected cultivar, Magnar, has been released which has high and viable seed production and high germination (Evans and Young 1983).

The purpose of this study was to determine the establishment of Magnar basin wildrye compared to that of Jose tall wheatgrass in relation to soil salinity and spring precipitation as simulated by irrigation in central Nevada.

Study Area and Methods

Two sites were chosen for their differences in soil salinity and their similarities in soil morphology and texture and potential to support mature basin wildrye plants. The nonsaline and saline sites are both in Grass Valley, Eureka and Lander counties, Nevada, at the University of Nevada's Gund Research and Development ranch on the east side of the dry lake bed of pluvial Lake Gilbert (Young and Evans 1980). The soil of the nonsaline site is of the fine, montmorillonitic, mesic family of Typic Camborthids (Appendix, Table 17) in a lagoon of Lake Gilbert while that of the saline site is a Gund silt-loam series of the fine-silty over clayey, mixed (calcareous), mesic family of Aquic Durorthidic Torriorthents (Appendix, Table 16) on the lake plain (Peterson 1981) of Lake Gilbert. The physical and chemical properties of these fine-textured soils are representative of many other flood plains and valley bottoms in the Great Basin (Roundy 1983¹ and Roundy et al. 1984). The soil of the saline site is saline/alkaline having an average SAR of 44 and an average E_c of 8.4 dS·m⁻¹ in the upper 30 cm with the predominant salts being NaCl and sodium sulfate Na₂SO₄. The nonsaline soil has an average E_c of less than 0.5 dS·m⁻¹. Both sites supported a shrub community of greasewood, salt rabbitbrush, and big sagebrush

¹ Roundy, B.A. 1983. Estimation of water potential components of saline soils of Great Basin rangelands. Soil Sci. Soc. Am. J. (submitted).

(Artemisia tridentata Nutt. ssp. tridentata) and a herbaceous understory of basin wildrye.

Brush on both sites was eliminated by applying $3.4 \text{ kg}\cdot\text{ha}^{-1}$ of 2,4-D in the spring and rotobearing later in the summer of 1980. The sites were fenced to exclude rabbits and livestock. In the fall of 1980, a moderately saline plot ($\text{ECe} = 7 \text{ dS}\cdot\text{m}^{-1}$) and a saline plot ($\text{ECe} = 9.7 \text{ dS}\cdot\text{m}^{-1}$) on the saline site were seeded to ^{locally collected?} basin wildrye. In the fall of 1981 a moderately saline plot and a nonsaline plot were seeded to both Jose tall wheatgrass and Magnar basin wildrye. Grasses were seeded 1 to 2-cm deep with a vegetable seeder calibrated for a rate of 1 seed per cm into circular concentric furrows, 35 cm apart and constructed by hand with a hoe to be similar to furrows made by a standard rangeland drill. The circular plots were 32 m in diameter and in 1980 were divided into three pie-shaped blocks seeded to Magnar basin wildrye and in 1981 were divided into six pie-shaped blocks seeded alternately to Jose tall wheatgrass and Magnar basin wildrye (Appendix, Figure 29).

In the spring of each year after fall seeding, water was applied using a single sprinkler with a 4.8 mm range by 2.4 mm spreader nozzle operated at 0.2 MPa on a 60 cm riser in the center of each circular plot to create an irrigation gradient (Hanks et al. 1976). Water applied decreased almost linearly with distance from the sprinkler head (Appendix, Figure 28). Amount of irrigation was measured in cans 14.5 cm diameter by 17.5 cm deep placed along three transects at 2.5, 6.5, 10.5 and 16 m from the center of each plot. Each irrigation was approximately 6 hr and added an average of 2 cm of water to the soil at 2.5 m from the plot center, and no water at 16 m from the plot center. There were five irrigations in the spring of 1981 and four in 1982 with the plots being irrigated approximately every two weeks from May through June. The irrigation water was hauled

to the plots from a nearby mountain stream and had an electrical conductivity of less than $0.02 \text{ dS}\cdot\text{m}^{-1}$.

Seedling counts were made as early as seedlings emerged, and thereafter every 2 weeks through July and again the following spring. Seedlings per m of row were recorded in the concentric rows at 2.5, 6.5, 10.5 and 16 m from the plot center and in the inside and outside row bordering these rows. Six observations per block, species and distance from the plot center were recorded at each sampling date. Once each year in June seedlings per 0.5 m of row were counted ^{on} ~~and for~~ old shrub mounds and interspaces separately.

Soil samples of one mound and one interspace were collected along three transects in 1981 and along two transects at 1982 at distances of 2.5, 6.5, 10.5 and 16 m from each plot center. Samples were collected starting in April and thereafter in 2 to 4-week intervals. Samples were generally collected 2 weeks after each irrigation on the day preceding the next irrigation. Samples were taken for depth intervals of 0-1, 1-5, 5-10, 10-15 and 25-30 cm and were analyzed for E_c, volumetric water content, and total, matric and osmotic soil water potential as described by Roundy (1983)¹ and reported by Roundy et al. (1984). Other chemical and physical characteristics of these soils are reported in Roundy (1983)¹, Roundy et al. 1984, and Table 1.

Predawn leaf water potentials of seedlings receiving the highest irrigation at 2.5 m from the plot center and those receiving no irrigation at 16 m from the plot center were measured periodically using a pressure bomb (Scholander et al. 1965).

Emergence and establishment of the highest irrigated seedlings and seedlings receiving no irrigation were compared using analysis of variance

and Duncan's multiple range test. Linear and polynomial regression were used respectively to compare seedling responses to soil water potential and to compare species establishment on the nonsaline, moderately saline, and saline plots in relation to cumulative irrigation plus precipitation.

Results and Discussion

Because natural precipitation was not controlled, seedling emergence and establishment results must be interpreted taking into account the natural precipitation in relation to irrigation each year. In 1980-1981, low winter precipitation was followed by high precipitation in March, April and May and low precipitation in June (Figure 12). In 1981-1982, winter and March precipitation was high followed by low precipitation in April, May and June. Generally, 1980-1981 could be characterized as a dry winter followed by a wet spring, while 1981-1982 could be considered a wet winter followed by a dry spring. Seedlings generally followed a pattern of initial emergence when temperatures became warm enough for germination in April and May, followed by mortality of some seedlings with the absence of rain. This was followed by additional seedling emergence associated with spring rains and irrigation followed by gradual mortality through the summer (Figure 13).

Emergence

Irrigation greatly increased Magnar basin wildrye seedling emergence in the spring of 1981, but had little effect on emergence of basin wildrye or tall wheatgrass in the spring of 1982 (Figure 13 and Table 3).

On the moderately saline plot, emergence of basin wildrye under the highest irrigation was much higher in 1981 than in 1982, but maximum emergence of the nonirrigated rows was less in 1981 than in 1982 (Table 3).

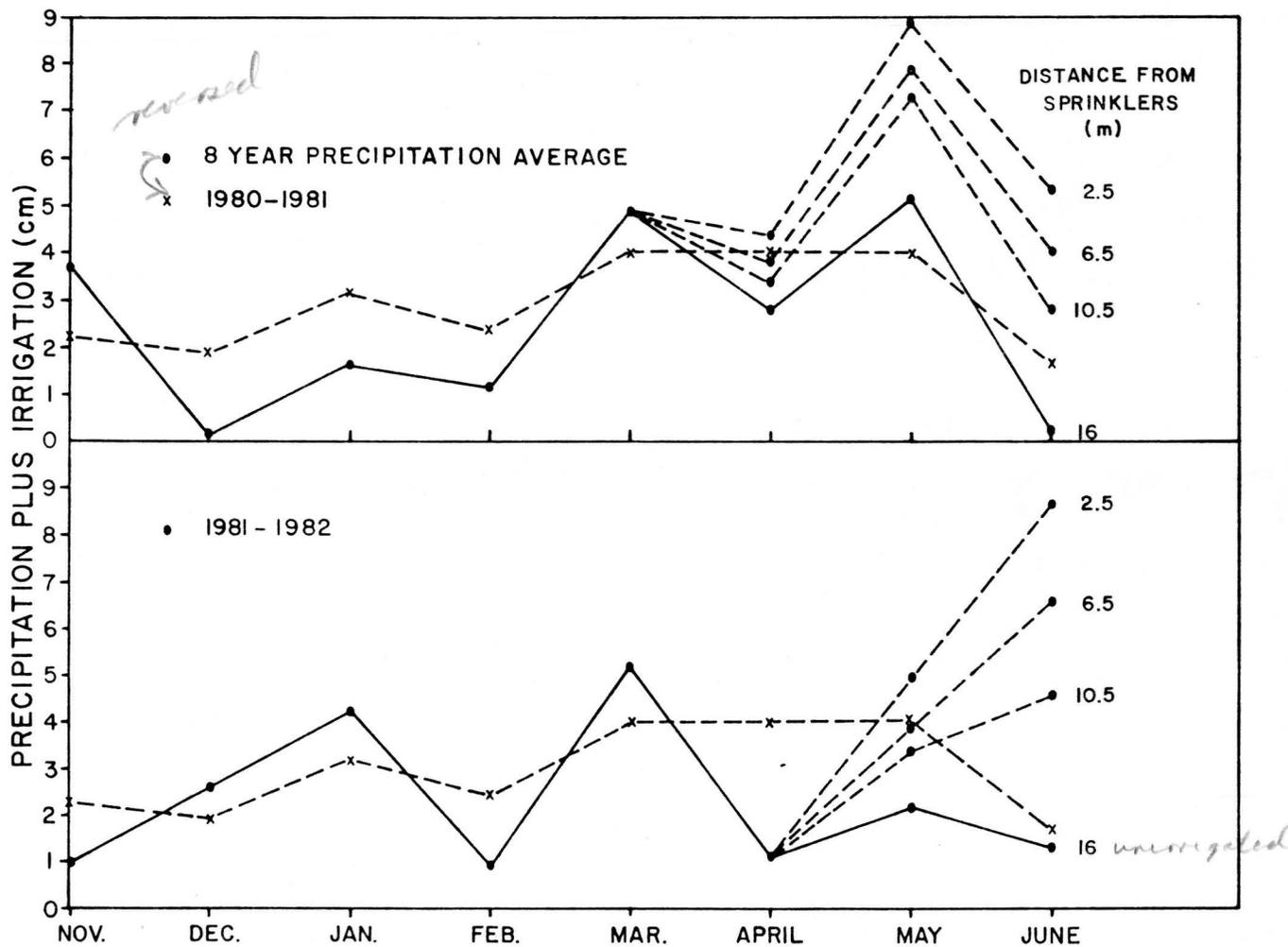


Figure 12. Monthly precipitation and irrigation for 1980 to 1982 and 8-year precipitation means at the Gund research and demonstration ranch, Grass Valley, Nevada.

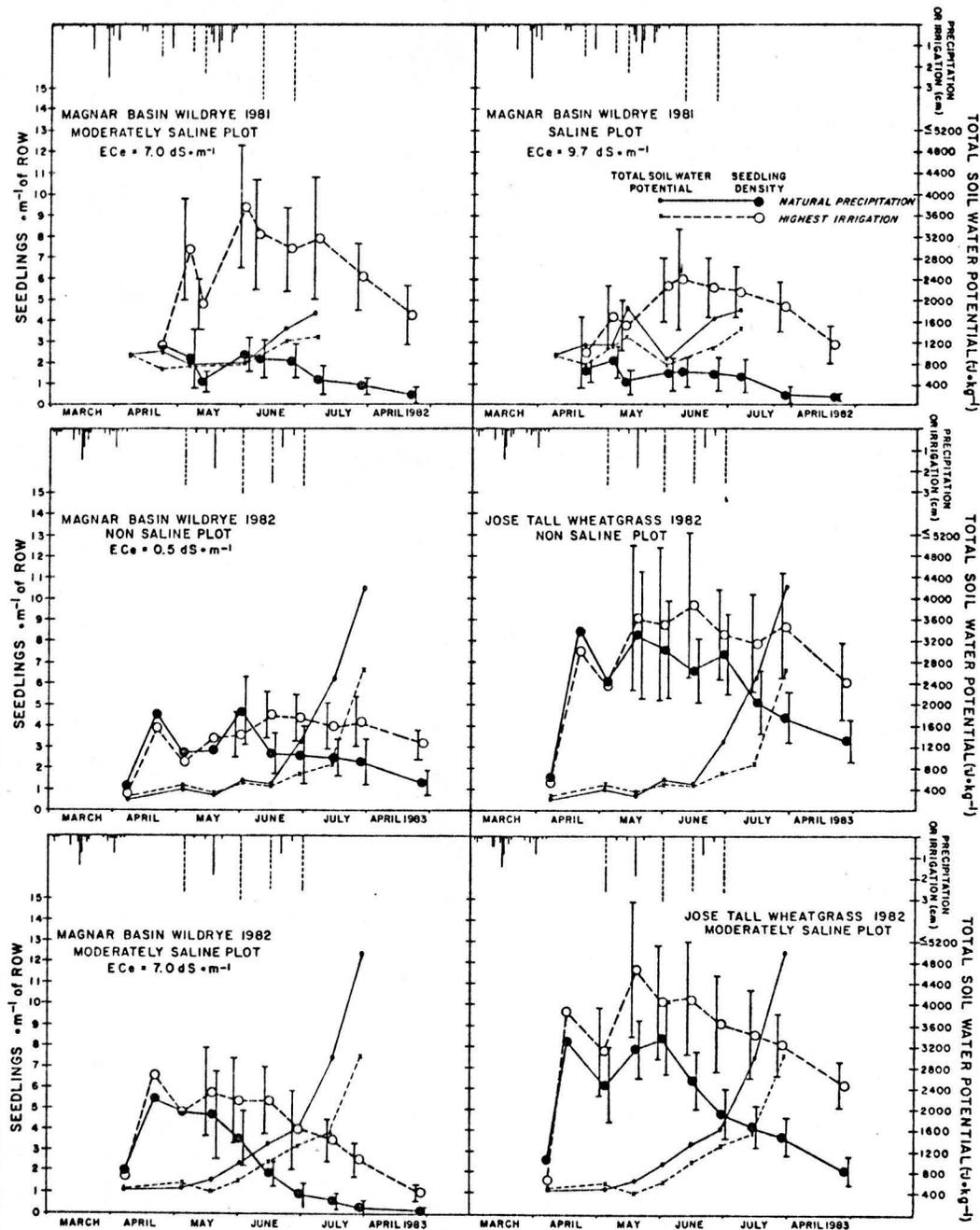


Figure 13. Seedling density with confidence intervals ($P=0.05$), daily precipitation and irrigation, and total soil water potential (5 to 15 cm interval) for plots with Magnar basin wildrye in 1981 and Magnar basin wildrye and Jose tall wheatgrass in 1982 in Grass Valley, Nevada.

Table 3. Emerged and established seedlings and seedling survival percentage of Jose tall wheatgrass and Magnar basin wildrye in central Nevada in relation to soil salinity and irrigation.*

| Cultivar | Year | Soil | Soil ECe (dS·m ⁻¹) | Treatment | Precipitation plus irrigation April-June (cm) | Maximum seedlings emerged (plants/m of row) | Seedlings established (plants/m of row) | Seedling Survival (%) |
|-----------------|------|-------------------|-----------------------------------|--------------------|--|---|---|-----------------------------|
| Basin wildrye | 1981 | Moderately saline | 7.0 | No irrigation | 8.3 | 2.8 e | 0.5 e | 18 |
| | | | | Highest irrigation | 18.7 | 9.4 ab | 4.3 b | 46 |
| | | Saline | 9.7 | No irrigation | 8.3 | 2.1 e | 0.4 e | 19 |
| | | | | Highest irrigation | 18.7 | 6.0 cd | 2.9 c | 48 |
| | 1982 | Nonsaline | 0.5 | No irrigation | 4.6 | 4.7 de | 1.3 de | 28 |
| | | | | Highest irrigation | 14.6 | 4.5 de | 3.1 c | 69 |
| | | Moderately saline | 7.0 | No irrigation | 4.6 | 4.7 de | 0.1 e | 2 |
| | | | | Highest irrigation | 14.6 | 5.8 c-e | 1.0 de | 17 |
| Tall wheatgrass | 1982 | Nonsaline | 0.5 | No irrigation | 4.6 | 8.3 bc | 3.3 bc | 40 |
| | | | | Highest irrigation | 14.6 | 9.7 ab | 6.1 a | 63 |
| | | Moderately saline | 7.0 | No irrigation | 4.6 | 8.4 bc | 2.1 cd | 25 |
| | | | | Highest irrigation | 14.6 | 11.7 a | 6.2 a | 53 |

*Means in the same column followed by the same letter are not significantly different at the 0.05 level as determined by Duncan's multiple range test.

These trends can be explained by the different patterns of winter and spring precipitation and irrigation in 1981 and 1982 and the associated differences in the water potential of the surface soil. Due to lack of winter soil water recharge (Figure 12), the surface soil water potential in the upper 1 to 5 cm of the moderately saline plot averaged -820 and $-300 \text{ J}\cdot\text{kg}^{-1}$, respectively, in 1981 and 1982. Due to the initially dry seedbed in 1981, emergence did not begin until after irrigation and natural storms in mid to late April, with maximum emergence occurring in June after substantial April and May irrigations and storms (Figure 13). In contrast, maximum emergence of Magnar basin wildrye on the moderately saline plot in 1982 occurred in April prior to any irrigations when temperatures were warm enough for germination and the soil was still wet from high winter precipitation. In 1981, irrigations combined with storms resulted in moisture events about 8 days apart for the irrigated rows compared to natural storms about 20 days apart for the nonirrigated rows, and resulted in about 4 times the seedling emergence on the highest irrigated rows compared to the nonirrigated rows (Table 3). In the absence of frequent rains, the surface soil rapidly dried out, resulting in extremely low soil water potentials (Roundy et al. 1984). The higher frequency of irrigations and storms on an initially dry seedbed in April and May in 1981 probably resulted in greater germination and emergence of the shallower basin wildrye seeds resulting in greater maximum emergence on the irrigated rows in 1981 than 1982. Due to an initially wet seedbed in 1982, maximum emergence occurred prior to irrigation and nonirrigated rows had higher emergence than in 1981, when the seedbed was initially much drier. These data illustrate the importance of frequent spring storms to seedling emergence following a dry winter and also show

that the highest seedling emergence will be produced by frequent spring storms when temperatures are warm enough for germination.

There was generally no difference in maximum emergence in relation to soil salinity for basin wildrye or tall wheatgrass seedlings except that in 1981 basin wildrye seedlings receiving the highest irrigation had greater emergence on the moderately saline plot than on the saline plot (Table 3).

In 1982, Jose tall wheatgrass had higher seedling emergence than Magnar basin wildrye on both the highest irrigated and nonirrigated rows and on both the nonsaline and moderately saline plots (Table 3). Jose tall wheatgrass has greater radicle growth at low osmotic potentials, has higher total germination and more rapid emergence at low osmotic and matric potentials than Magnar basin wildrye and germinates at lower osmotic and matric potentials than Magnar basin wildrye². Magnar basin wildrye appears to require more frequent storms or irrigation as occurred in 1981 to equal the emergence produced by Jose tall wheatgrass following a wet winter and relatively dry spring as in 1982.

In 1981, basin wildrye had higher emergence on old shrub mound soils than on interspace soils, but in 1982 there was no difference in emergence between mound and interspace soils for basin wildrye or tall wheatgrass seedlings (Table 4). Frelich et al. (1973) have shown that a combination of low osmotic potentials and hard soil crusts reduces and delays emergence of both tall wheatgrass and basin wildrye. Mound soils are more penetrable than interspace soils which become much more penetrable following irrigation or precipitation, but harden rapidly as they

² Roundy, B.A., J.A. Young and R.A. Evans. 1983. Germination of basin wildrye and tall wheatgrass in relation to osmotic and matric potential. Agron. J. (submitted).

Table 4. Seedling density of Jose tall wheatgrass and Magnar basin wildrye seeded on old shrub mounds and interspaces.*

| <u>Species</u> | <u>Date</u> | <u>Mound</u> | <u>Interspace</u> |
|-----------------|--------------|---------------------------|-------------------|
| | | <u>Seedlings/m of row</u> | |
| Basin wildrye | 24 June 1981 | 7.3 a | 4.0 b |
| Basin wildrye | 16 June 1982 | 4.3 b | 3.7 b |
| Tall wheatgrass | 16 June 1982 | 10.3 a | 9.0 a |

*Means for the same date followed by the same letter are not significantly different at the 0.05 probability level by Duncan's multiple range test.

dry out (Roundy et al. 1984). However, both in 1981 and 1982, total water potential of mound soils averaged $-300 \text{ J}\cdot\text{kg}^{-1}$ lower than interspace soils (Roundy et al. 1984). This difference in total water potential was generally due to a difference in the relationship of soil water content to matric potential for the mound and interspace soils and was generally not due to salinity (Roundy et al. 1984). Greater frequency of storms and irrigation in 1981 may have allowed mound surface soils to remain at high matric potentials for a long enough period of time to result in higher emergence on the more penetrable mound than interspace soils.

Although the saline soil in this study had boron concentrations ranging up to 100 ppm in the saturation extract, boron probably had little effect on seed germination since both species had high germination in boron concentrations up to 450 ppm in laboratory tests³. However, boron may have reduced emergence and survival of some seedlings since radicle growth greater than 5 mm of both species is reduced at concentrations above 150 ppm and root yield of both species is reduced by half at concentrations above 30 ppm³.

Establishment

As soil water potential decreased through the summer, seedling density decreased (Figure 13). The highest irrigation generally increased the number of seedlings of both species established on both the nonsaline and saline soils (Table 3). Seedling establishment generally increased with increased irrigation (Figure 14).

An acceptable stand of Magnar basin wildrye seedlings (at least two seedlings per m of row) on the saline site was produced only in 1981 and

³ Roundy, B.A. 1983. Germination and growth of basin wildrye and tall wheatgrass in relation to boron. Agron. J. (Submitted).

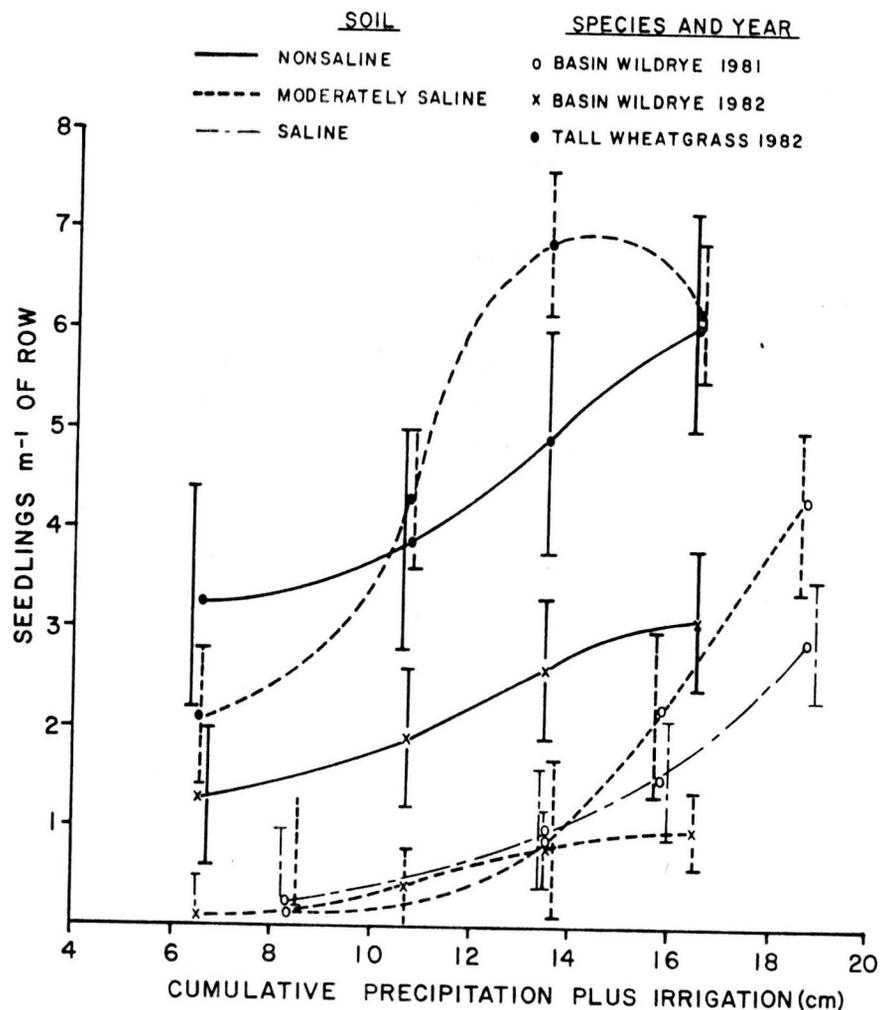


Figure 14. Established seedling density and confidence intervals ($P = 0.05$) of Magnar basin wildrye and Jose tall wheatgrass in plots of different soil salinity as a third-degree polynomial function of cumulative precipitation plus irrigation from April through June at Grass Valley, Nevada.

required at least 16 cm of irrigation plus precipitation from April through June (Figure 14). Basin wildrye failed to produce an acceptable stand of seedlings in 1982 on the moderately saline plot, even at the highest irrigation (Table 3, Figure 14). The lower established density of basin wildrye in 1982 than in 1981 on the saline site was due mainly to lower emergence and somewhat to lower survival (Table 3). In 1981, peak seedling emergence was preceded by a series of natural storms in May (Figures 12 and 13). Irrigation before and after these storms not only resulted in greater seedling emergence, but also resulted in somewhat higher survival of emerged seedlings.

In 1981, seedlings receiving the highest irrigation received 8.9 cm of water from two irrigations and a series of storms in May compared to 4.6 cm received in May of 1982 from one irrigation and one large storm. The additional water and the reduced evaporative demand associated with the natural storms in May of 1981 resulted in low plant water stress in June (Table 5) and higher total soil water potential in early June in 1981 than 1982. For example, total soil water potential of the 1-5 cm interval in the highest irrigated rows of the moderately saline plot averaged -560 and $-1500 \text{ J}\cdot\text{kg}^{-1}$, respectively, on June 1, 1981 and 1982. Frequent precipitation on saline soils maintains higher total water potentials by increasing soil water content which increases soil matric and osmotic potentials and by leaching salts which also increases soil osmotic potential (Roundy et al. 1984). Even though Magnar basin wildrye seedlings received 8.5 cm of water from irrigations and natural storms of June of 1982, they still failed to establish on the moderately saline plot. These differences in establishment in 1981 and 1982 suggest that high and frequent precipitation in May when evaporative demands are low are more

Table 5. Predawn leaf water potential of Jose tall wheatgrass and Magnar basin wildrye seedlings receiving natural precipitation (no irrigation) and the highest irrigation treatment.

| | | | 1981 | | | | |
|---------|-----------------------------------|--------------------|---|------------|-----------|-----------|-----------|
| | | | Leaf water potential \pm standard deviation ($J \cdot kg^{-1}$) | | | | |
| Species | Soil ECe ($dS \cdot m^{-1}$) | Treatment | 2 June | 10 June | 24 June | 8 July | 29 July |
| Magnar | 7.0 | No irrigation | -580:150 | -1090:490 | -1090:200 | -1150:380 | -2940:490 |
| | | Highest irrigation | -390:30 | -440:80 | -520:170 | -1050:160 | -1730:130 |
| | 9.7 | No irrigation | -390:180 | -1230:510 | -1430:70 | -1480:330 | -2370:980 |
| | | Highest irrigation | -600:130 | -320:80 | -1050:70 | -1360:400 | -1170:160 |
| | | | 1982 | | | | |
| | | | Leaf water potential \pm standard deviation ($J \cdot kg^{-1}$) | | | | |
| | | | 17 June | 16 July | 28 July | 17 August | |
| Magnar | 0.5 | No irrigation | -860:150 | -1420:270 | -790:290 | -2680:430 | |
| | | Highest irrigation | -260:40 | -790:180 | -610:290 | -2670:590 | |
| | 7.0 | No irrigation | -1210:370 | -2470:430 | - | - | |
| | | Highest irrigation | -600:180 | -1290:400 | -600:300 | -2760:480 | |
| Jose | 0.5 | No irrigation | -980:530 | -910:420 | -850:530 | -2900:760 | |
| | | Highest irrigation | -310:70 | -600:90 | -460:210 | -2430:260 | |
| | 7.0 | No irrigation | -1270:310 | -3780:1080 | -2200:780 | -6770:260 | |
| | | Highest irrigation | -420:120 | -910:320 | -510:240 | -1660:440 | |

effective than in June for emergence and establishment of Magnar basin wildrye on moderately saline soils.

Basin wildrye seedlings had greater establishment on the nonsaline plot than the saline plot in 1982 (Table 3, Figure 14). Precipitation plus irrigation of 14 cm in April through June produced an acceptable stand of Magnar basin wildrye seedlings on the nonsaline plot while 16 cm failed to produce an acceptable stand on the moderately saline plot in 1982. Greater plant water stress was associated with higher soil salinity (Table 5). The lower total water potential of the saline than the nonsaline soil could generally be attributed to its osmotic potential where the matric potential of the two soils was similar (Roundy et al. 1984).

Jose tall wheatgrass produced an acceptable stand of seedlings with no irrigation, but produced excellent seedling stands (six seedlings per m of row) with irrigation on both the nonsaline and moderately saline plots (Table 3, Figure 14). Although tall wheatgrass was not seeded in 1981, it probably would have had high establishment since basin wildrye had much higher establishment in 1981 than 1982.

Greater establishment of tall wheatgrass than basin wildrye was due not only to higher emergence, but also generally greater seedling survival. Although water stress of tall wheatgrass was greater on the moderately saline than the nonsaline plot (Table 5), salinity did not reduce survival of tall wheatgrass seedlings as much as it reduced survival of basin wildrye seedlings.

Magnar basin wildrye seedling survival associated with decreasing soil water potential was significantly ($P = 0.05$) lower on the moderately saline plot than the nonsaline plot, while that of Jose tall wheatgrass

was similar for both plots and similar to Magnar basin wildrye on the nonsaline plot (Table 6). This suggests that Jose tall wheatgrass salinity tolerance is greater than that of Magnar basin wildrye. Jose tall wheatgrass has greater absolute growth of roots and shoots under decreasing osmotic potentials than Magnar basin wildrye (Roundy 1983). Because Jose tall wheatgrass has more rapid root and shoot elongation than Magnar basin wildrye in nonsaline and saline soils,⁴ it would be expected to be more competitive and have higher establishment on nonsaline and saline soils than Magnar basin wildrye.

Although basin wildrye is definitely adapted to drier, saline soils, such as those seeded in this study, high and frequent spring precipitation or irrigation is necessary to establish it from seed on these soils. This suggests that high establishment of natural basin wildrye seedlings occurs only during years of unusually high precipitation as may be the case for other species growing in harsh environments (Noy-Meir 1973, Went 1955).

Although tall wheatgrass is able to establish on dry saline soils, as in this study, spring precipitation or irrigation can make the difference between an acceptable stand and an excellent stand on these soils. However, due to its inability to persist on many sites receiving less than 30 cm annual precipitation, tall wheatgrass may not be the best plant material to revegetate dry, saline lowlands. Use of irrigation or *introduction or breeding and selection* development of more drought and salt-tolerant plant materials is needed before many saline, arid sites may successfully be seeded.

⁴ Roundy, B.A. 1983. Root and shoot elongation of basin wildrye and tall wheatgrass in relation to drought and salinity. J. Range Manage. (Submitted).

Table 6. Statistics for the linear regressions of seedling percentage survival on total soil water potential ($J \cdot kg^{-1}$) at the 1-15 cm depth interval for Jose tall wheatgrass and Magnar basin wildrye seedlings in 1982 on nonsaline and saline soils in central Nevada.

| <u>Species</u> | <u>Soil</u> | <u>Intercept</u> | <u>Slope*</u> | <u>r⁺</u> |
|-----------------|-------------------|------------------|---------------|----------------------|
| Tall wheatgrass | Nonsaline | 99.1 | 0.00977 b | 0.86 |
| | Moderately saline | 104.6 | 0.01055 b | 0.90 |
| Basin wildrye | Nonsaline | 104.1 | 0.01126 b | 0.83 |
| | Moderately saline | 100.8 | 0.01697 a | 0.88 |

*Values followed by the same letter are not significantly different at the 0.05 level as determined by the slope test method of Snedecor and Cochran (1971).

+All r values are significant at the 0.01 level.

In conclusion, the ^{results of} hypotheses ^{testing} can be reported as follows:

- III. A. Precipitation generally increased seedling emergence and establishment. Irrigation to simulate precipitation increased seedling emergence after a dry winter more than after a wet winter. Irrigation to ^{augment} ~~simulate~~ precipitation always increased seedling survival.
- B. Salinity decreased establishment of basin wildrye, but had little effect on emergence of basin wildrye or emergence and establishment of tall wheatgrass.
- C. Seedling emergence was generally similar on mound and interspace soils.
- D. Jose tall wheatgrass had higher emergence and establishment than Magnar basin wildrye on the saline and nonsaline soils and at all irrigation levels.

Precipitation affected seedling emergence and establishment, salinity affected seedling establishment, and microtopography generally had little effect on seedling emergence.

GERMINATION OF BASIN WILDRYE AND TALL WHEATGRASS
IN RELATION TO OSMOTIC AND MATRIC POTENTIAL

Introduction

Increasing forage production on lowland rangelands in the arid west once dominated by basin wildrye may require seeding species ^{or cultivars} which can germinate and persist in saline, rapidly-drying seedbeds. Young and Evans (1981) have summarized the ^{degradation} ~~decimation~~ of basin wildrye on these rangelands and the problems associated with revegetating them with desirable forages. Germination in the associated soils is limited by low soil matric and osmotic potentials and possibly toxic concentrations of specific ions. Tall wheatgrass is well known for its salt tolerance at germination and at the seedling stage (Dewey 1960, Rauser and Crowle 1963, McElgunn and Lawrence 1973) but germination responses at low soil matric potentials are unknown. Germination and emergence of native collections of basin wildrye at low osmotic potentials have been reported by Choudhuri (1968), Frelich, et al. (1973) and Young and Evans (1981). Native collections of basin wildrye have a reputation for low seed germination, but a newly released cultivar, Magnar, has high and viable seed production and high germination (Evans and Young 1983). Because germination and seedling tolerance of low soil osmotic potentials may not be correlated for a particular plant material (McGinnies 1960, Sharma 1973), both germination and seedling studies are necessary in evaluating plant material adaptability to saline, arid rangelands. In a previous study (Roundy 1983) Jose tall wheatgrass seedlings were more tolerant of low

soil osmotic potentials than Magnar basin wildrye seedlings. The present study compares the germination responses of these two cultivars to low soil matric potentials and low osmotic potentials of specific ions.

Methods

A two-factor analysis of covariance experiment was conducted to determine the effects of the covariate, osmotic potential, on germination responses of the two species in four osmoticum. Twenty-five seeds each of tall wheatgrass and basin wildrye were placed in plastic boxes 10-cm square by 7-cm deep filled with 5 g of ground polystyrene foam to support the seedlings following the procedures of Young et al. (1968). Four replications each were filled with solutions of NaCl, Na₂SO₄, CaCl₂ and polyethylene glycol (PEG) with a molecular weight of 6000 prepared to have osmotic potentials of 0, -100, -200, -400, -600, -800, -1000, -1200, -1500, -2000 and -2500 J·kg⁻¹ at 15°C. Appropriate concentrations of the salts for each osmotic potential were determined by using osmotic coefficients and the calculations of Robinson and Stokes (1959) where:

$$\Psi_{\pi} = - \frac{v RT W_A}{1000 \bar{V}_A} \phi m$$

and Ψ_{π} is the osmotic potential, v is the number of moles of ions that can be ionized from one mole of salt, R is the universal gas constant, T is the absolute temperature, W_A is the molecular weight of the solvent, \bar{V}_A is the partial molal volume of the solvent, m is the molality of the solution and ϕ is the molal osmotic coefficient. For water at 25°C this can be simplified to:

$$\Psi_{\pi} \text{ (J·kg}^{-1}\text{)} = -(2471.5) (v) (m) (\phi)$$

Osmotic potential of the solutions at 15°C was then calculated by:

$$\Psi_{\pi} \text{ at } 15^{\circ}\text{C (J}\cdot\text{kg}^{-1}) = (\Psi_{\pi} \text{ at } 25^{\circ}\text{C}) \left(\frac{288.2\text{K}}{289.2\text{K}} \right)$$

Polyethylene glycol solutions were mixed according to the calibration procedures of Michel and Kaufmann (1973). Germinated seedlings were counted every 2 or 3 days for 3 weeks and radicle length of 5 seedlings per cultivar were measured for each osmotic potential replication at the end of 3 weeks. Average rates of germination were calculated after MaGuire (1962) where:

$$\text{Average germination rate (\% day}^{-1}\text{)} = \frac{n}{\sum_i} [g_n - g_{(n-1)}] / n$$

in which g is the total germination percentage on an incubation day n minus the total germination percentage on the previous day $g(n-1)$ divided by the incubation day n . Germination responses were estimated as a function of a multiple regression equation using dummy variables for species and osmotica and using the linear, quadratic and cubic covariates of osmotic potential and interaction terms as independent variables. Main effects and interactions of species, osmotica and osmotic potential were tested for significance as outlined by Nie et al. (1975) and Ott (1977).

A multiple regression experiment was conducted to determine the effects of soil matric potential on emergence of the two species. Different amounts of water were added to 200 g of air-dried nonsaline Gund silt loam series of the fine-silty over clayey, mixed (calcareous), mesic family of Aquic Durorthidic Torriorthents in plastic boxes 10-cm square by 7-cm deep to create a range of soil matric potentials. After an equilibrium period of 1 week, the soil in each box was thoroughly mixed by shaking and then was compressed to a bulk density of 1.5 g cm^{-3} .

Twenty-five seeds of each species were planted in rows 1-cm deep for each box. Four replications of 17 different gravimetric soil water contents from 0.25 to 0.06 were prepared. Soil matric potential of each replication was determined at the end of the experiment by placing approximately 2 g of soil in psychrometer chambers described by Johnson and Brown (1977) and by measuring microvolt output after a 15-sec cooling period following 4-hour equilibration in a constant temperature water bath at 25°C. Water potential was calculated from microvolt output using the model of Brown and Bartos (1982). Emerged seedlings were counted every 2 or 3 days for 3 weeks. Total emergence and emergence over time were estimated as a third-degree polynomial function of soil matric potential and incubation days.

Emergence in relation to soil osmotic and matric potentials was studied by adding NaCl solutions to 200 g of Gund silt loam to create all possible combinations of matric and osmotic potential in $-500 \text{ J}\cdot\text{kg}^{-1}$ increments from a total potential of 0 to $-2000 \text{ J}\cdot\text{kg}^{-1}$. Solutions and soil were mixed and seeds were sown in the soil in boxes as described above with 4 replications each with 25 seeds of each cultivar for each replication. Total soil water potential of each replication was checked at the end of the experiment with thermocouple psychrometers. Emerged seedlings were counted at the end of 3 weeks.

A multiple regression experiment was conducted to determine the effects of seed water content and seed water potential on germination of the two species. Seeds were soaked for different periods of time and the seed water content, water potential, and germination were subsequently determined. Four replications of 50 seeds of each cultivar were weighed and then soaked in distilled water in petri dishes for 1.5, 2.5, 4.5, 6.5,

8, 12.5, 18.5, 24, 36.5 and 48 hours. After seeds were soaked, they were blotted dry and weighed to determine gravimetric water content. Water potential of 25 seeds of each replication was measured in thermocouple psychrometer chambers after a 24-hr equilibration period in a constant temperature water bath at 25°C. The other 25 seeds of each replication were transferred to petri dishes 5.5 cm in diameter and 1 cm deep. The dishes were covered with parafilm and the lid was pressed on to prevent evaporation. Germinated seeds were counted every 2 or 3 days for 3 weeks. Germination was estimated as a third-degree polynomial function of seed water content or seed water potential.

In all experiments, seeds were soaked or incubated in dark germinators at a constant 15°C. Seeds in plastic foam were considered germinated when the radicle had emerged 0.5 cm and seedlings in soil were considered emerged when the coleoptile was visible above the soil surface.

Comparisons of germination responses in osmotic solutions and in soils at low matric potentials were made by comparing multiple regression estimates and confidence intervals (Ott 1977) of germination or emergence at different water potentials.

Results

Germination in Different Osmotica

Total germination, rate of germination, and radicle length varied statistically between species and among different osmotica (Table 7). When adjusted for each other, linear, quadratic and cubic effects of osmotic potential were significant for total and rate of germination, but only the linear effects of osmotic potential were significant for

Table 7. Analysis of covariance of total germination, rate of germination, and radicle length according to species and osmoticum and linear, quadratic, cubic, and combined covariates of osmotic potential for Jose tall wheatgrass and Magnar basin wildrye.

| Source of Variation | F Value | | |
|-----------------------------|-------------|---------------------|----------------|
| | Germination | Rate of Germination | Radicle length |
| Species (S) | 89.2** | 53.6** | 143.9** |
| Osmoticum (O) | 16.7** | 41.3** | 307.3** |
| Osmotic potential (P) | 378.8** | 587.9** | 467.6** |
| Linear (p) | 18.8** | 16.6** | 76.6** |
| Quadratic (p ²) | 33.7** | 4.6* | 3.1 NS |
| Cubic (p ³) | 27.6** | 7.0* | 0.2 NS |
| S X O | 5.4** | 2.8* | 43.1** |
| S X P | 199.3** | 59.0** | 21.8** |
| S X p | 9.2** | 2.2 NS ⁺ | 21.5** |
| S X p ² | 34.3** | 4.3* | 9.8* |
| S X p ³ | 41.9** | 12.8** | 6.9** |
| O X P | 3.9** | 6.0** | 75.0** |
| O X p | 2.0 NS | 5.9** | 108.7** |
| O X p ² | 1.5 NS | 3.4** | 85.5** |
| O X p ³ | 1.2 NS | 1.9 NS | 55.9** |
| S X O X P | 6.6** | 1.8 NS | 5.7** |
| S X O X p | 1.4 NS | 0.7 NS | 6.9** |
| S X O X p ² | 1.3 NS | 0.5 NS | 4.5** |
| S X O X p ³ | 1.3 NS | 0.4 NS | 3.1* |

*, **Significant at the 0.05 and 0.01 levels, respectively.

⁺NS = not significant at the 0.05 level.

radicle length (Table 7). Because most of the interactions of species, osmotica, and osmotic potential were significant (Table 7), interpretations are based on response surface estimates of the germination parameters for each species and osmoticum at decreasing osmotic potentials (Table 8). Jose tall wheatgrass had higher total germination, higher rate of germination and greater radicle growth at low osmotic potentials in all the salts tested and in PEG than Magnar basin wildrye (Table 8). Tall wheatgrass had greater germination and a higher rate of germination than basin wildrye at osmotic potentials less than $-800 \text{ J}\cdot\text{kg}^{-1}$ and also had greater radicle growth than basin wildrye at all the osmotic potentials tested. Tall wheatgrass germinated at lower osmotic potentials than basin wildrye and its greatest initial drop in germination occurred from -1500 to $-2000 \text{ J}\cdot\text{kg}^{-1}$ osmotic potential, while that of Magnar occurred from -1000 to $-1200 \text{ J}\cdot\text{kg}^{-1}$. Reductions of 50% in 3-week germination, average rate of germination, and radicle length occurred at osmotic potentials less than -2000 to -2500 , -1500 to -2000 and -600 to $-2000 \text{ J}\cdot\text{kg}^{-1}$, respectively, for tall wheatgrass and less than -1200 to -1500 , -800 to -1000 and -400 to $-2000 \text{ J}\cdot\text{kg}^{-1}$, respectively, for basin wildrye, depending on the osmoticum.

Generally, germination responses were lower when the cultivars were incubated in salts than in PEG. Specific salts had a more negative effect on germination rate and especially on radicle growth than on total germination. For example, tall wheatgrass had higher total germination in NaCl than PEG at osmotic potentials below $-1500 \text{ J}\cdot\text{kg}^{-1}$ (Table 8 and Figure 15), but the rate of germination and radicle growth in NaCl was lower than in PEG at most of the osmotic potentials tested. Basin wildrye germination responses were generally similar for the different salts

Table 8. Estimates of total germination, rate of germination, and radicle length of Jose tall wheatgrass and Magnar basin wildrye after 3 weeks of incubation as a function of species and osmotic dummy variables, and the linear, quadratic and cubic covariates of osmotic potential and interaction terms. R^2 values for the complete model were 0.94, 0.92, and 0.78 for total germination, rate of germination and radicle length, respectively.

| | | Osmotic potential ($-J\text{ Kg}^{-1}$) | | | | | | | | | | |
|-----------------|---------------------------------|--|------|------|------|------|------|------|------|------|------|------|
| | | 0 | 100 | 200 | 400 | 600 | 800 | 1000 | 1200 | 1500 | 2000 | 2500 |
| | | Germination (%) | | | | | | | | | | |
| Tall wheatgrass | PEG | 88.9 | 87.6 | 86.7 | 85.3 | 84.5 | 83.8 | 82.9 | 81.4 | 77.5 | 62.9 | 33.6 |
| | NaCl | 88.4 | 86.8 | 85.5 | 83.8 | 83.0 | 82.6 | 82.4 | 82.0 | 80.5 | 72.7 | 53.7 |
| | Na ₂ SO ₄ | 84.8 | 83.9 | 83.0 | 81.0 | 78.6 | 75.8 | 72.3 | 68.2 | 60.4 | 42.1 | 15.5 |
| | CaCl ₂ | 84.5 | 82.1 | 80.2 | 77.8 | 76.7 | 76.1 | 75.6 | 74.4 | 70.1 | 50.9 | 8.1 |
| Basin wildrye | PEG | 88.4 | 93.5 | 96.6 | 98.0 | 93.7 | 84.8 | 72.6 | 58.6 | 36.0 | 5.1 | 0.0 |
| | NaCl | 94.9 | 95.7 | 95.4 | 91.7 | 84.4 | 74.5 | 62.8 | 50.0 | 30.9 | 5.7 | 0.0 |
| | Na ₂ SO ₄ | 89.0 | 90.9 | 91.4 | 88.9 | 82.3 | 72.6 | 60.8 | 47.9 | 28.4 | 3.6 | 1.3 |
| | CaCl ₂ | 89.1 | 90.1 | 89.9 | 86.1 | 78.6 | 68.4 | 56.3 | 43.3 | 24.0 | 0.5 | 0.2 |
| | | Rate of Germination (% day ⁻¹) | | | | | | | | | | |
| Tall wheatgrass | PEG | 15.5 | 15.8 | 16.0 | 16.0 | 15.6 | 14.8 | 13.7 | 12.3 | 10.0 | 5.6 | 1.6 |
| | NaCl | 13.8 | 13.6 | 13.4 | 13.0 | 12.6 | 12.1 | 11.6 | 11.1 | 10.0 | 7.5 | 3.7 |
| | Na ₂ SO ₄ | 15.2 | 14.6 | 14.1 | 12.9 | 11.8 | 10.7 | 9.7 | 8.6 | 7.0 | 4.3 | 1.3 |
| | CaCl ₂ | 14.9 | 14.0 | 13.2 | 11.7 | 10.4 | 9.2 | 8.2 | 7.2 | 5.8 | 3.5 | 0.5 |
| Basin wildrye | PEG | 18.0 | 17.7 | 17.2 | 16.0 | 14.3 | 12.4 | 10.4 | 8.3 | 5.3 | 1.7 | 0.0 |
| | NaCl | 15.9 | 15.3 | 14.6 | 13.0 | 11.2 | 9.2 | 7.2 | 5.3 | 2.7 | 0.0 | 0.0 |
| | Na ₂ SO ₄ | 15.9 | 15.3 | 14.6 | 13.0 | 11.1 | 9.1 | 7.0 | 5.1 | 2.4 | 0.0 | 0.0 |
| | CaCl ₂ | 16.0 | 14.9 | 13.8 | 11.6 | 9.5 | 7.5 | 5.6 | 3.9 | 1.7 | 0.0 | 0.0 |
| | | Radicle length (cm) | | | | | | | | | | |
| Tall wheatgrass | PEG | 5.8 | 6.1 | 6.3 | 6.8 | 6.7 | 6.2 | 5.6 | 4.7 | 3.3 | 1.1 | 0.2 |
| | NaCl | 6.1 | 5.5 | 4.9 | 3.7 | 2.8 | 2.2 | 1.8 | 1.5 | 1.3 | 1.0 | 0.3 |
| | Na ₂ SO ₄ | 5.3 | 4.6 | 3.9 | 2.5 | 1.6 | 1.0 | 0.6 | 0.4 | 0.3 | 0.4 | 0.0 |
| | CaCl ₂ | 6.0 | 5.0 | 4.0 | 2.0 | 1.5 | 1.1 | 0.9 | 0.7 | 0.6 | 0.5 | 0.0 |
| Basin wildrye | PEG | 3.3 | 3.6 | 3.9 | 4.5 | 4.5 | 4.2 | 3.7 | 3.0 | 1.9 | 0.3 | 0.0 |
| | NaCl | 3.2 | 3.0 | 2.8 | 2.4 | 2.0 | 1.6 | 1.2 | 0.9 | 0.4 | 0.0 | 0.0 |
| | Na ₂ SO ₄ | 3.3 | 2.9 | 2.5 | 1.6 | 1.0 | 0.7 | 0.4 | 0.3 | 0.2 | 0.2 | 0.0 |
| | CaCl ₂ | 3.5 | 3.1 | 2.8 | 2.0 | 1.5 | 1.1 | 0.9 | 0.7 | 0.5 | 0.3 | 0.0 |

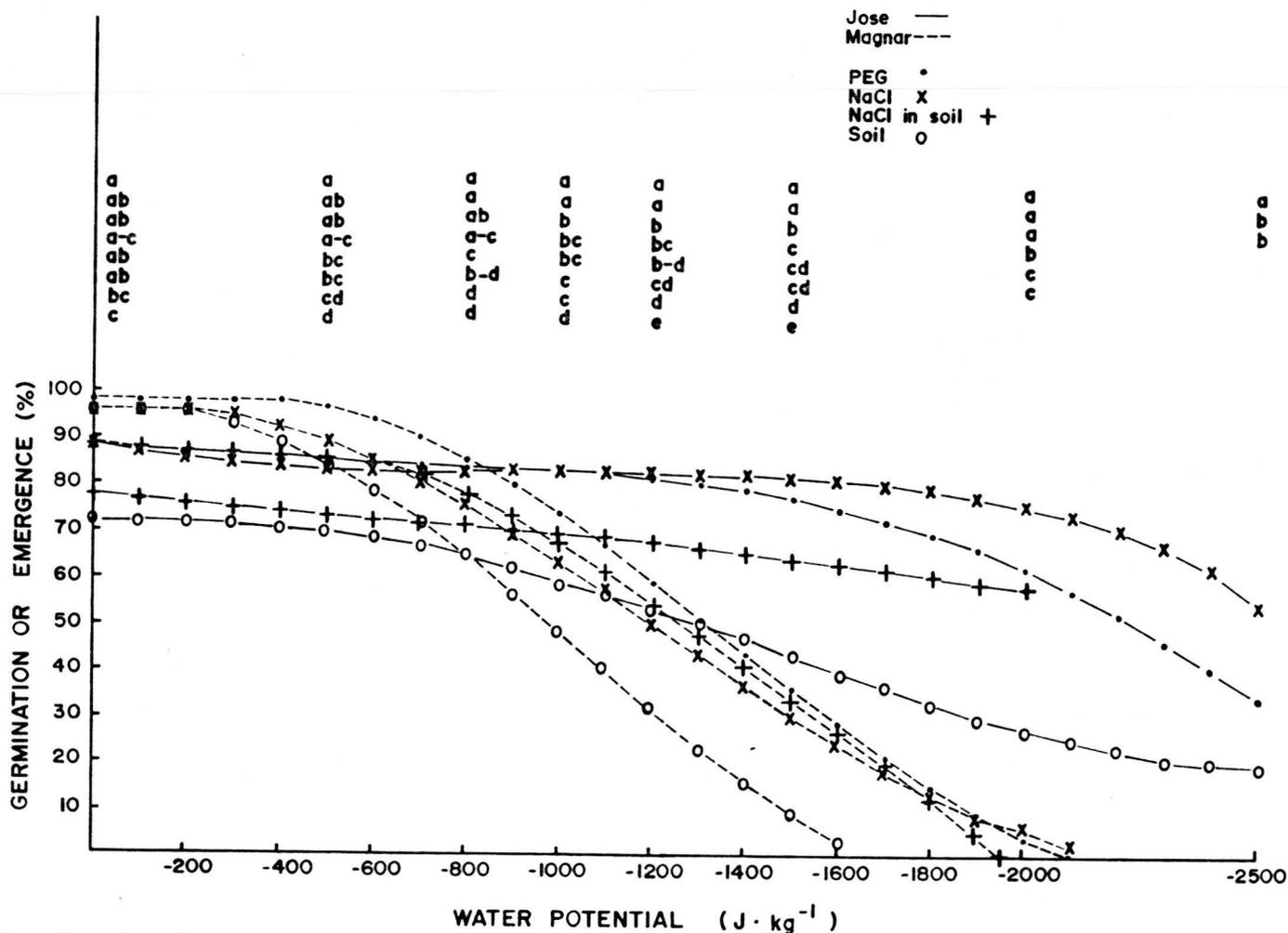


Figure 15. Germination or emergence of Jose tall wheatgrass and Magnar basin wildrye as a function of osmotic or matric potentials. Regressions are of the form: Germination or emergence (%) = $a + b_1\Psi + b_2\Psi^2 + b_3\Psi^3$ where Ψ = matric or osmotic potential ($-J \cdot kg^{-1}$). All regressions were significant at the 0.01 level except for tall wheatgrass in NaCl in soil which was significant at the 0.1 level. Letters above apply to regression lines in order and any regression lines having the same letter have overlapping 95% confidence intervals at that water potential.

except that CaCl_2 reduced total germination and rate of germination more than the other salts at low osmotic potentials (Table 8). Tall wheatgrass had higher germination responses in NaCl than Na_2SO_4 and CaCl_2 indicating a higher tolerance to sodium and chloride than calcium or sulfate ions.

Emergence at Low Soil Matric Potentials

Basin wildrye had higher emergence than tall wheatgrass at matric potentials higher than $-600 \text{ J}\cdot\text{kg}^{-1}$, but tall wheatgrass had higher emergence than basin wildrye at matric potentials below $-900 \text{ J}\cdot\text{kg}^{-1}$ (Figure 15). Basin wildrye had little emergence at matric potentials below $-1500 \text{ J}\cdot\text{kg}^{-1}$, while tall wheatgrass still had almost 30% emergence at $-2000 \text{ J}\cdot\text{kg}^{-1}$.

Emergence of both species was less in soil at low matric potentials than in PEG and NaCl in plastic foam or in NaCl solutions in soil at reduced osmotic potentials (Figure 15 and Table 9). Emergence in soil with osmotic potentials reduced by NaCl was less than germination in NaCl in foam for tall wheatgrass, but was similar in the two media for basin wildrye. For both species, emergence in soil was similar at equal total potentials of matric and osmotic potential combinations where the matric potential was less than $0 \text{ J}\cdot\text{kg}^{-1}$ (Table 9).

Low matric potentials decreased the rate of emergence of Magnar basin wildrye more than Jose tall wheatgrass seedlings (Figure 16). From Figure 15 it can be seen that it took tall wheatgrass 7 days and basin wildrye 12 days to reach 20% emergence at a matric potential of $-1000 \text{ J}\cdot\text{kg}^{-1}$. At a matric potential of $-1200 \text{ J}\cdot\text{kg}^{-1}$, it took tall wheatgrass 8 days and basin wildrye 17 days to reach 20% emergence.

Table 9. Mean emergence of Jose tall wheatgrass and Magnar basin wildrye seedlings after 3 weeks incubation in Gund silt-loam soil at various soil matric potentials and NaCl-induced osmotic potentials. Values in parentheses are one-half the calculated 95% confidence intervals.

| Matric Potential ($J \cdot kg^{-1}$) | Emergence (%) | | | | | | | | | |
|---|---|-------------|--------------|--------------|--------------|---------------|-------------|--------------|--------------|--------------|
| | Tall wheatgrass | | | | | Basin wildrye | | | | |
| | Osmotic Potential ($J \cdot kg^{-1}$) | | | | | | | | | |
| | <u>0</u> | <u>-500</u> | <u>-1000</u> | <u>-1500</u> | <u>-2000</u> | <u>0</u> | <u>-500</u> | <u>-1000</u> | <u>-1500</u> | <u>-2000</u> |
| 0 | 78(11) | 69(13) | 67(25) | 69(18) | 56(16) | 88(10) | 83(10) | 65(19) | 20(9) | 1(3) |
| -500 | 71(13) | 78(17) | 52(26) | 39(8) | | 84(16) | 31(18) | 3(3) | 0 | |
| -1000 | 54(26) | 46(22) | 33(17) | | | 27(11) | 4(9) | 1(3) | | |
| -1500 | 25(8) | 27(8) | | | | 1(3) | 0 | | | |
| -2000 | 28(12) | | | | | 3(3) | | | | |

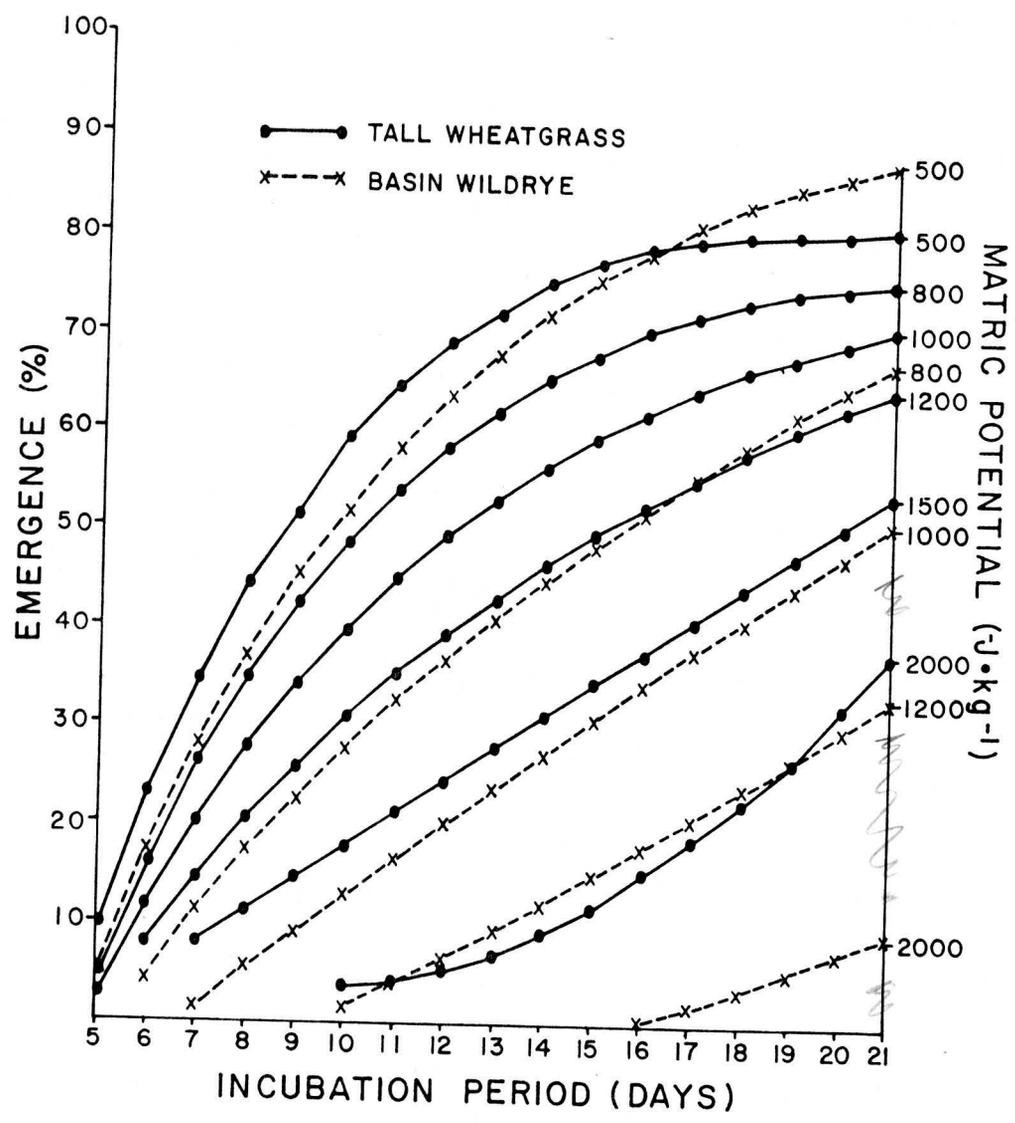


Figure 16. Emergence of Jose tall wheatgrass and Magnar basin wildrye as a function of soil matric potential (Ψ_m) and incubation days (t) of the form: Emergence (%) = $a + b_1\Psi_m + b_2\Psi_m^2 + b_3\Psi_m^3 + b_4t + b_5\sqrt{t} + b_6\Psi_mt + b_7\Psi_m\sqrt{t} + b_8\Psi_m^2t + b_9\Psi_m^2\sqrt{t}$. R^2 values were 0.81 for both tall wheatgrass and basin wildrye and are significant at the 0.01 level.

Imbibition

Seed water potential increased greatly after 4 and 6 hours of soaking in distilled water for Magnar basin wildrye and Jose tall wheatgrass, respectively. For a given soaking period, basin wildrye seeds had a higher water potential than tall wheatgrass seeds. This was partly because at a given water content below 0.6, Magnar seeds had higher water potential than tall wheatgrass seeds and partly because basin wildrye seeds had higher water contents than tall wheatgrass seeds for a given soaking period over 4 hours. Jose tall wheatgrass seeds have about twice the mass of Magnar basin wildrye seeds averaging 6.3 and 3.3. mg per seed, respectively. Tall wheatgrass had higher germination and germinated at lower seed water contents and seed water potentials than basin wildrye (Figure 17).

Discussion

Seed germination is influenced by the direct effects of low water potentials on seed hydration as well as indirect effects associated with low soil matric and osmotic potentials. Seeds of different species may have different critical water potentials or hydration levels below which the physiological processes of germination are slowed or prevented (Hillel 1972, Hadas and Stibbe 1973). This direct effect of water potential on germination can be tested by determining germination responses in polyethylene glycols of high molecular weight which do not enter the seed or by allowing seeds to imbibe to different water potentials and noting subsequent germination. Both experimental approaches in this study indicate that Jose tall wheatgrass has a lower threshold water potential at which its germination processes operate than Magnar basin

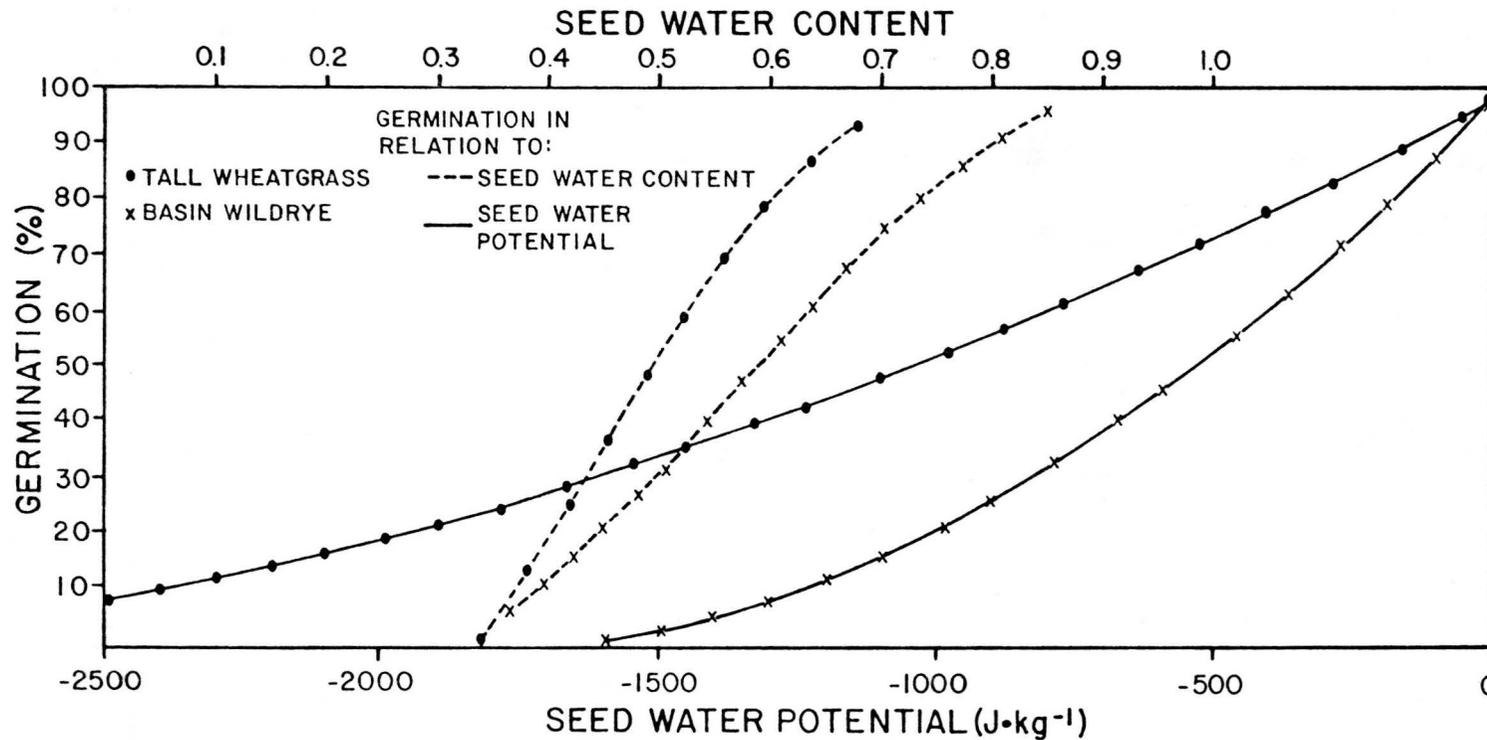


Figure 17. Germination of Jose tall wheatgrass and Magnar basin wildrye as third-degree polynomial functions of seed water content or seed water potential. R^2 values for tall wheatgrass are 0.86 and 0.83 while those for basin wildrye are 0.80 and 0.85 for seed water content and seed water potential, respectively. All regressions were significant at the 0.01 level.

wildrye. This is probably the main reason tall wheatgrass germinates at lower osmotic and matric potentials than basin wildrye.

When seeds are incubated in solutions with osmotic potentials reduced by salts, ion entry into the seed may increase or decrease germination, depending on the toxicity of ions to the species. Entering ions lower the seed osmotic potential, which facilitates hydration of the seed (Sharma 1973) by allowing a higher seed matric potential than the osmotic potential of the solution surrounding the seed. The extent to which this favorable effect of increased hydration is equally or dominantly offset by interference of the ions with germination processes varies with the species and salts (Ungar 1978) and can be tested by comparing the germination in PEG versus germination in different salts at the same osmotic potentials.

Total germination of tall wheatgrass and basin wildrye in this study was generally more affected by reduced osmotic potentials than by toxicity of NaCl, Na₂SO₄ and CaCl₂. That these ions did interfere with germination and growth processes of both species is indicated by their lower germination rate and radicle growth in the salt solutions than in PEG. Higher total germination of Jose tall wheatgrass in NaCl than in PEG, Na₂SO₄ and CaCl₂ at low osmotic potentials indicates the higher tolerance of this species to sodium and chloride ions. The greater radicle growth of Jose tall wheatgrass than Magnar basin wildrye at reduced osmotic potentials is correlated with its larger seed size as has been shown to be the case of Young et al. (1968) for a number of grass species.

In addition to the direct effect of low water potentials on seed hydration, low soil matric potentials may reduce water entry into the seed by reduced seed-soil contact and lowered soil hydraulic conductivity

(Sharma 1973, Hadas and Russo 1974 a,b, Thill et al. 1979). Germination in soil can also be reduced due to seed microbial damage (Sharma 1973) or for some seeds the presence of an air gap between the seed coat and the pericarp (McWilliam and Phillips 1971). Lower emergence of tall wheatgrass, but not basin wildrye in soil at matric potentials greater than $-600 \text{ J}\cdot\text{kg}^{-1}$ compared with germination in PEG suggests seed-soil contact was limiting to tall wheatgrass, but not to basin wildrye germination at these higher soil matric potentials. Jose tall wheatgrass seeds are about twice the mass of Magnar basin wildrye seeds and it has been shown by Harper and Benton (1966) and Hadas and Russo (1974b) that the larger the seed, the smaller the wetted area for a given soil aggregate size.

Emergence of both cultivars in soil with $0 \text{ J}\cdot\text{kg}^{-1}$ matric potential (and high hydraulic conductivity) but with NaCl-reduced osmotic potentials was similar to emergence at equivalent soil matric potentials higher than $-800 \text{ J}\cdot\text{kg}^{-1}$ (Figure 15). At potentials below $-800 \text{ J}\cdot\text{kg}^{-1}$, emergence in soil was higher for NaCl-reduced osmotic potentials than at equivalent soil matric potentials. This suggests that hydraulic conductivity or seed-soil contact became limiting to germination of both cultivars at soil matric potentials below about $-800 \text{ J}\cdot\text{kg}^{-1}$ and that ions may have entered the seeds in the NaCl-in-soil treatment, thereby facilitating seed hydration as mentioned earlier.

The ability of Jose tall wheatgrass to emerge sooner than Magnar basin wildrye at low soil matric potentials (Figure 16) is a definite advantage to emergence on arid rangelands where spring seedbed matric potentials rapidly decrease due to infrequent rains. Tall wheatgrass would also be expected to emerge and establish better than basin wildrye on saline soils due to higher germination and radicle growth at reduced

osmotic potentials. The results of these laboratory studies are correlated with those of field trials. On a nonsaline and on a moderately saline soil in central Nevada emergence and establishment of Jose tall wheatgrass was higher than that of Magnar basin wildrye for a range of irrigation-simulated spring rainfall conditions.¹

Although Magnar basin wildrye had lower germination than Jose tall wheatgrass at reduced osmotic potentials, Magnar basin wildrye had higher germination and germinated at lower osmotic potentials than basin wildrye collections tested by Choudhuri (1968) and Young and Evans (1981). Magnar basin wildrye thus should be the seed of choice when seeding basin wildrye on saline soils.

results of testing the
The hypotheses can be reported as follows:

- IV. A. Tall wheatgrass had higher emergence in the field and had higher germination and germinated at lower matric and osmotic potentials than basin wildrye.
- B. Germination was higher at low osmotic potentials than at low matric potentials; probably due to the reduced seed soil contact and hydraulic conductivity associated with low matric potentials.
- C. Although reduced water potentials affected germination more than specific ions, ion toxicity was evidenced by generally lower germination, germination rate, and radicle growth in salts than in isosmotic PEG-6000 solutions. Tall wheatgrass exhibited high tolerance to sodium and chloride ions.

¹Roundy, B.A. 1983. Emergence and establishment of basin wildrye and tall wheatgrass in relation to moisture and salinity. J. Range Manage. (Submitted).

The ability of a species to rapidly germinate under decreasing osmotic and especially matric potentials is important for successful emergence on saline, arid soils.

RESPONSE OF BASIN WILD RYE AND
TALL WHEATGRASS TO SALINATION

Introduction

Since the ^{degradation} decimation of most basin wildrye stands by heavy grazing and mowing before the turn of the century, forage production on many saline/alkaline ranges of the arid west has been far below potential (Lesperance et al. 1978). Those ranges might be improved by seeding grasses that can emerge and persist in the associated arid and saline soils. Although native collections of wildrye have a reputation for low seed germination and poor seedling vigor (Young and Evans 1981), an improved cultivar, Magnar, has been released which has high and viable seed production and high germination (Evans and Young 1983). Besides basin wildrye, one of the forage species best adapted to saline rangelands is tall wheatgrass. Tall wheatgrass is generally used as a standard for comparison of salt tolerance of forage grasses and its salt and sodium tolerances are well documented (Dewey 1960, Carter and Peterson 1962, Rauser and Crowle 1963, Moxley et al. 1978, Shannon 1978).

Seedling survival on arid, saline soils may be a function of tolerance to low osmotic potentials and avoidance of low soil matric potentials. Seedlings that can maintain growth under low osmotic, high matric potentials of saline soils recharged by winter precipitation may later avoid much lower matric and osmotic potentials by sending their roots below the upper soil-drying front. Reviews of osmotic adjustment, turgor maintenance (Hsiao et al. 1976, Turner and Jones 1980) and salinity tolerance

(Poljakoff-Mayber and Gale 1975) suggest that plant growth under low soil osmotic potentials is dependent on osmotic adjustment to maintain turgor necessary for cell elongation and tolerance of high concentrations of specific ions used in osmotic adjustment.

My purpose was to investigate the growth, survival and water potential responses of Magnar basin wildrye and Jose tall wheatgrass to soil osmotic potential decreased by different salts. Comparisons between these species of relative salt tolerance, effects of specific ions, growth responses to osmotic adjustment and maintenance of turgor will aid in their evaluation for seeding arid, saline rangelands.

Methods

Seeds of Magnar basin wildrye and Jose tall wheatgrass were sown in washed silica sand in 3.8 cm diameter by 20 cm deep plastic containers in a greenhouse. Day and night temperatures averaged 25 and 15°C, respectively, and relative humidity ranged from 30% during the day to 60% at night. The sand was kept wet with a complete nutrient solution (Hoaglund and Arnon 1938) and after 2 weeks, when plant emergence was complete, plants were thinned to one per container. The relationships of molarity to osmotic potential and electrical conductivity of CaCl_2 , NaCl , Na_2SO_4 , equimolar Na_2SO_4 plus NaCl and equimolar CaCl_2 plus NaCl were determined using a freezing-point depression osmometer and electrical conductivity meter (Table 10). When seedlings were 3 weeks old, salination was begun and continued in ^{MPa} -2.5 bar increments to final soil osmotic potentials of -5, -10, -15, -20, -25, -30, and -35 ^{MPa} bars for each salt. There were 14 containers each containing 1 plant, salinized for each salt and for each final soil osmotic potential. Plants were irrigated

Table 10. Estimated electrical conductivity ($\text{dS}\cdot\text{m}^{-1}$) of final treatment osmotic potentials, calculated sodium adsorption ratios (SAR) and regression equations of electrical conductivity and molarity on salt and nutrient solution osmotic potentials.

| Osmotic potential (-bars) | Electrical conductivity ($\text{dS}\cdot\text{m}^{-1}$) | | | | | | | | | |
|---|---|-------|-----|---------------------------------|-----|---------------------------------------|-----|---|-----|-------------------|
| | CaCl ₂ | NaCl | SAR | Na ₂ SO ₄ | SAR | Equimolar CaCl ₂ + NaCl | SAR | Equimolar Na ₂ SO ₄ + NaCl | SAR | Salts combined |
| 5 | 15.6 | 13.0 | 39 | 15.1 | 39 | 15.4 | 6 | 15.1 | 52 | 14.9 |
| 10 | 25.4 | 22.0 | 84 | 28.1 | 82 | 24.6 | 9 | 24.9 | 119 | 25.1 |
| 15 | 35.3 | 31.1 | 129 | 41.1 | 125 | 33.8 | 12 | 34.6 | 187 | 35.2 |
| 20 | 45.1 | 40.1 | 175 | 54.1 | 170 | 43.0 | 14 | 44.4 | 254 | 45.4 |
| 25 | 55.0 | 49.2 | 220 | 67.1 | 210 | 52.2 | 15 | 54.1 | 321 | 55.6 |
| 30 | 64.8 | 58.2 | 265 | 80.1 | 255 | 61.4 | 17 | 63.9 | 388 | 65.7 |
| 35 | 74.7 | 67.3 | 310 | 93.1 | 295 | 70.6 | 18 | 73.6 | 455 | 75.8 |
| Regression statistics | | | | | | | | | | |
| Electrical conductivity ($\text{dS}\cdot\text{m}^{-1}$) = a + b × osmotic potential (-bars) | | | | | | | | | | |
| a | 5.7 | 3.9 | | 2.1 | | 6.2 | | 5.4 | | 4.8 |
| b | 2.0 | 1.8 | | 2.6 | | 1.8 | | 1.9 | | 2.0 |
| r | 0.99 | 0.99 | | 0.99 | | 0.99 | | 0.99 | | 0.97 |
| Osmotic potential (-bars) = a + b × molarity (moles/L) | | | | | | | | | | |
| a | 0.20 | 0.69 | | 0.42 | | 0.16 | | 1.13 | | 1.33 |
| b | 58.52 | 41.78 | | 51.22 | | 51.61 | | 42.17 | | 46.32 |
| r | 0.99 | 0.99 | | 0.99 | | 0.99 | | 0.99 | | 0.97 |

above soil saturation with the appropriate salt and nutrient solution every other day such that old solution was leached out with each irrigation and matric potentials were 0 bars. Salination to the final osmotic potential of -35 bars took 4 weeks. Control plants were watered with nutrient solution having an osmotic potential greater than -1 bar. Starting when seedlings were 5 weeks old, leaf segments were harvested at predawn of the day after irrigation for determination of leaf water potential components. Leaf water potential was measured, leaf osmotic plus matric potential was estimated, and turgor pressure calculated using psychrometer chambers and methods similar to those detailed by Johnson and Brown (1977) and Johnson (1978). Excised leaf segments were inserted in water-tight psychrometer chambers which were placed in a constant-temperature water bath at 25°C for 3 hours. Total leaf water potential was measured by reading psychrometer microvolt output after a 15-sec cooling period. Psychrometer chambers were then placed on dry ice for 15 minutes and then allowed to slowly warm to room temperature. Water potential of the frozen-thawed leaf tissue was again determined psychrometrically and is an estimation of the osmotic plus matric potential of the leaf. Turgor pressure was calculated by subtracting the osmotic plus matric potential from the total leaf water potential. Over 400 plant water potential measurements were made over a 4 week period in order to obtain 3 to 4 replications for each cultivar, salt and soil osmotic potential combination. In addition, water was withheld from some control plants and water potential components of 57 leaf segments of each cultivar were measured over a 2 week period as soil matric potential decreased. When seedlings were 9 weeks old, live and dead plants were counted. Shoots of 9 to 11 plants and roots of 8 plants per cultivar, salt, and

soil osmotic potential combination were harvested, oven-dried and weighed. Regression slopes and intercepts of soil osmotic potential on shoot and root weight and of leaf water potential on turgor pressure were statistically compared for different salts and species by the method of Snedecor and Cochran (1971). Confidence intervals of leaf water potentials at zero turgor were calculated according to Sokal and Rohlf (1969).

Results and Discussion

Yield of Jose and Magnar shoots and roots decreased rapidly with decreasing soil solution osmotic potentials (Figure 18). Shoot and growth of both species was minimal below a soil osmotic potential of -15 and -10 bars, respectively (Figures 18 and 19). Growth of shoots and roots of both species tended to be least inhibited by Na_2SO_4 and equimolar Na_2SO_4 plus NaCl and most inhibited by CaCl_2 , but the difference in yield response in relation to salt was generally statistically significant ($p = 0.05$) only for Jose tall wheatgrass shoots (Appendix, Table 3). Excessive Ca concentration may produce nutritional imbalances, unless accompanied by other cations such as Na or K (Goodin and Mozafar 1972). High concentrations of Ca were especially toxic to Magnar basin wildrye seedlings; salination by CaCl_2 to soil osmotic potentials below -15 bars resulted in greater than 38% mortality. Mortality was less than 10% of Jose tall wheatgrass seedlings for all salt solutions and of Magnar basin wildrye seedlings for all solutions but CaCl_2 and equimolar CaCl_2 plus NaCl . Choudhuri (1968) found that 50% of basin wildrye seedlings collected from nonsaline and saline areas permanently wilted after gradual salination by NaCl to a soil saturation extract osmotic potential of -11 bars. Since he maintained the plants at a field capacity water content, which is generally 1/2 that at saturation, the actual soil solution osmotic

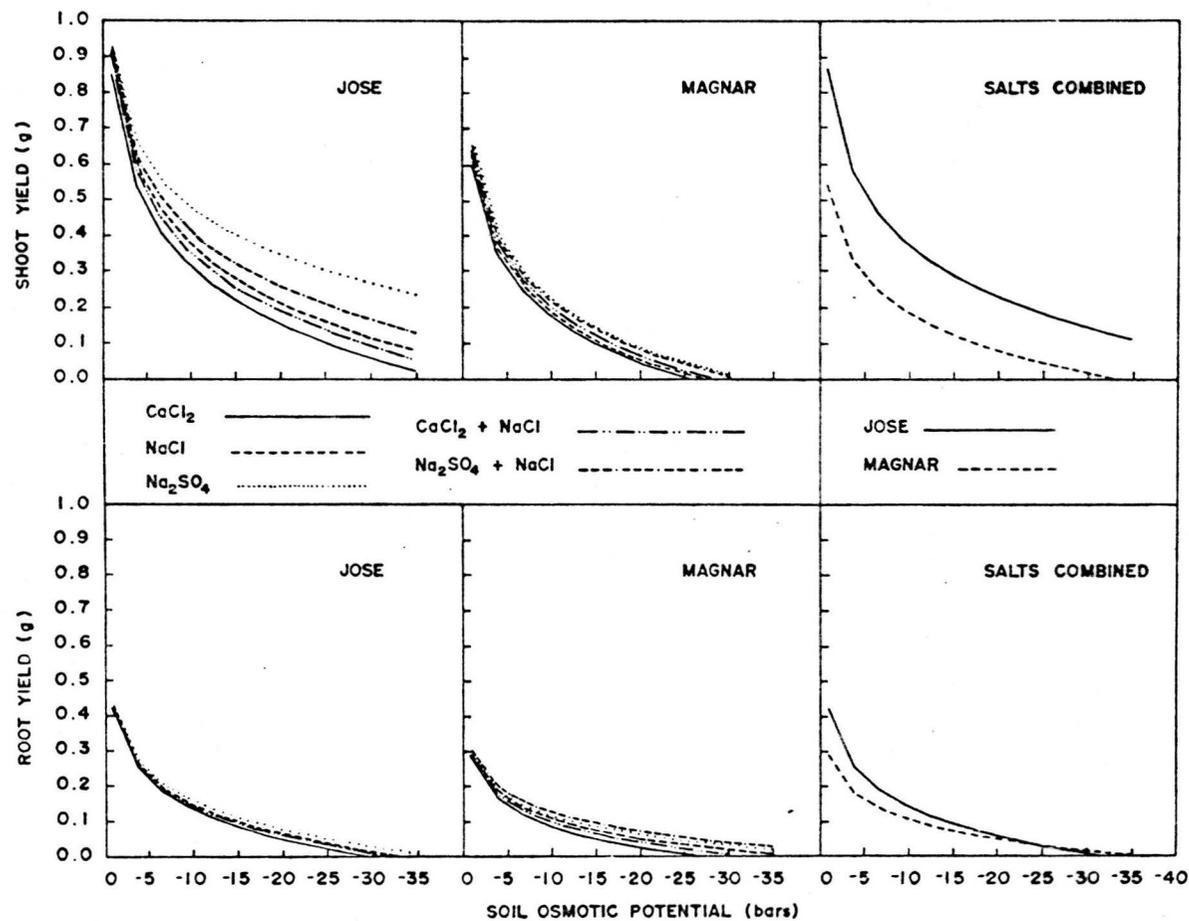


Figure 18. Dry weight yield of Jose tall wheatgrass and Magnar wildrye seedling shoots and roots as a function of soil osmotic potentials as decreased by different salt plus nutrient solutions. Regressions are of the form: $\text{yield (g)} = a + b \times \ln [\text{soil osmotic potential (- bars)}]$. All regressions were significant at the 0.01 level.

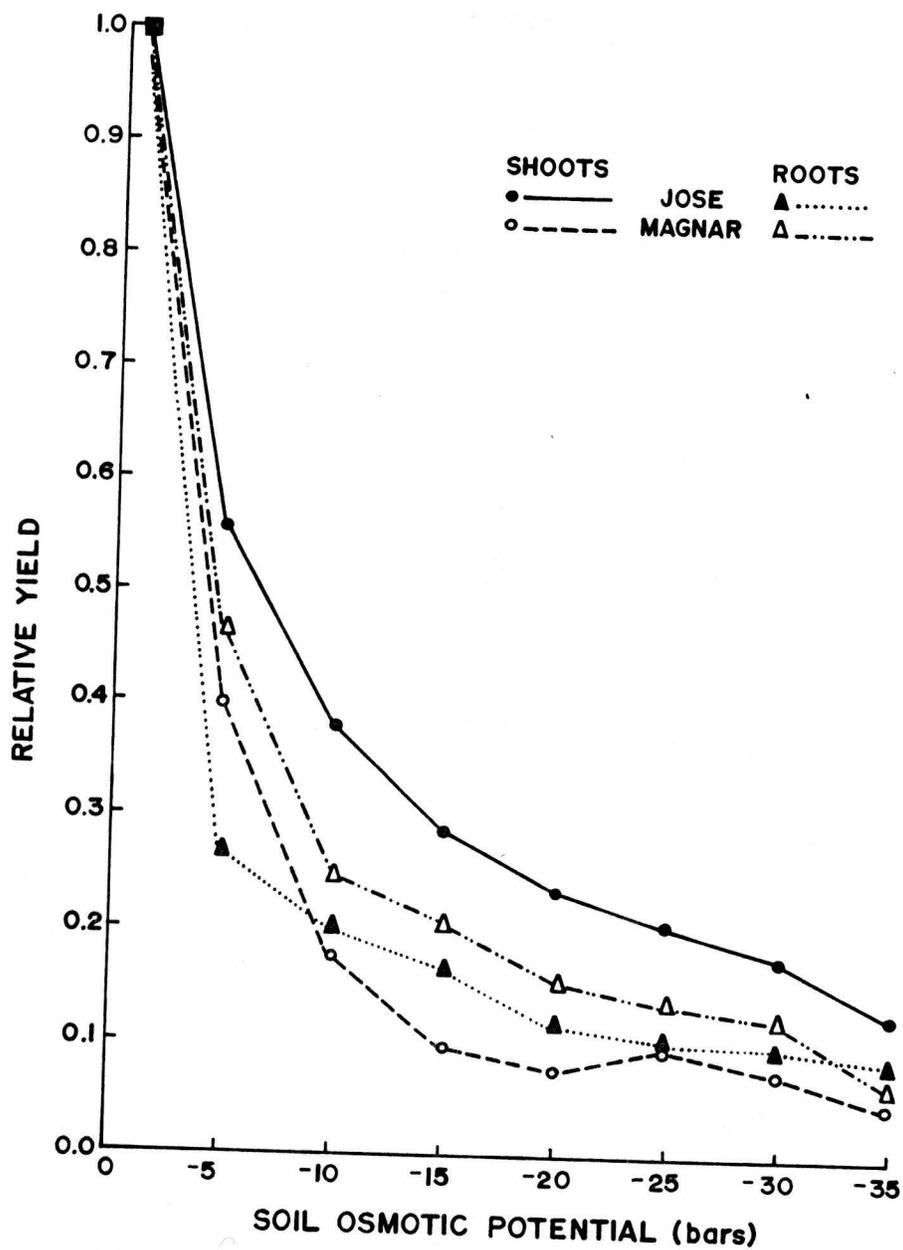


Figure 19. Relative shoot and root weight of Jose tall wheatgrass and Magnar wildrye as a function of soil osmotic potential.

potential at 50% wilt would have been approximately -22 bars. In the present study with a similar greenhouse temperature environment, Magnar basin wildrye seedlings generally survived much lower osmotic potentials which may indicate that this improved wildrye cultivar has a higher salinity tolerance than the basin wildrye collection tested by Choudhuri.

High ratios of Na to Ca commonly reduce growth by inducing Ca deficiencies (LaHaye and Epstein 1969). Elzam and Epstein (1969) found that sharp decreases in root yield of tall wheatgrass associated with salination from 50 to 100 mM NaCl also coincided with a sharp decrease of Ca in the roots. They suggested that some salt damage may be due to lack of Ca to maintain the integrity of the cell membrane for selective absorption of K in the presence of Na. In the present study, inhibition of shoot and root growth was similar for both high concentrations of Ca and Na in the root medium. Both species had a greater or similar growth at isosmotic potentials of NaCl as equimolar CaCl₂ plus NaCl even though the sodium adsorption ratios of the former were much higher than that of the latter salt solution and Cl concentrations were very similar for both solutions (Figure 18 and Table 10). This suggests that reductions in yield of tall wheatgrass under high exchangeable Na percentages (Rausser and Crowle 1963, Choudhuri 1968) probably should not necessarily be attributed to Na-induced nutritional imbalances. Saline soils on western rangelands in the Great Basin are low in Ca and Mg, while Na₂SO₄ and NaCl are the dominant salts (Table 1). Calcium toxicity would not be expected on these saline rangelands, and the tolerance of both cultivars to high Na should have high adaptive value.

On an absolute yield basis, Jose tall wheatgrass produced much more

shoot and slightly more root matter than Magnar basin wildrye (Figure 18). Decreasing soil osmotic potential inhibited shoot growth more of basin wildrye than of tall wheatgrass, and inhibited root growth more of tall wheatgrass than of basin wildrye (Figure 19). Salt tolerance indices (electrical conductivity of the saturation extract where 50% reduction in yield occurs) of 13 (Moxley et al. 1978), 14 (Dewey 1960), and 18 (Bernstein 1964) $\text{dS}\cdot\text{m}^{-1}$ have been reported for tall wheatgrass. Using Figure 19 to determine the osmotic potential at 50% yield reduction and the regression equations of Table 10, salt tolerance indices for all salts combined were calculated as 18 and 13 $\text{dS}\cdot\text{m}^{-1}$ for Jose tall wheatgrass and Magnar basin wildrye shoots and 12 and 14 $\text{dS}\cdot\text{m}^{-1}$ for Jose and Magnar roots, respectively. This differential effect of decreasing soil osmotic potential on tall wheatgrass and basin wildrye roots and shoots resulted in large differences in root/shoot ratios of the two cultivars as soil osmotic potential decreased.

Magnar basin wildrye root/shoot ratios doubled when salinized to -15 bars and then decreased with decreasing soil osmotic potential. In contrast, the root/shoot ratio of Jose tall wheatgrass seedlings decreased by half when salinized to -5 bars and then increased slightly to remain constant with increasing salinization. Although tall wheatgrass had greater growth than basin wildrye at all soil osmotic potentials, the increased root/shoot ratio of basin wildrye may be of adaptive value on arid soils where reduced transpiration may result in a longer period of higher soil water potentials and an extended growth period.

Regression coefficients and intercepts for regressions of turgor pressure on leaf water potential generally did not differ statistically ($p = 0.05$) among salts, so data from all salts were combined for comparisons of turgor maintenance between species and between unwatered and

salinized plants (Table 11). The response of turgor pressure to decreasing leaf water potential was similar for both species and salinized plants of both cultivars maintained positive turgor at lower leaf water potentials than did unwatered plants. Leaf water potentials at zero turgor averaged -35.7 and -23.7 bars for salinized and unwatered plants, respectively. Turgor maintenance by osmotic adjustment is affected by the rate of development (Begg and Turner 1976) and degree of water stress, and the light and temperature environment (Turner and Jones 1980). Development of stress in small, unwatered sand and soil cultures could be very rapid because the soil matric potential decreases greatly with a small reduction in soil water content after a certain water content has been reached. The ability of salinized plants to maintain greater turgor than unwatered plants at low leaf water potentials could be explained by a slower development of stress for the salinized plants or possible increased ion uptake facilitating osmotic adjustment. Shannon (1978) suggested that ion uptake and increase in proline and soluble sugar all contributed to osmotic adjustment of tall wheatgrass lines. However, he found that the most salt-tolerant lines restricted accumulation of Na in the root and Na, Ca and Cl in the shoot and had higher soluble sugar contents than the less tolerant lines. Sepaskhah and Boersma (1979) found that NaCl-decreased soil osmotic potentials increased turgor of wheat leaves at high soil matric potentials (-0.3 bars) but not at lower matric potentials (-2.5 to -7.5 bars). The water-holding characteristics and osmotic potential of the soil, the temperature and light environment, and the plant growth responses may all interact to affect the rate of water stress development and the ability of the plant to maintain turgor at low water potentials. Jose tall wheatgrass and Magnar basin wildrye

Table 11. Statistics for the linear regressions of turgor pressure (bars) on leaf water potential (bars) for unwatered and salinized Jose tall wheatgrass and Magnar basin wildrye seedlings.

| <u>Treatment</u> | <u>Cultivar</u> | Turgor pressure at zero leaf water potential (bars) | <u>Slope*</u> | Leaf water potential at zero turgor [‡] 90% confidence interval (bars) [†] | <u>r[†]</u> |
|------------------|-----------------|---|---------------|--|----------------------|
| Unwatered | Jose | 10.6 | 0.48a | -22.1 ± 7.1 | 0.90 |
| | Magnar | 10.22 | 0.41a | -25.2 ± 7.8 | 0.84 |
| Salinized | Jose | 10.61 | 0.29b | -36.7 ± 19.0 | 0.73 |
| | Magnar | 9.69 | 0.28b | -34.7 ± 19.2 | 0.77 |

*Values followed by the same letter are not significantly different at the 0.05 level as determined by the slope test method of Snedecor and Cochran (1971).

†All r values are significant at the 0.01 level.

‡90% confidence intervals calculated according to Sokal and Rohlf (1969).

apparently have similar ability to osmotically adjust to maintain positive turgor at low osmotic potentials when soil matric potentials are high.

Small initial reductions in turgor pressure were associated with large reductions in shoot growth of both cultivars (Figure 20). Average losses in turgor pressure of only 0.77 and 0.95 bars accompanied a 50% reduction in shoot yield for Jose and Magnar, respectively. Small losses in turgor associated with large decreases in growth may indicate that the turgor pressure has fallen below some critical turgor necessary for cell elongation (Cleland 1971, Loescher and Nevins 1973) or that ionic imbalances or energy expenditures associated with osmotic adjustment for limiting growth (Bernstein 1963, Hsiao et al. 1976). A threshold turgor pressure may be necessary for biochemical modification of cell wall properties to take place and provide the force for cell wall extension (Cleland 1971). Decreases in cell osmotic potentials that maintain turgor may reduce growth by affecting enzymes that are sensitive to low osmotic potentials, high salt concentration, or specific ions (Bernstein 1963). Although Jose tall wheatgrass was less sensitive than Magnar basin wildrye to decreasing soil osmotic potentials, both cultivars had similar ability to osmotically adjust to maintain turgor and similar patterns of greatly reduced growth with relatively high turgor.

In conclusion, the ^{results of testing} hypotheses can be reported as follows:

- V. A. Tall wheatgrass had greater establishment and survival on a saline soil in the field and also had greater root and shoot yield under decreasing soil osmotic potentials in this greenhouse experiment.
- B. Salinized plants adjusted osmotically, but did not maintain growth at low soil osmotic potentials.

- C. Low osmotic potentials decreased growth more than specific salts, but growth of both species was inhibited more by calcium than sodium salts.
- D. Both species had similar osmotic adjustment, but salinized plants had greater osmotic adjustment than unwatered plants, probably due to the more rapid development of water stress in the unwatered plants.

The ability to grow at decreasing osmotic potentials is important to establishment on saline soils. Both tall wheatgrass and basin wildrye had similar osmotic adjustment, but tall wheatgrass had greater growth at a given turgor pressure. The greater salt tolerance of tall wheatgrass, due to its ability to tolerate or exclude ions, is apparently more important than osmotic adjustment in maintaining growth at low osmotic potentials.

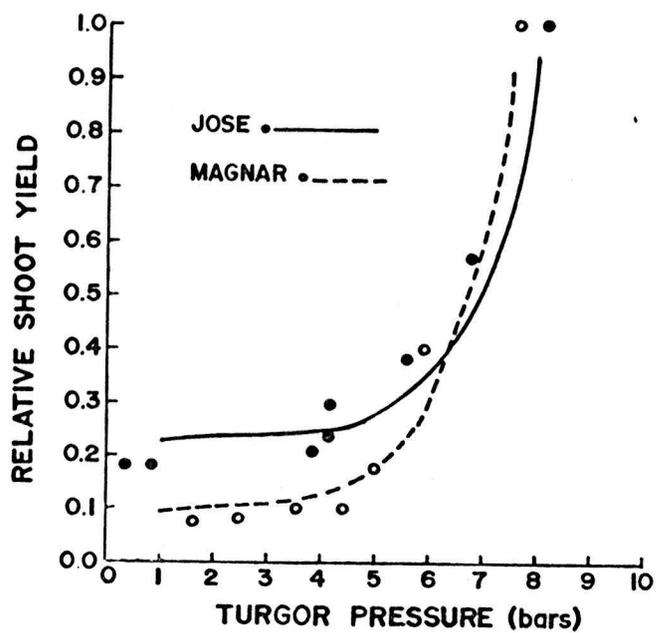


Figure 20. Relative yield of shoots of Jose tall wheatgrass and Magnar basin wildrye seedlings as a function of turgor pressure. For tall wheatgrass shoots, $y = 0.233 + 0.00024e^x$, $r = 0.97$. For basin wildrye shoots, $y = 0.103 + 0.00045e^x$, $r = 0.98$.

ROOT AND SHOOT ELONGATION OF BASIN WILDRYE AND TALL
WHEATGRASS IN RELATION TO SALINITY AND DROUGHT

Introduction

Basin wildrye and tall wheatgrass may have potential for increasing forage production of many saline rangelands in the Great Basin. Basin wildrye is a tall, robust grass which once dominated many of these rangelands before it was ~~decimated~~^{reduced or degraded} by heavy grazing and mowing around the turn of the century (Lesperance et al. 1978). Tall wheatgrass is known for its salt and sodium tolerance (Carter and Peterson 1962, Dewey 1960, Moxley et al. 1978, Shannon 1978, Rauser and Crowle 1963).

Since precipitation in the Great Basin mainly occurs in fall, winter, and spring, matric and osmotic potentials of saline soils decrease rapidly in the spring and summer after temperatures become warm enough for plant growth (Roundy et al. 1984). Successful seedling establishment on these soils may be dependent on the ability of seeded species to rapidly germinate and grow as soil matric and osmotic potentials decrease. In a field experiment in central Nevada, Jose tall wheatgrass had higher seedling emergence and survival on a saline soil (electrical conductivity of the saturation extract, E_{ce} , of $7.0 \text{ dS}\cdot\text{m}^{-1}$) than Magnar basin wildrye¹. The greater emergence of tall wheatgrass than basin wildrye can be attributed to its higher germination and ability to germinate at lower soil

¹Roundy, B.A. 1983. Emergence and establishment of basin wildrye and tall wheatgrass in relation to moisture and salinity. J. Range Manage. (Submitted).

matric and osmotic potentials than basin wildrye.² Greater survival of tall wheatgrass on this saline, arid soil may be due to its greater salt tolerance and greater absolute root growth at low osmotic potentials than basin wildrye (Roundy 1983). Seedlings that can maintain growth under low osmotic potentials of saline soils recharged by winter precipitation may later avoid much lower matric and osmotic potentials by sending their roots below the upper soil-drying front. Ability to grow in saline soils may be dependent on osmotic adjustment to maintain turgor necessary for cell elongation (Hsiao et al. 1976, Turner and Jones 1980) and tolerance of high concentrations of specific ions used in osmotic adjustment (Poljakoff-Mayber and Gale 1975). Caldwell (1974) has suggested availability of ions for uptake and accumulation may aid in osmotic adjustment to low soil water potentials. Osmotic adjustment and morphological adjustments induced by salinity may help maintain a favorable plant water balance where soil water is limited (Gale 1975, Maas and Nieman 1978, and Stark and Jarrell 1980). Maize (Zea mays L.) with a salinity pretreatment had continued leaf elongation at lower predawn leaf water potentials as water stress increased than did unsalinized plants (Stark and Jarrell 1980). Jensen (1982) found that salinization of barley (Hordeum vulgare L.) before a drying cycle resulted in slower soil desiccation and an increased growth period, but no differences in yields, transpiration coefficients or wilting percentages compared to unsalinized plants. He speculated that the delay in water uptake due to salinity may be advantageous when the water supply is limited by intermittent periods of drought.

² Roundy, B.A., J.A. Young, and R.A. Evans. 1983. Germination of basin wildrye and tall wheatgrass in relation to osmotic and matric potential. Agron. J. (Submitted).

Salinized tall wheatgrass and basin wildrye plants maintained turgor pressure at lower leaf water potentials than unsalinized plants in which water stress developed rapidly when water was withheld (Roundy 1983). The present study was conducted to determine the effects of salinity on root and shoot elongation of Jose tall wheatgrass and Magnar basin wildrye and to determine the interactions of decreasing soil osmotic and matric potentials, plant water stress, osmotic adjustment and turgor maintenance, and growth.

Methods

Solutions having an E_{Ce} of less than 1.0, 10 and 20 dS·m⁻¹ were prepared by adding equimolar NaCl plus CaCl₂ to complete nutrient solution (Hoagland and Arnon 1938). Clear plastic columns 7-cm diam. by 60-cm deep were filled with sandy clay loam soil and saturated with the different salt solutions. Ten columns each were saturated with the three salt solutions for each grass species. Thermocouple psychrometers were buried at depths of 10, 20, 35, and 55 cm in three columns for each species and salinity treatment. Two-week old seedlings of Jose tall wheatgrass and Magnar basin wildrye were transplanted into the columns with one seedling per column. All columns were placed in a growth chamber set for 12 hr at 10°C and 12 hr at 15°C when lights were on. Day-time radiation averaged 300 μeinsteins m⁻² s⁻¹ and relative humidity averaged 30 and 60% during day and night, respectively. Columns were tilted at a 65° angle within a plywood frame which shaded the roots in the columns. Total shoot length and depth of the deepest root were measured weekly until shoots stopped growing or until roots reached the bottom of the column. When seedlings were 3-months old, visible root

length was estimated for each column using a 2-cm by 2-cm grid and calculations of Marsh (1971) reported in Tennant (1975). Soil psychrometers were read weekly 1 hr before lights came on when temperature gradients in the columns were minimal. After seedlings were about 2-months old, 2 to 4-cm leaf segments were harvested 1 hr prior to lights on for determination of leaf water potential components. Samples were collected every 1 to 2-weeks until plants wilted. Leaf water potential was measured, leaf osmotic plus matric potential was estimated, and turgor pressure calculated using methods similar to those detailed by Johnson (1978) and Johnson and Brown (1977). Excised leaf segments were inserted in water-tight psychrometer chambers 0.64 cm diameter by 1-cm long, which were placed in a constant-temperature water bath at 25°C for 3 hours. Total leaf water potential was measured by reading psychrometer micro-volt output after a 15-sec cooling period. Psychrometer chambers were then placed on dry ice for 15 min and then allowed to slowly warm to room temperature. Water potential of the frozen-thawed leaf tissue was again determined psychrometrically and is an estimation of the osmotic plus matric potential of the leaf. Turgor pressure was calculated by subtracting the osmotic plus matric potential from the total leaf water potential.

Water potential was calculated from soil and chamber psychrometer output using the model of Brown and Bartos (1982) adjusted for individual psychrometer calibrations against NaCl solutions of known solute potential.

Shoot and root elongation data were fit to third-order polynomial regression equations using time as the independent variable. Regression slopes of leaf water potential on turgor pressure were compared by the method of Snedecor and Cochran (1971). Water potential components

of growth cessation and visible root length were compared among species and salinity treatments using analysis of variance and Duncan's multiple range test.

Results

Absolute growth of shoots and root elongation of tall wheatgrass was greater than that of basin wildrye for all soil salinities (Figures 21 and 22). Salinity decreased growth of shoots and elongation of roots of both species. Most rapid shoot elongation was 11.5, 9.6 and 5.0 $\text{cm}\cdot\text{day}^{-1}$ for tall wheatgrass and 2.0, 1.0 and 1.3 $\text{cm}\cdot\text{day}^{-1}$ for basin wildrye for soil salinities of 1, 10, and 20 $\text{dS}\cdot\text{m}^{-1}$, respectively. Growth differences due to salinity were apparent even when there were minimal differences in leaf water potential of plants growing in nonsaline and saline soil. For example, predawn leaf water potentials after 55 days, when large growth differences were evidenced (Figures 21 and 22) were -1450, -1640, and -1500 $\text{J}\cdot\text{kg}^{-1}$ for tall wheatgrass and -1120, -1070, and -1090 $\text{J}\cdot\text{kg}^{-1}$ for basin wildrye for soil salinities of 1, 10 and 20 $\text{dS}\cdot\text{m}^{-1}$, respectively. Tall wheatgrass shoots grew rapidly and ceased growth abruptly, while basin wildrye grew less rapidly and gradually ceased growth. Maximum rate of root elongation was 1.4, 1.1, and 0.9 $\text{cm}\cdot\text{day}^{-1}$ for tall wheatgrass and 1.0, 0.6 and 0.5 $\text{cm}\cdot\text{day}^{-1}$ for basin wildrye for soil salinities of 1, 10 and 20 $\text{dS}\cdot\text{m}^{-1}$, respectively. Shoot growth of basin wildrye at an ECe of 20 $\text{dS}\cdot\text{m}^{-1}$ was less initially, then exceeded growth of that at an ECe of 10 $\text{dS}\cdot\text{m}^{-1}$. Salinity decreased root elongation of basin wildrye more than that of tall wheatgrass. Tall wheatgrass required 30, 35 and 41 days and basin wildrye required 38, 52 and 72 days to reach a rooting depth of 30 cm in soil salinities of 1, 10 and 20 $\text{dS}\cdot\text{m}^{-1}$, respectively (Figure 22).

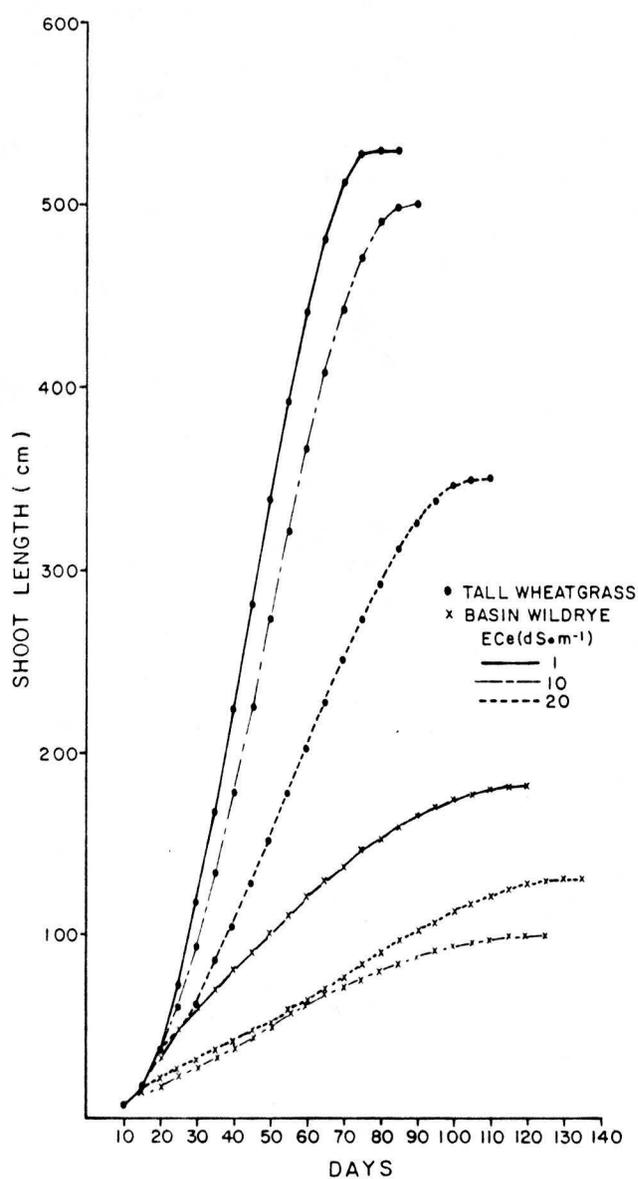


Figure 21. Cumulative shoot length as a third-degree polynomial function of time for Jose tall wheatgrass and Magnar basin wildrye growing in soils of different salinities. R^2 values were 0.89, 0.88, 0.69, and 0.88, 0.77, 0.85, for soil electrical conductivities of 1, 10 and 20 $\text{dS}\cdot\text{m}^{-1}$, for tall wheatgrass and basin wildrye, respectively. All regressions were significant at the 0.05 level.

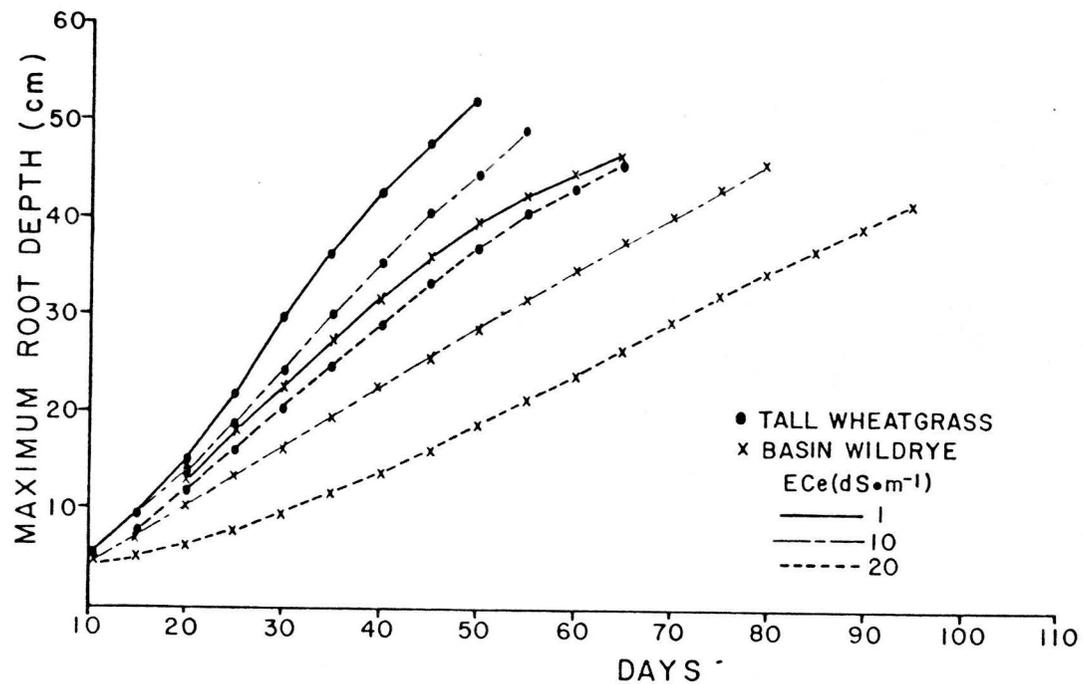


Figure 22. Maximum root depth as a third-degree polynomial function of time for Jose tall wheatgrass and Magnar basin wildrye growing in soils of different salinities. R^2 values were 0.92, 0.80, 0.78, and 0.78, 0.89, and 0.76 for soil electrical conductivities of 1, 10, and 20 $\text{dS}\cdot\text{m}^{-1}$, for tall wheatgrass and basin wildrye, respectively. All regressions were significant at the 0.05 level.

Visible root length generally increased from a depth of 10 to 20 cm, then decreased with increasing soil depth (Figure 23). Due to soil drying, roots were difficult to see, so the root lengths were probably underestimated and estimates were probably more variable than the actual root lengths. Jose tall wheatgrass generally had greater root length at all depths than Magnar basin wildrye and salinity decreased root length of both species similarly.

Slopes of the linear regressions of turgor pressure on leaf water potential were similar for tall wheatgrass grown at different salinities as were leaf water potentials at zero turgor (Table 12). For basin wildrye, the decrease in leaf turgor with decreasing leaf water potential tended to be less and leaf water potential at zero turgor tended to be more negative as soil salinity increased. Tall wheatgrass tended to have higher turgor at a given leaf water potential, but generally had a greater turgor loss with decreasing leaf water potential than basin wildrye.

Tall wheatgrass generally had lower leaf and soil water potential after shoot growth cessation than basin wildrye (Table 13, Figure 24). Tall wheatgrass had lower leaf and soil water potential and lower turgor pressure in nonsaline than salinized soil after growth cessation. Tall wheatgrass had lower soil water potential at depths greater than 20 cm than basin wildrye after growth cessation (Figure 24). Basin wildrye leaf water potential components after growth cessation were generally similar for different soil salinities (Table 13). Basin wildrye had lower soil water potential in the upper 35 cm of nonsaline soil than in saline soil at growth cessation (Figure 24).

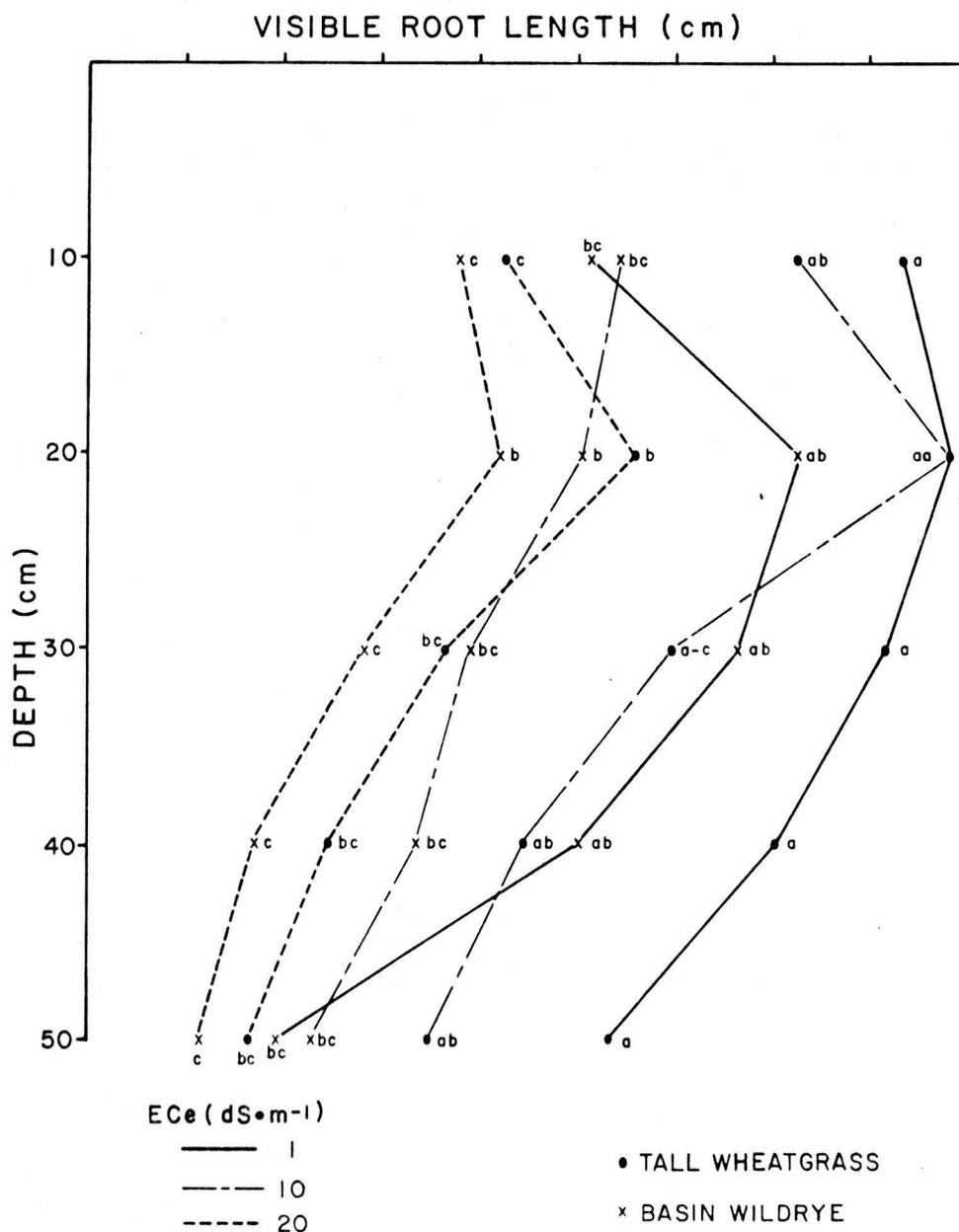


Figure 23. Visible root length of Jose tall wheatgrass and Magnar basin wildrye after 3-months growth in soils of different salinities. Means at each depth followed by the same letter are not significantly different at the 0.05 level as determined by Duncan's multiple range test.

Table 12. Statistics for the linear regressions of turgor pressure on leaf water potential ($\text{J}\cdot\text{kg}^{-1}$) for Jose tall wheatgrass and Magnar basin wildrye seedlings growing in soils at different salinities.

| Species | Soil ECe ($\text{dS}\cdot\text{m}^{-1}$) | Turgor pressure at zero leaf water potential ($\text{J}\cdot\text{kg}^{-1}$) | Slope* | Leaf water potential at zero turgor ($\text{J}\cdot\text{kg}^{-1}$) | r^{\dagger} |
|-----------------|---|---|---------|--|---------------|
| Tall wheatgrass | 1 | 1620 | 0.300ab | -5400 | 0.83 |
| | 10 | 1662 | 0.333a | -4991 | 0.84 |
| | 20 | 1744 | 0.312ab | -5590 | 0.72 |
| Basin wildrye | 1 | 1552 | 0.353a | -4397 | 0.81 |
| | 10 | 1356 | 0.272ab | -4985 | 0.69 |
| | 20 | 1326 | 0.247b | -5368 | 0.70 |

* Values followed by the same letter are not significantly different at the 0.05 level as determined by the slope test method of Snedecor and Cochran (1971).

[†]All r values are significant at the 0.01 level.

Table 13. Predawn leaf water potential and turgor pressure ($\text{J}\cdot\text{kg}^{-1}$) within 1-week of cessation of shoot elongation of Jose tall wheatgrass and Magnar basin wildrye grown in soils of different salinities.

| Species | Soil E_{ce} ($\text{dS}\cdot\text{m}^{-1}$) | Leaf Water Potential ($\text{J}\cdot\text{kg}^{-1}$) | Turgor Pressure ($\text{J}\cdot\text{kg}^{-1}$) |
|-----------------|--|---|--|
| Tall wheatgrass | 1 | -5477c* | 0b |
| | 10 | -3381b | 574ab |
| | 20 | -2988ab | 994a |
| Basin wildrye | 1 | -3269b | 407ab |
| | 10 | -1767a | 810a |
| | 20 | -2964ab | 666ab |

* Means in the same column followed by the same letter are not significantly different at the 0.05 level as determined by Duncan's multiple range test.

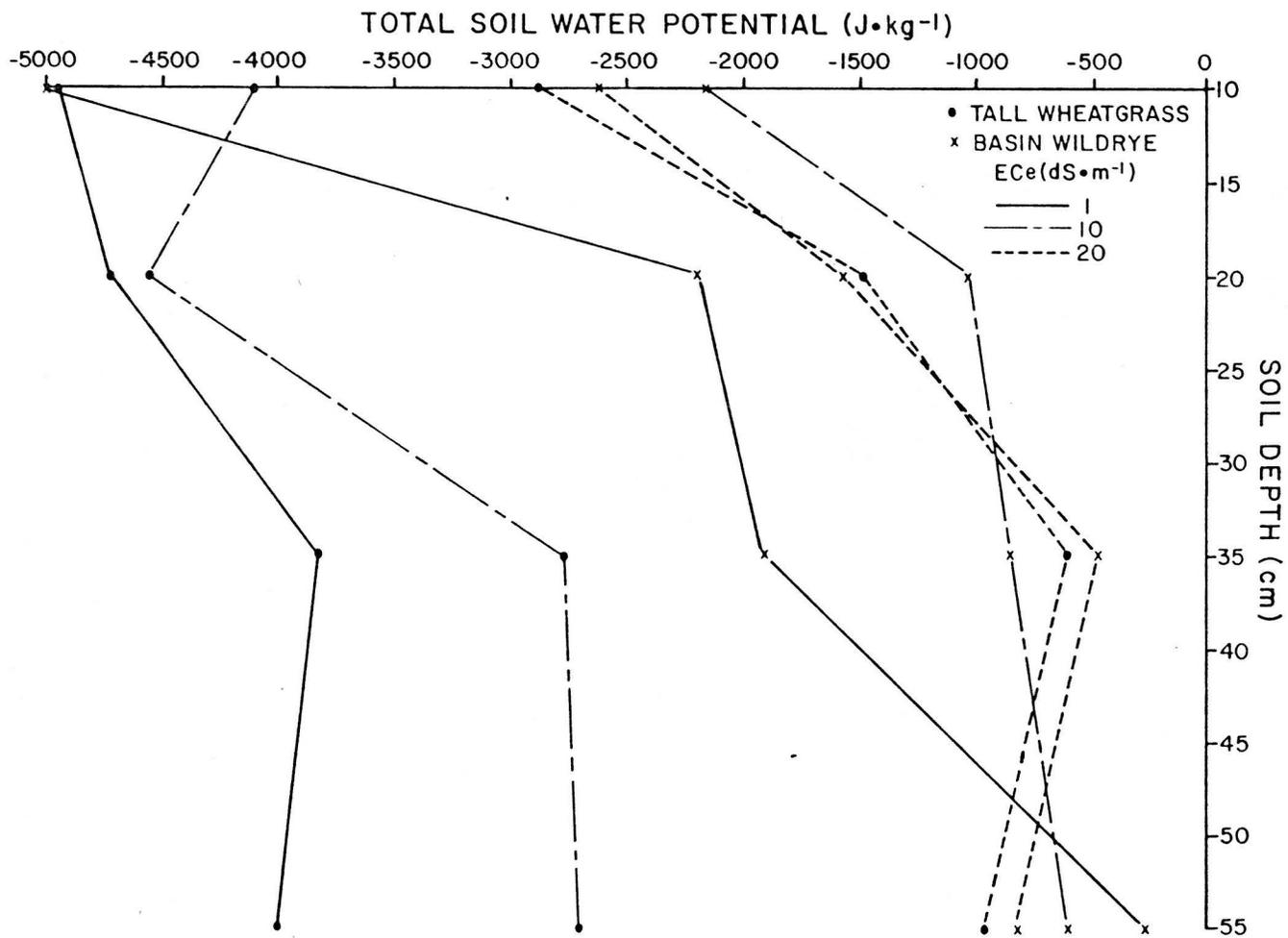


Figure 24. Total soil water potential in soil columns of different salinities within 1-week of cessation of shoot elongation of Jose tall wheatgrass and Magnar basin wildrye.

Discussion

The ability of plants to postpone dehydration by water conservation mechanisms by extensive root growth or by osmotic adjustment (Turner and Kramer 1980) may be important to seedling survival on saline, arid rangelands. Magnar basin wildrye showed a trend toward slightly greater osmotic adjustment and turgor maintenance in salinized than nonsalinized soil (Table 12). Osmotic adjustment and turgor maintenance of Jose tall wheatgrass was similar in nonsaline and saline soil. Much lower osmotic adjustment of these two species when unwatered than when salinized in small containers as reported by Roundy (1983) was probably due to a faster rate of development of water stress for the unwatered plants. Turgor maintenance by osmotic adjustment is affected by the rate of development (Begg and Turner 1976) and degree of water stress, and the light and temperature environment (Turner and Jones 1980). The slow development of water stress in the present study resulted in maintenance of turgor at very low leaf water potentials of both species both in nonsaline and saline soil. Even though both species maintained turgor as well in saline as nonsaline soil, salinity substantially reduced growth of both species. These growth differences were apparent even during periods when there were no differences between leaf or soil water potentials for nonsaline and saline soil treatments. This strongly suggests that the effects of salinity on growth were not due to water stress, but rather due to salt toxicity (Strogonov 1964) or nutritional imbalances due to accumulated ions (Storey and Wyn Jones 1978). Basin wildrye evidenced a slight increase in salinity tolerance with time. Plants in the soil with an E_{c_e} of $20 \text{ dS}\cdot\text{m}^{-1}$ initially grew less, but then finally grew more than plants in the soil with an E_{c_e} of $10 \text{ dS}\cdot\text{m}^{-1}$ (Figure 21).

This pattern of growth was associated with decreased initial water use by the plants in the higher salinity treatment followed by higher leaf water potentials later than the plants in the lower salinity treatment.

Salinity decreased growth of both species and plants in the non-saline soil had more rapid water use, greater soil water depletion, and a shorter period of growth than plants in saline soil. It has been suggested that conservation of water due to reduced water use associated with soil salinity may allow maintenance of a favorable water balance during drought periods (Stark and Jarrell 1980, Jensen 1982). Reduced root growth of plants in saline soil in this study resulted in less water use at lower soil depths than plants in nonsaline soil (Figure 24). Reduced growth and water use would probably be much less adaptive to saline, arid rangelands than extensive root growth and associated greater water use. High evaporative demands result in rapid decreases of surface soil water potentials in the absence of precipitation on these rangeland seedbeds (Roundy et al. 1984). Reduced water use in the surface soil could also allow invasion of seeded rangelands by less desirable weedy species. The greater survival of Jose tall wheatgrass than Magnar basin wildrye on a saline soil in Nevada¹ is best explained by greater initial radicle growth of tall wheatgrass under decreasing osmotic potentials² and continued greater root elongation than basin wildrye in saline soil as shown in this study. High tolerance to salinity as evidenced by rapid and extensive root growth should be a foremost consideration when selecting for plants that can establish on saline, arid rangelands.

results
finding
The hypotheses can be reported as follows:

- VI. A. Tall wheatgrass had greater establishment and survival in the field and also had more rapid root elongation and grew at lower soil water potentials than basin wildrye.
- B. Osmotic adjustment was generally similar for plants growing in saline and nonsaline soil as water stress developed slowly. Salinity decreased growth even when water stress was minimal or when osmotic adjustment maintained high turgor.

Rapid elongation of roots under decreasing soil osmotic and matric potentials is especially important to seedling survival on saline, arid soils. In the absence of spring rains, surface soil water potentials will result in desiccation of shallow-rooted seedlings.

GERMINATION AND SEEDLING GROWTH OF BASIN WILD RYE
AND TALL WHEATGRASS IN RELATION TO BORON

Introduction

Many saline/alkaline rangelands in the arid west could be highly productive once adapted forage species are established. In addition to high sodium concentrations, and low soil osmotic and matric potentials, high boron concentrations may limit seedling emergence and establishment on the associated saline/alkaline, arid soils. Great Basin playas have accumulated boron from hot springs waters which become boron-enriched from late-stage differentiates of granitic magmas (Papke 1976). Sediments high in boron are then eroded from playa surfaces and deposited by wind on lowland soils¹. Two grasses which may have the greatest potential for establishing on these soils are tall wheatgrass and basin wildrye. Tall wheatgrass is well known for its sodic and salt tolerance (Dewey 1969, Carter and Peterson 1962, Shannon 1978, Roundy 1983) and the high boron tolerance of three cultivars, Alkar, Nebraska, and Largo, has been documented by Schuman (1969). Basin wildrye is a native grass adapted to many saline-sodic soils (Young and Evans 1981). Pratt et al. (1971) have shown basin wildrye to be tolerant to mine spoils containing 5 ppm soluble boron in the saturation extract. An improved cultivar of basin wildrye called Magnar has much higher seed viability and germination than native wildrye collections (Young and Evans 1983) and also has

¹ Young, J.A. and R.A. Evans. 1984. Erosion and deposition of fine sediments from playas. *J. Arid. Envir.* (Submitted).

high sodic and salt tolerance (Roundy 1983). However, Magnar basin wildrye had much lower emergence and establishment than Jose tall wheatgrass on a saline soil in central Nevada.² The purpose of this study was to compare the germination and seedling growth of Jose tall wheatgrass with that of Magnar basin wildrye in relation to boron. This information will help determine if boron may limit field establishment of these species on Great Basin saline soils.

Methods

Germination tests were conducted by placing twenty-five seeds of each species in plastic boxes containing 5 g of polystyrene foam (Young et al. 1968) and boric acid solutions containing 0, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 120, 150, 180, 200, 250, 300, 350, 400, 450, 500 ppm of boron. There were 4 replications of each boron concentration and all replicates were incubated in a dark germinator at a constant 15°C. Germinated seedlings were counted every 2 or 3 days for 3 weeks and radicle length of 20 seedlings per cultivar for each boron concentration were measured at the end of 3 weeks. Average rates of germination were calculated after MaGuire (1962) where:

$$\text{Average germination rate (\%}\cdot\text{day}^{-1}) = \sum_i^n [g_n - g_{(n-1)}] / n$$

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

Seedling response to boron concentrations were determined in 11.5 cm diameter by 11 cm deep plastic pots filled with sandy loam soil and

² Roundy, B.A. 1983. Emergence and establishment of basin wildrye and tall wheatgrass in relation to moisture and salinity. J. Range Manage. (Submitted).

irrigated to saturation every other day with complete nutrient solution (Hoagland and Arnon 1938) and boron concentrations of 0, 10, 20, 40, 60, 80 and 100 ppm from boric acid. Twenty-five seeds of each cultivar were seeded separately in four pots for each boron concentration and pots were finally thinned to ten seedlings. The experiment was conducted in the greenhouse with average day and night temperatures of 20 and 30°C, respectively, and relative humidity ranged from 30% during the day to 70% at night. Soil boron concentrations were checked at the end of the experiment, using a liquid ion exchange electrode (Carlson and Paul 1968, 1969) and were within 7 ppm of the boron treatment concentrations. Roots and shoots were harvested, oven dried and weighed 45 days after seeds were sown. Cultivar responses to increasing boron concentrations were fit to polynomial regression equations and confidence intervals ($P = 0.05$) were calculated according to Ott (1977). A saline soil (electrical conductivity of the saturation extract = $7.0 \text{ dS} \cdot \text{m}^{-1}$) was sampled at depth intervals of 0-1, 1-5, 5-10 and 10-15 cm in the spring of 1981 in conjunction with a seedling establishment study² to determine the associated range of soil boron concentrations. Four samples were taken for each depth interval for soil microtopographical areas appearing high in salinity and areas appearing low in salinity as evidenced by the presence or absence of a thin salt crust on the soil surface. Soluble boron concentrations of the saturation extracts of these soil samples were determined with a liquid ion exchange electrode (Carlson and Paul 1968, 1969).

Results

Total germination of Jose tall wheatgrass was not reduced even at boron concentrations of 500 ppm. Magnar basin wildrye germination was

reduced from 92 to 80% by 200 to 450 ppm of boron and then dropped to 47% at 500 ppm of boron. Rate of germination of Jose tall wheatgrass was not significantly reduced ($P = 0.05$) by boron, but that of Magnar basin wildrye was reduced at boron concentrations above 350 ppm (Figure 25). Jose tall wheatgrass had greater absolute radicle growth than Magnar basin wildrye at boron concentrations less than 200 ppm (Figure 26). Boron concentrations greater than 100 ppm decreased radicle growth of both species (Figure 26), but boron decreased relative radicle growth of Jose tall wheatgrass more than that of Magnar basin wildrye so that absolute radicle growth of both species was similar at boron concentrations greater than 200 ppm (Figure 26).

Absolute growth of tall wheatgrass shoots and roots generally exceeded that of basin wildrye at all boron concentrations (Figure 27). Leaves of tall wheatgrass and basin wildrye exhibited pronounced tip burn and some chlorosis at 80 and 60 ppm of boron, respectively. Root growth of both species was more sensitive to boron than shoot growth (Table 14). Root and shoot growth of basin wildrye was more sensitive to increasing boron concentrations than that of tall wheatgrass (Table 14). Seedling survival of tall wheatgrass in pots in the greenhouse was not affected by boron even at 100 ppm, but basin wildrye survival was reduced to 53, 45 and 23% at boron concentrations of 60, 80 and 100 ppm, respectively.

Boron content in the saturation extract of a saline soil where Jose tall wheatgrass and Magnar basin wildrye were seeded² ranged from 2 to 96.7 ppm (Table 15). Highest boron samples averaged about 30 ppm while low boron samples averaged about 5 ppm. Boron concentrations in the soil

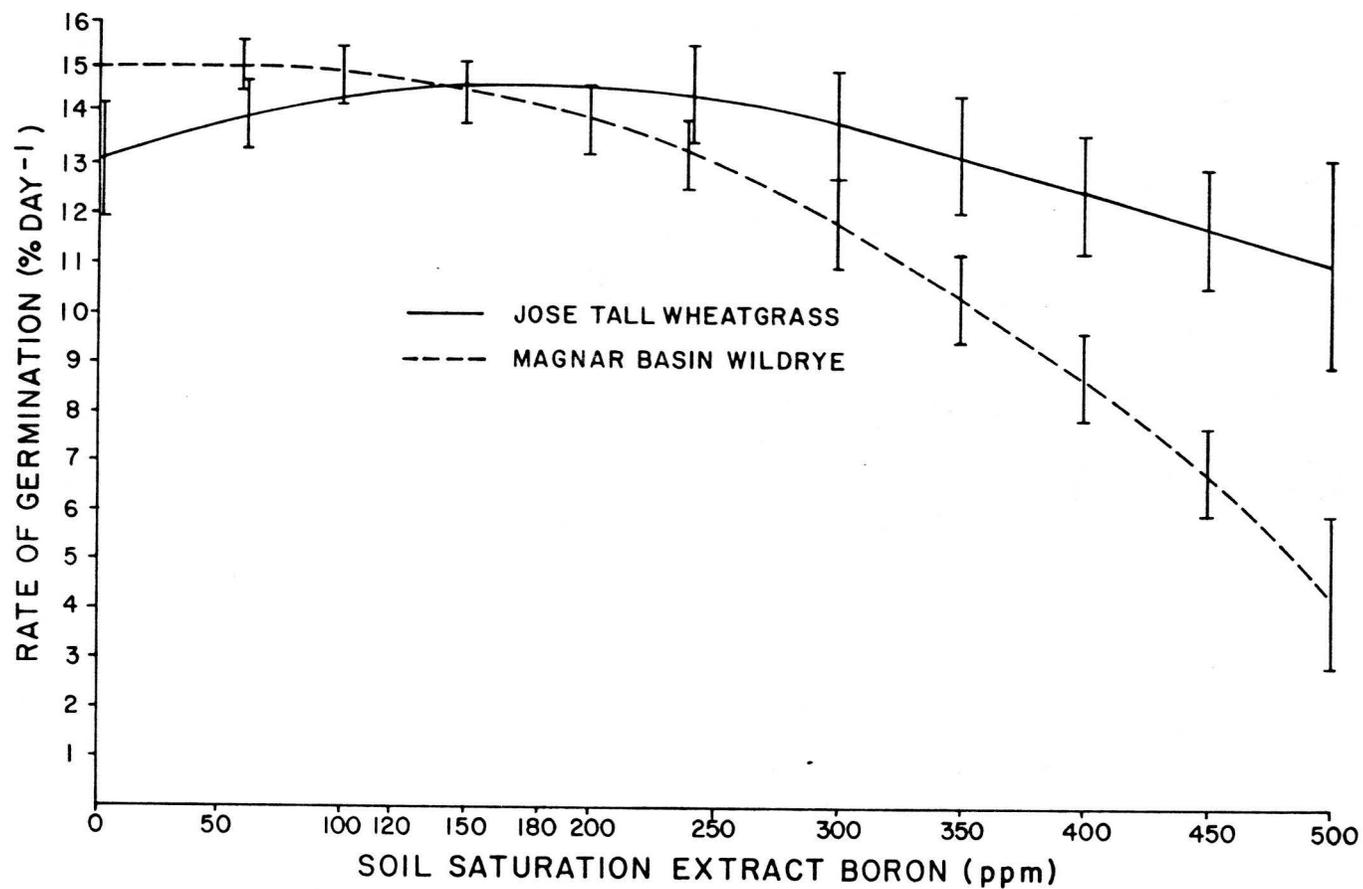


Figure 25. Rate of germination of Jose tall wheatgrass and Magnar basin wildrye as a third degree polynomial function of soil boron concentration in the saturation extract. Vertical bars indicate confidence limits ($P = 0.05$) for the regression lines. R values for tall wheatgrass and basin wildrye are 0.38 and 0.86, respectively, and are both significant at the $P = 0.01$ level.

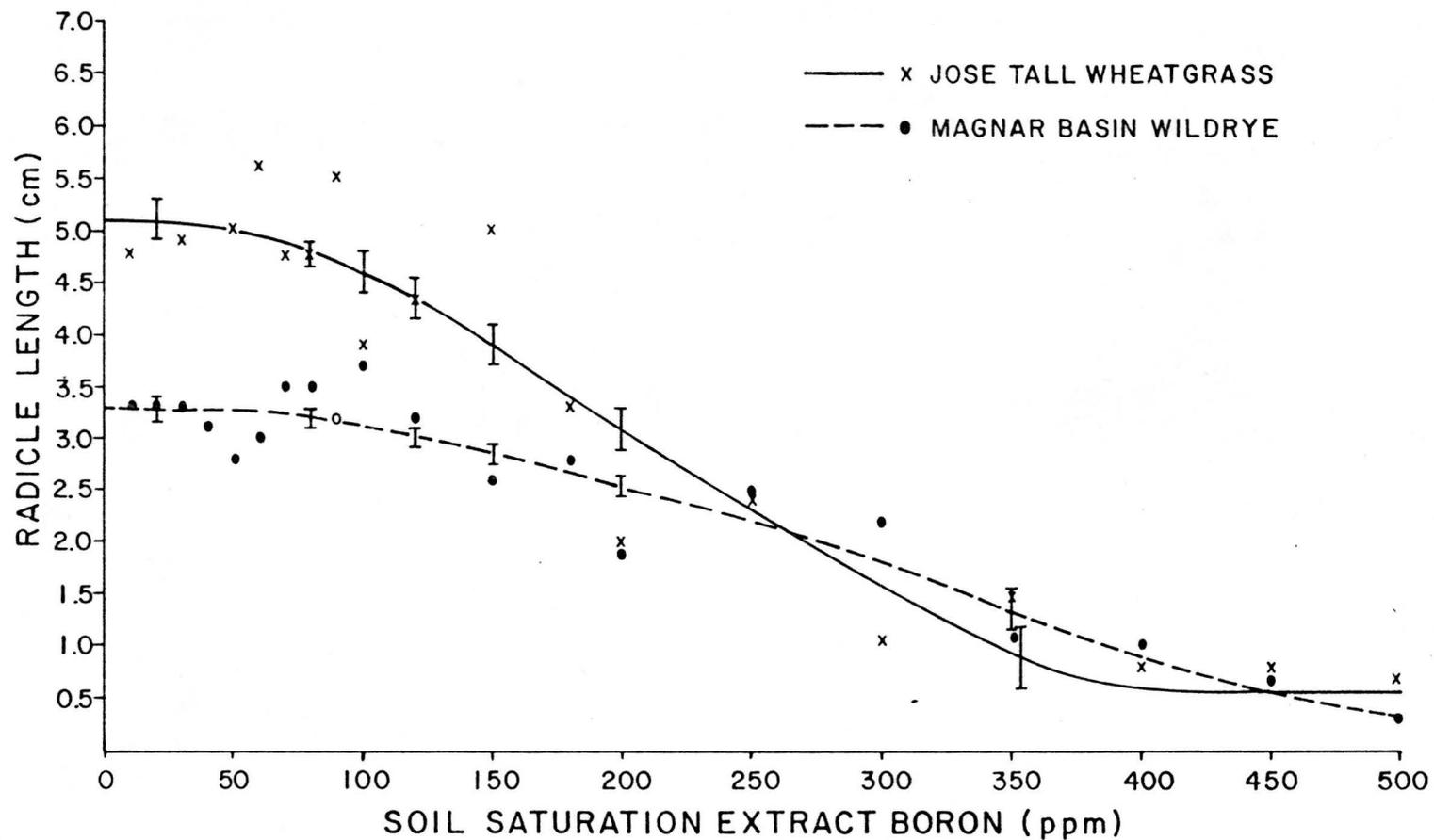


Figure 26. Radicle length of Jose tall wheatgrass and Magnar basin wildrye seedlings as a second degree polynomial function of boron concentration in the germinating medium. Vertical bars indicate confidence limits ($P = 0.05$) for the regression lines and each value is the mean of 20 radicle measurements. R values for tall wheatgrass and basin wildrye are 0.77 and 0.69, respectively, and both are significant at the $P = 0.05$ level.

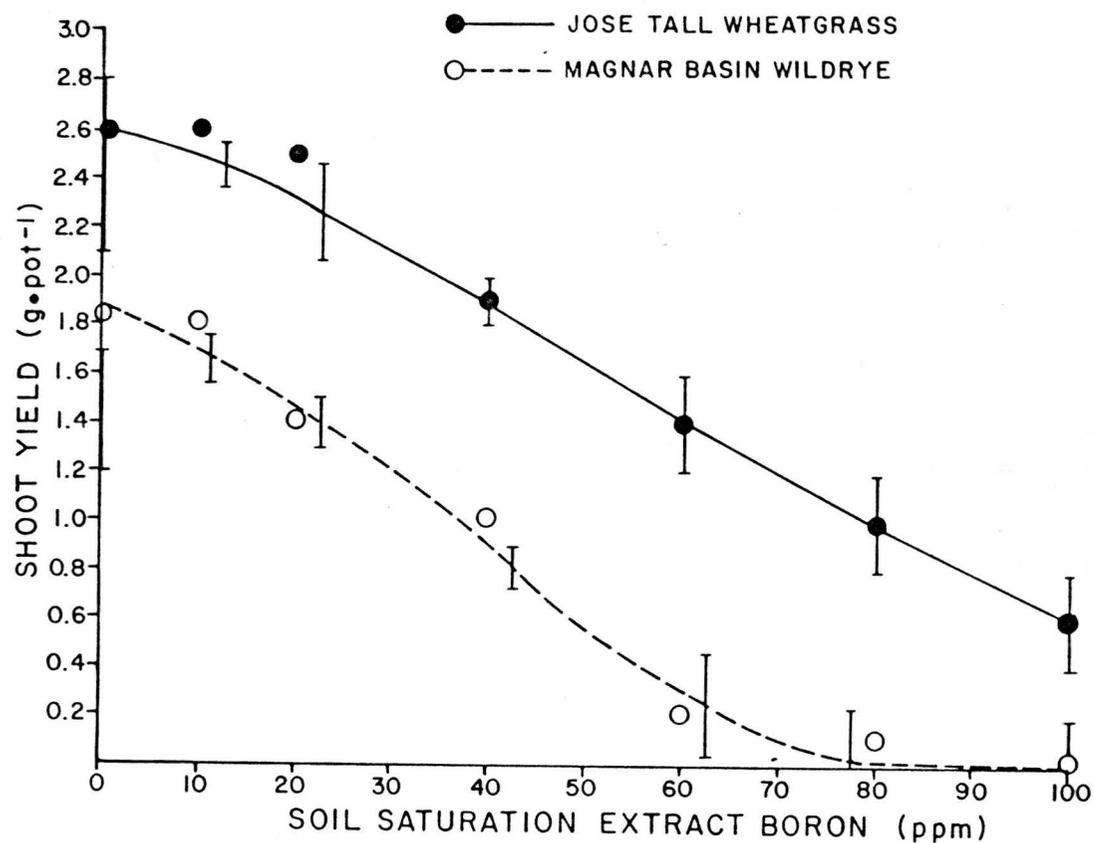


Figure 27. Dry weight yield of Jose tall wheatgrass and Magnar basin wildrye seedling shoots (above) and roots (next page) as a third degree polynomial function of soil boron concentration in the saturation extract. Vertical bars indicate confidence intervals ($P = 0.05$) for the regression lines and each value is the mean of 4 replications. R values are 0.96 and 0.98 for tall wheatgrass shoots and roots and 0.96 and 0.97 for basin wildrye shoots and roots, respectively. All R values are significant at the $P = 0.05$ level.

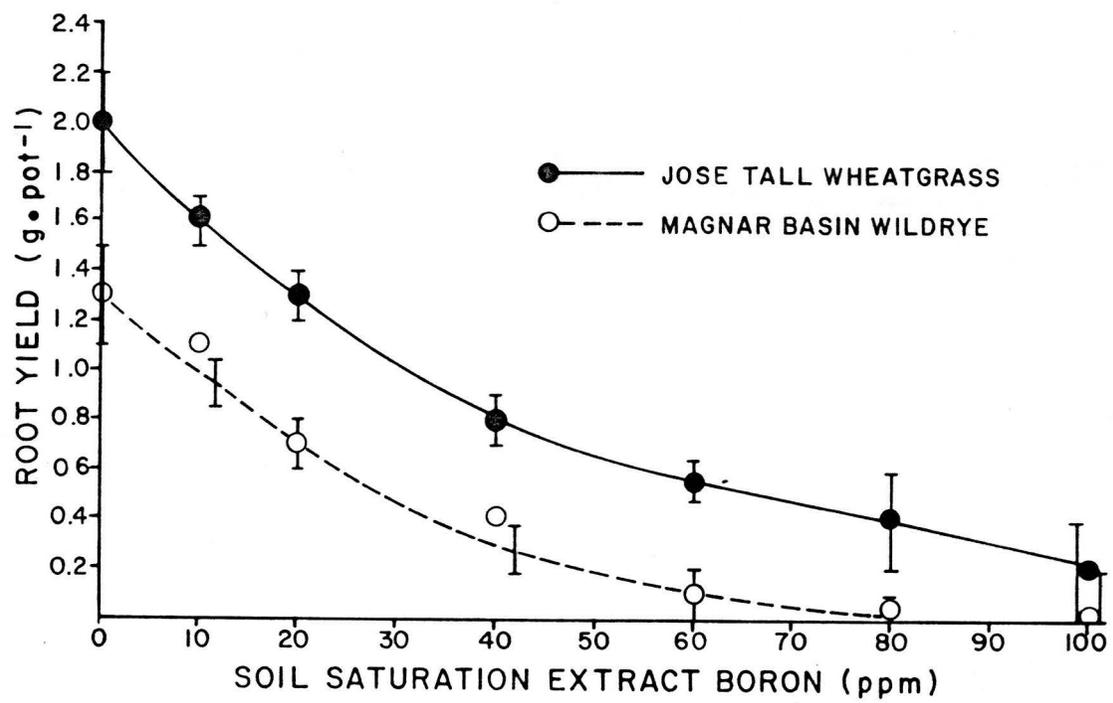


Figure 27 (continued).

Table 14. Boron concentrations associated with Jose tall wheatgrass and Magnar basin wildrye germination and growth reductions.

| Parameter | <u>Significant Reduction⁺</u> | | <u>50% reduction</u> | |
|---------------------------------|--|----------------------|------------------------|----------------------|
| | <u>Tall wheatgrass</u> | <u>Basin wildrye</u> | <u>Tall wheatgrass</u> | <u>Basin wildrye</u> |
| | Boron Concentration of Soil saturation extract (ppm) | | | |
| Total germination after 3 weeks | NS* | 200 | NS | 500 |
| Rate of germination | NS | 350 | NS | 450 |
| Radicle length | 100 | 120 | 230 | 325 |
| Shoot yield | 30 | 20 | 65 | 37 |
| Root yield | 10 | 10 | 30 | 22 |
| Survival | NS | 60 | NS | 60 |

⁺Statistically significant reduction ($P = 0.05$) compared to control treatments with no added boron as determined by nonoverlapping regression line confidence intervals.

*NS = no statistically significant ($P = 0.05$) reduction occurred at a boron concentration of 500 ppm for germination or rate of germination or at 100 ppm for survival.

Table 15. Mean boron concentrations of Gund silt-loam soil samples representing high and low boron concentrations at saturation water content (saturation) and corresponding maximum possible soil solution boron concentrations at field capacity soil water content (FC) and at the soil water content where the soil matrix potential is less than $-1500 \text{ J}\cdot\text{kg}^{-1}$ (dry).

| <u>Depth interval (cm)</u> | <u>Boron (ppm)</u> | | | | | | | <u>Range Saturation</u> |
|----------------------------|---------------------------|-----------|------------|--------------------------|-----------|------------|----------|-------------------------|
| | <u>High boron samples</u> | | | <u>Low boron samples</u> | | | | |
| | <u>Saturation</u> | <u>FC</u> | <u>Dry</u> | <u>Saturation</u> | <u>FC</u> | <u>Dry</u> | | |
| 0-1 | 61.6 | 104.7 | 251.3 | 4.1 | 7.0 | 16.7 | 2.6-96.7 | |
| 1-5 | 30.2 | 51.3 | 123.2 | 5.8 | 9.9 | 23.7 | 2.0-42.2 | |
| 5-10 | 32.9 | 55.9 | 134.2 | 6.1 | 10.4 | 24.9 | 2.5-44.0 | |
| 10-15 | 27.5 | 46.8 | 112.2 | 5.0 | 8.5 | 20.4 | 2.3-40.1 | |

were highly variable horizontally as is the case for other soluble salts.³

As the soil dries, the boron concentration of the soil solution would be expected to increase even though some salt precipitation and adsorption of boron by the soil occurs (Bresler et al. 1982). In Table 15 are listed maximum possible soil solution concentrations of boron at field capacity water content where the soil matric potential is less than $-1500 \text{ J}\cdot\text{kg}^{-1}$ as calculated by simple linear dilution. Actual soil solution boron concentrations would be less than the table values due to soil adsorption and salt precipitation, but these maximum values may serve as a basis for discussing potential boron toxicity in the field.

Discussion

Both Jose tall wheatgrass and Magnar basin wildrye had high germination and high rates of germination at extremely high boron concentrations. The highest boron concentrations in the soil sampled in this study would not reduce rate and total germination of these species, but might slightly reduce radicle growth (Tables 14 and 15). Emergence of these species on saline soils would generally be expected to be limited by low soil osmotic and matric potentials⁴ rather than by high boron concentrations.

The boron concentration in the soil sampled could directly reduce tall wheatgrass and basin wildrye shoot and especially root growth. Root growth of both species could be reduced even on the microtopographical areas of low boron concentrations (5 ppm in the saturation extract) at

³ Roundy, B.A. 1983. Estimation of water potential components of saline soils of Great Basin rangelands. Soil Sci. Soc. Am. J. (Submitted).

lower soil water contents. Areas of high boron concentration (30 ppm in the saturation extract) could be expected to directly reduce survival of Magnar basin wildrye, but probably not of Jose tall wheatgrass as the soil dries (Table 14 and 15). Boron may indirectly reduce seedling survival by reducing root growth so that roots are unable to stay below the soil surface drying front. Rollins et al. (1968) attributed failure of tall wheatgrass and basin wildrye to establish on barren interspace soils in Nevada to high total salts and excessive sodium or boron. High seedling mortality of Magnar basin wildrye reported by Roundy² on the moderately saline soil sampled in this study could have been due, in part, to reduced root growth due to high boron concentrations. Although both species reported here are tolerant of boron compared to most plants (Wilcox 1960), Jose tall wheatgrass has greater absolute growth and its root and shoot growth are less sensitive to high boron concentrations than Magnar basin wildrye. These differences may allow Jose tall wheatgrass roots to stay below the soil drying front and avoid reduced osmotic and matric potentials and increased boron concentrations better than Magnar basin wildrye. This may explain, in part, greater field survival reported by Roundy² of tall wheatgrass than basin wildrye seedlings on a moderately saline rangeland soil and greater seedling survival of basin wildrye on a nonsaline than a moderately saline soil.

⁴ Roundy, B.A., J.A. Young and R.A. Evans. 1983. Germination of basin wildrye and tall wheatgrass in relation to moisture and salinity. J. Range Manage. (Submitted).

results testing
The hypotheses are reported as follows:

- VII. A. Boron concentrations on the saline soil in some areas were high enough to decrease seedling growth, but probably not high enough to decrease germination.
- B. Tall wheatgrass had greater growth under high soil boron concentrations and also higher survival on the saline soil in the field. Both species had high boron tolerance.

Boron tolerance may be important to seedling establishment on saline soils, but differences in boron tolerance between tall wheatgrass and basin wildrye probably account for only a small part of the difference in seedling survival for the two species in the field.

SUMMARY AND CONCLUSIONS

Great Basin lowlands once dominated by basin wildrye generally have saline soils and limited and unpredictable growing season precipitation. The potential of Magnar basin wildrye and Jose tall wheatgrass to establish on these rangelands in relation to soil water and salinity was compared in a series of field and laboratory experiments. Field experiments were conducted to determine the effects of soil salinity and precipitation on plant emergence and establishment, and to determine related effects of precipitation on soil salinity, penetrability, and soil total, matric, and osmotic potentials. Emergence and establishment of basin wildrye and tall wheatgrass and salinity and water potential components were compared on a nonsaline and on a saline soil in relation to precipitation and a sprinkler-induced gradient in spring irrigation. Water potential component estimates from salinity and psychrometer measurements were analyzed for accuracy. Soil osmotic potential was calculated by linear dilution, E_c and water content measurements and matric potential was calculated as the difference between total water potential as measured by thermocouple psychrometers and osmotic potential. Due to predominantly highly soluble salts (Table 1) soil osmotic potentials calculated this way were similar to those calculated using a chemical equilibrium model (Tillotson et al. 1980, Figure 3) and matric potentials were similar to those determined by a pressure plate at volumetric water contents greater than 0.09 (Figure 4).

Salinity of the surface cm of soil was lowest in early spring, following winter precipitation, then increased greatly in mid-spring as the

soil began drying and salts accumulated in the surface (Figure 8a). Total water potential of the surface cm increased and decreased rapidly in response to precipitation and drying periods (Figure 8b). Interspace soil crusts were greatly softened by precipitation, but rapidly rehardened as they dried out (Figure 11). The surface seedbed can be a harsh environment for germination in the absence of precipitation due to its high salinity and low soil osmotic and matric potentials and hard interspace soil crusts. Ability to rapidly germinate at low osmotic and matric potentials would be important to seedling emergence in this environment.

Subsurface salinity (1-15 cm) increased gradually from early spring through summer due to an upward movement of water and salts from lower depths as the soil surface dried (Figure 8a). Irrigation decreased this upward movement of salts and increased the subsurface soil osmotic and matric potentials by leaching salts and increasing soil water content (Figure 8). The nonsaline soil generally had higher total water potentials than the saline soil. Salinity of the saline soil increased with depth. Without frequent precipitation or irrigation, soil water potentials decreased rapidly in June and July. In field experiments, seedling emergence and establishment varied with natural precipitation, irrigation to simulate spring precipitation, and soil salinity. The winter and spring of 1980 to 1981 could be characterized as a dry winter and a wet spring receiving 8.3 cm of rain in April through June. The highest irrigation added about 10 cm of water to the natural rain that fell in April through June. Due to the dry winter and the initially dry surface soil, plus the timing of irrigations between major storms, irrigation greatly increased the emergence of basin wildrye on the saline soil in

1981 (Figure 13). Supplemental irrigation plus precipitation of 16 cm was necessary to produce an acceptable stand of basin wildrye seedlings (at least two seedlings per m of row) on the saline soil in 1981 (Figure 14).

The winter and spring of 1981 to 1982 could be characterized as a wet winter and dry spring with the highest irrigation adding 10 cm to the 4.6 cm of rain that fell in April through June. Due to an initially wet seedbed and less frequent natural storms and irrigation, irrigation had little effect on emergence of either Jose tall wheatgrass or Magnar basin wildrye on either the nonsaline or saline soil in the spring of 1982 (Table 3). Tall wheatgrass had higher emergence and establishment than basin wildrye on both the nonsaline and saline soils (Table 3). Basin wildrye did not produce an acceptable seedling stand on the saline soil even with the highest irrigation and required approximately 14 cm of precipitation plus irrigation to produce an acceptable stand on the nonsaline soil in 1981 (Figure 14). In contrast, tall wheatgrass produced excellent seedling stands (6 seedlings per m of row) with the highest irrigation and acceptable seedling stands with no irrigation on both the nonsaline and saline soils (Figure 14). The practical conclusion is that Jose tall wheatgrass but not Magnar basin wildrye would be expected to establish on soils of similar salinity during a normal spring. Basin wildrye would require much higher precipitation than normal or supplemental irrigation to establish on similar saline soils.

To understand plant responses which might explain the field differences in emergence and establishment between these two species, laboratory, greenhouse and growth chamber experiments were conducted. An understanding of differences in plant responses to salinity and low water

potentials which are consistent with field results is useful in determining selection criteria to determine potential of other plant materials for revegetating saline, arid range sites.

In a series of germination experiments, Jose tall wheatgrass had higher total germination, a higher rate of germination, and greater radicle growth at decreasing osmotic potentials and higher emergence at decreasing soil matric potentials than Magnar basin wildrye. Ion toxicity was evidenced by generally lower total germination, lower germination rates and less radicle growth of both species in NaCl, Na₂SO₄ and CaCl₂ than in PEG-6000 at isosmotic potentials (Table 8). Tall wheatgrass seeds were more tolerant of sodium and chloride than calcium or sulfate ions. Tall wheatgrass required fewer incubation days to emerge and emerged at lower soil matric potentials than basin wildrye (Figures 15 and 16). Both species had lower emergence in soil at reduced matric potentials than in PEG and salt solutions of equivalent osmotic potentials where seed-soil contact and hydraulic conductivity were not limiting factors (Figure 15). Tall wheatgrass also germinated at lower seed water contents and seed water potentials than basin wildrye (Figure 17). Conclusions are that Jose tall wheatgrass has a lower threshold water potential at which the physiological processes of germination operate and is therefore more likely to germinate and emerge in saline, arid seedbeds than Magnar basin wildrye. These laboratory differences in germination are consistent with differences in emergence in the field.

Since the osmotic and matric potentials of saline soils decrease rapidly with the absence of spring rains (Figure 8), tolerance to salinity as exhibited by rapid root growth should be important to

establishment. Plants that can rapidly elongate roots in soil with high matric but low osmotic potentials in the early spring would later avoid much lower matric and osmotic potentials in the rapidly drying surface soil later in the spring and summer. Turgor maintenance by osmotic adjustment either by accumulation or synthesis of solutes may be important to growth and survival of plants during a change in water status (Turner and Jones 1980). Osmotic adjustment may help plants growing in low soil water potentials due to drought or salinity to maintain a favorable water balance and continue growth at low leaf water potentials. Osmotic adjustment may be facilitated by availability of ions in the solution of saline soils for uptake and accumulation (Caldwell 1974). Two experiments were conducted to compare the root and shoot growth and osmotic adjustment of basin wildrye and tall wheatgrass under salinity and drought-induced water stress. A salination experiment (Roundy 1983) compared the root and shoot yield of seedlings in sand cultures in the greenhouse in relation to soil osmotic potentials decreased to $-3500 \text{ J}\cdot\text{kg}^{-1}$ by NaCl , Na_2SO_4 and CaCl_2 . Calcium inhibited growth of both species more than the other salts and both species exhibited high tolerance to sodium (Figure 18). Absolute yield of tall wheatgrass shoots and roots exceeded that of basin wildrye at all soil osmotic potentials (Figure 18). Salination reduced root growth of tall wheatgrass more than basin wildrye and reduced shoot growth of basin wildrye more than that of tall wheatgrass (Figure 19). Even though both species maintained relatively high turgor at low leaf water potentials small initial losses in turgor were associated with greatly reduced growth (Figure 20). Gradually salinized plants maintained positive turgor at average leaf water potentials of $1200 \text{ J}\cdot\text{kg}^{-1}$ lower than

did unsalinized plants in which water stress developed rapidly due to decreasing soil matric potentials when water was withheld (Table 11). Both species survived soil osmotic potentials down to $-3500 \text{ J}\cdot\text{kg}^{-1}$ but grew very little below $-1000 \text{ J}\cdot\text{kg}^{-1}$. Another experiment compared the shoot and root elongation and osmotic adjustment of plants grown in a growth chamber until desiccation. The plants were grown in 60-cm deep columns filled with soil initially saturated with equimolar NaCl and CaCl_2 solutions having EC's of less than 1, 10, and $20 \text{ dS}\cdot\text{m}^{-1}$. Jose tall wheatgrass had greater and more rapid shoot and root elongation at all soil salinities than ^{Magnat} basin wildrye (Figures 21 and 22). Basin wildrye, but not tall wheatgrass, exhibited a trend toward greater osmotic adjustment in saline than nonsaline soil (Table 12). Despite greater or similar turgor maintenance in saline as nonsaline soil, salinity decreased shoot and root growth and water use of both species. These growth reductions due to salinity were apparent early in the experiment when plant water stress was minimal and there were no differences in predawn leaf water potentials between plants grown in nonsaline and saline soil. Apparently, nutritional imbalances or ion toxicity limited growth despite high turgor maintenance. It has been suggested that conservation of water due to reduced water use associated with reduced growth in saline soils may allow maintenance of a favorable water balance during drought periods (Stark and Jarrell 1980, Jensen 1982). Due to high evaporative demands and associated rapid decreases in soil water potentials, plus the potential for soil water loss to invading weedy species, reduced water use at the expense of root growth would not facilitate establishment of seeded species on western rangelands. For tall wheatgrass and basin wildrye, ions available for osmotic adjustment

would not increase drought tolerance due to reduced root growth due to ion toxicity. Both species had much greater root growth in nonsaline than saline soil as evidenced by lower soil water potentials at growth cessation in nonsaline than saline soil (Figure 24). Tall wheatgrass also exhibited more extensive root growth than basin wildrye by lower soil water potentials at growth cessation than basin wildrye (Figure 24). The more rapid and extensive root growth and greater absolute radicle growth of tall wheatgrass than basin wildrye best explain the greater seedling survival and establishment of tall wheatgrass than basin wildrye on the nonsaline and saline soil in the field experiments. Rapid and extensive root growth in relation to salinity should be an important factor in screening plant materials for adaptability to arid, saline soils.

In addition to being highly sodic, Great Basin lowland soils may accumulate boron from wind eroded and deposited playa sediments rich in boron.¹ Boron tolerance of Jose tall wheatgrass and Magnar basin wildrye was studied in germination and seedling-growth experiments. Both species had very high tolerance to boron. Rate and total germination of both species was unaffected by boron concentrations below 200 ppm in the saturation extract while radicle length was unaffected at less than 100 ppm (Figures 25 and 26). Seedling growth of both species were more sensitive to boron than were germination responses. Reductions in root and shoot yield of 50% occurred at soil saturation extract concentrations of 30 and 65 ppm of boron, respectively, for tall wheatgrass and 22 and 37 ppm of boron, respectively, for basin wildrye

¹ Young, J.A. and R.A. Evans. 1984. Erosion and deposition of fine sediments from playas. J. Arid Envir. (Submitted).

(Figure 27, Table 14). Boron concentrations in the saline soil of the field experiment ranged from 2 to 96.7 ppm in the saturation extract (Table 15). Boron concentrations in the soil solution will increase as the soil dries, but probably not linearly as some salt precipitation and adsorption of boron by the soil occurs (Bresler et al. 1982). Emergence of both species on the saline soil in this study was probably not reduced by boron. However, the greater tolerance of tall wheatgrass to boron at the seedling stage may have been partly responsible for its greater seedling survival than basin wildrye on the saline soil.

In conclusion, the ^{results of testing the} main hypotheses may be reported as follows:

- I. Water potential components were accurately estimated from psychrometer measurements of total water potential and electrical conductivity measurements. Most accurate estimates were at soil water contents above 0.09 and E_{Ce}'s below 15 dS·m⁻¹.
- II. Precipitation and irrigation decreased surface soil salinity and increased soil matric and osmotic potentials and briefly increased interspace soil penetrability. Salinity decreased total soil water potentials. In the absence of frequent spring rains, surface soil water potentials rapidly decreased. Mound soils averaged similar salinity, lower total water potential, and greater penetrability than interspace soils.
- III. Irrigation to simulate precipitation increased seedling emergence on a year when the soil was initially dry in early spring and when later, natural storms and irrigations were frequent. Precipitation simulated by irrigation increased survival of both species on both the nonsaline and saline soils. Salinity decreased establishment of Magnar basin wildrye, but had little effect on emergence of basin wildrye or emergence and establishment of Jose tall wheatgrass.

Supplemental irrigation is necessary to establish Magnar basin wildrye on sites of similar salinity and precipitation. Seedling emergence and establishment were generally similar on mound and interspace soils.

- IV. The ability of Jose tall wheatgrass to have greater germination and germinate more rapidly than Magnar basin wildrye at low osmotic and matric potentials is consistent with its higher emergence in the field. The ability to germinate under low water potentials is important to seedling emergence on arid nonsaline and saline soils.
- V. The greater growth of tall wheatgrass under low osmotic potentials is consistent with its greater survival than basin wildrye on a saline soil in the field. This greater growth was not due to greater osmotic adjustment, but due to greater growth at a given turgor pressure than basin wildrye. Growth at low osmotic potentials is important to seedling survival on saline, arid soils.
- VI. The greater and more rapid root elongation of tall wheatgrass under decreasing soil osmotic and matric potentials is consistent with its greater seedling survival than basin wildrye on a nonsaline and a saline soil. Rapid root elongation is important to seedling survival on saline, arid soils, because soil surface water potentials rapidly decrease in the absence of frequent rains.
- VII. Greater growth of tall wheatgrass than basin wildrye at high boron concentrations may explain, in part, its greater seedling survival than basin wildrye on a saline soil. Both species germinated in high boron concentrations, so emergence in the field was probably not limited by boron. Boron tolerance is important to seedling establishment due to locally high boron concentrations of many saline soils in the west.

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The overall hypothesis that species must be able to rapidly germinate and grow under decreasing soil osmotic and matric potentials to establish on saline, arid soils is accepted. In the absence of rains, surface soil water potentials of these soils rapidly decrease. The greater and more rapid growth of Jose tall wheatgrass than Magnar basin wildrye best accounts for its greater establishment on both nonsaline and saline soils. The greater salt tolerance of tall wheatgrass than basin wildrye is probably due to its ability to tolerate or exclude ions which interfere with growth. Both species exhibited similar ability to adjust osmotically to low water potentials, but tall wheatgrass had greater growth than basin wildrye at similar turgor pressures. Root elongation may be one of the most important characteristics in determining potential of establishment of new plant materials on saline, arid rangelands.

Suggestions for further research

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APPENDIX

Table 16. Pedon Description of Gund Silt Loam Series of Saline Soil Sampled and Seeded in Field Experiment in Grass Valley, Nevada

Classification: fine-silty, over clayey, mixed (calcareous), mesic Aquic Durorthidic Torriorthent

| Horizon | Depth (cm) | Description |
|---------|------------|--|
| A1 | 0 - 10 | Pale brown (10YR 6/3) silt loam, dark brown (10YR 3/3) moist; moderate thin and medium platy structure; soft, very friable, sticky, slightly plastic; common very fine and fine roots; many very fine interstitial and vesicular pores; strongly alkaline (pH 8.7); gradual smooth boundary. |
| C1Si | 10 - 36 | Pale brown (10YR 6/3) silt loam, brown (10 YR 4/3) moist; moderate thin and medium platy structure, hard, friable, sticky, plastic; common very fine and fine roots; common very fine tubular pores; 40 percent discontinuous weak silica cementation; strongly alkaline (pH 9.0); gradual smooth boundary. |
| C2si | 36 - 58 | Very pale brown (10YR 7/3) silt loam, pale brown (10YR 6/3) moist; moderate thin and medium platy structure; hard, firm, brittle, slightly sticky, nonplastic; few very fine to coarse roots; common very fine tubular pores; continuous weak silica cementation; strongly effervescent; moderately alkaline (pH 8.0); clear wavy boundary. |
| IIC3 | 58 - 97 | Light gray (2.5Y 7/2) clay, light brownish gray (2.5Y 6/2) moist; common medium distinct olive yellow (2.5Y 6/6) mottles moist; strong medium prismatic structure; hard, friable, sticky, very plastic; few very fine, fine and medium roots; many very fine and fine interstitial and tubular pores; continuous moderately thick pressure faces; 60 percent of the faces of ped, pores and root channels are coated with reddish brown (5YR 4/4) iron-manganese stains; strongly effervescent; strongly alkaline (pH 8.9); clear wavy boundary. |
| IIC4cs | 97 - 152 | Pale yellow (5Y 7/3) silty clay light olive gray (5Y 6/2) moist; many medium distinct olive yellow (2.5Y 6/6) mottles moist, massive, hard, friable, very sticky, plastic, very few very fine roots, many very fine tubular pores; common fine white (10YR 8/1) gypsum flecks; strongly effervescent; strongly alkaline (pH 9.0) |

Table 16. Continued

| | |
|------------------|---|
| Location: | Lander County, Nevada, 488 m north and 380 m west of the SE corner of section 1a, T. 23 N., R. 48E. |
| Physiography: | Lake terrace |
| Elevation: | 1720 m |
| Slope: | 0-2% |
| Aspect: | West |
| Drainage | Poorly drained |
| Parent material: | Silty alluvium over lacustrine sediments derived from loess and mixed rock sources |
| Vegetation: | Greasewood, salt rabbitbrush, basin big sagebrush, basin wildrye |
| Described by: | Soil Conservation Service October 1977 |

Table 17. Pedon Description of Nonsaline Soil Sampled and Seeded in Field Experiment in Grass Valley, Nevada.

Classification: fine, montmorillonitic, mesic Typic Camborthid

| Horizon | Depth (cm) | Description |
|---------|------------|--|
| A11 | 0 - 3 | Very pale brown (10YR 7/3) silty clay loam, brown (10YR 5/3) moist; very fine platy structure; soft, very friable, sticky, slightly plastic; common very fine and medium roots; slightly acid (pH 6.3); clear smooth boundary. |
| A12 | 3 - 8 | Pale brown (10YR 6/3) silty clay, brown to dark brown (10YR 4/3) moist; medium platy structure; soft, very friable, sticky, plastic; many very fine and medium roots; neutral (pH 6.5); clear smooth boundary. |
| B1 | 8 - 18 | Pale brown (10YR 6/3) silty clay, brown to dark brown (10YR 4/3) moist; fine platy structure; soft, very friable, sticky, plastic; common very fine and medium roots; neutral (pH 6.8); clear smooth boundary. |
| B2 | 18 - 30 | Very pale brown (10YR 7/3) silty clay, brown to dark brown (10YR 4/3) moist; very fine platy structure; soft, very friable, sticky, plastic; common fine and medium roots; neutral (pH 6.7); clear smooth boundary. |
| C1 | 30 - 76 | Very pale brown (10YR 7/4) silty clay, brown to dark brown (10YR 4/3) moist; fine subangular blocky structure; soft, very friable, very sticky, plastic; common very fine and medium roots; neutral (pH 6.6); gradual smooth boundary. |
| C2 | 76 - 152 | Very pale brown (10YR 7/4) silty clay, brown to dark brown (10YR 4/3) moist; medium subangular blocky structure; hard, very friable, very sticky, plastic; common very fine roots, neutral (pH 6.6); gradual smooth boundary. |
| C3 | >152 | Very pale brown (10YR 7/4) silty clay loam, dark yellowish brown (10YR 4/4) moist; coarse subangular blocky structure; slightly hard, very friable, sticky, plastic, few very fine roots; slightly effervescent; neutral (pH 6.6). |

Table 17. Continued

| | |
|------------------|---|
| Location: | Eureka County, Nevada, approximately 200 m west of the SE corner of section 17, T.23 No., R. 48E. |
| Physiography: | Lagoon |
| Elevation: | 1740 m |
| Slope: | 0-2% |
| Aspect: | West |
| Drainage: | Poorly drained |
| Parent material: | Alluvium derived from loess and mixed rock sources. |
| Vegetation: | Greasewood, salt rabbitbrush, basin big sagebrush, green rabbitbrush and basin wildrye. |
| Described by: | Bruce Roundy October 1982. |

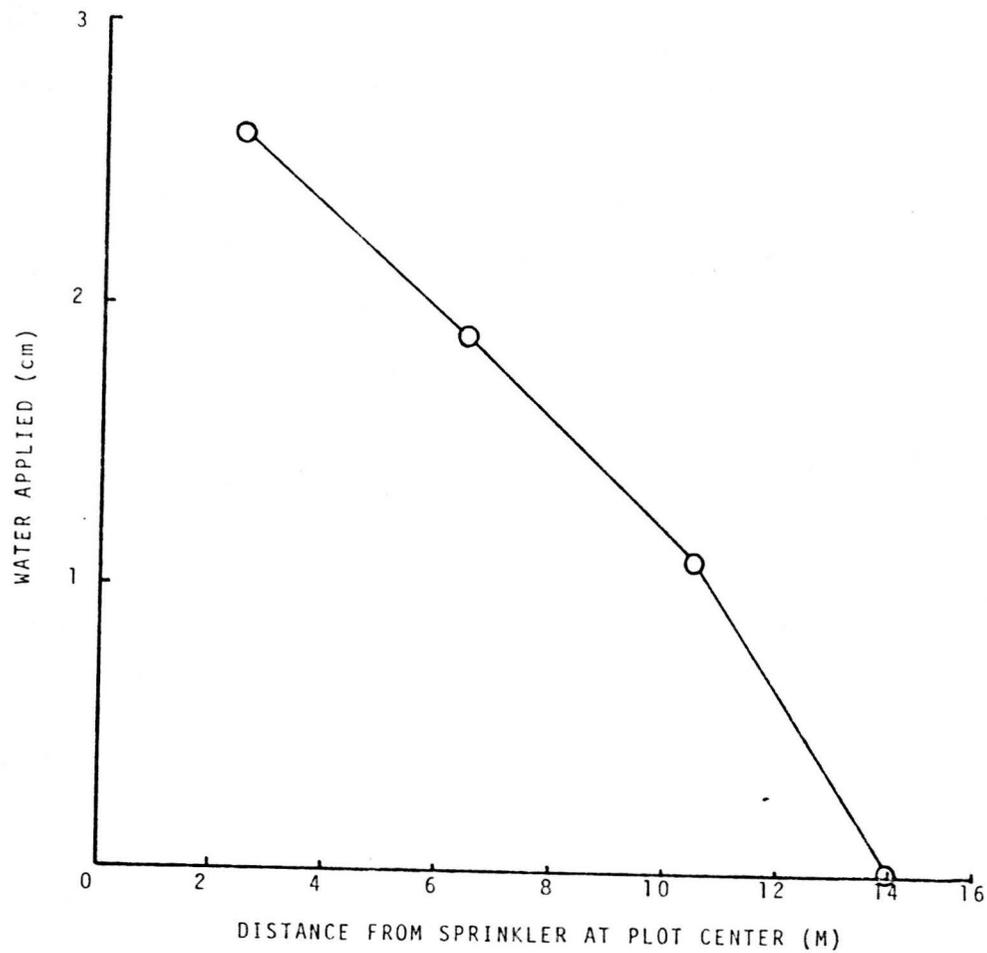


Figure 28. Water applied as a function of distance from a single sprinkler with a 4.8 mm range by 2.4 mm spreader nozzle operated for 6 hr at 0.2 MPa on a 60 cm riser.

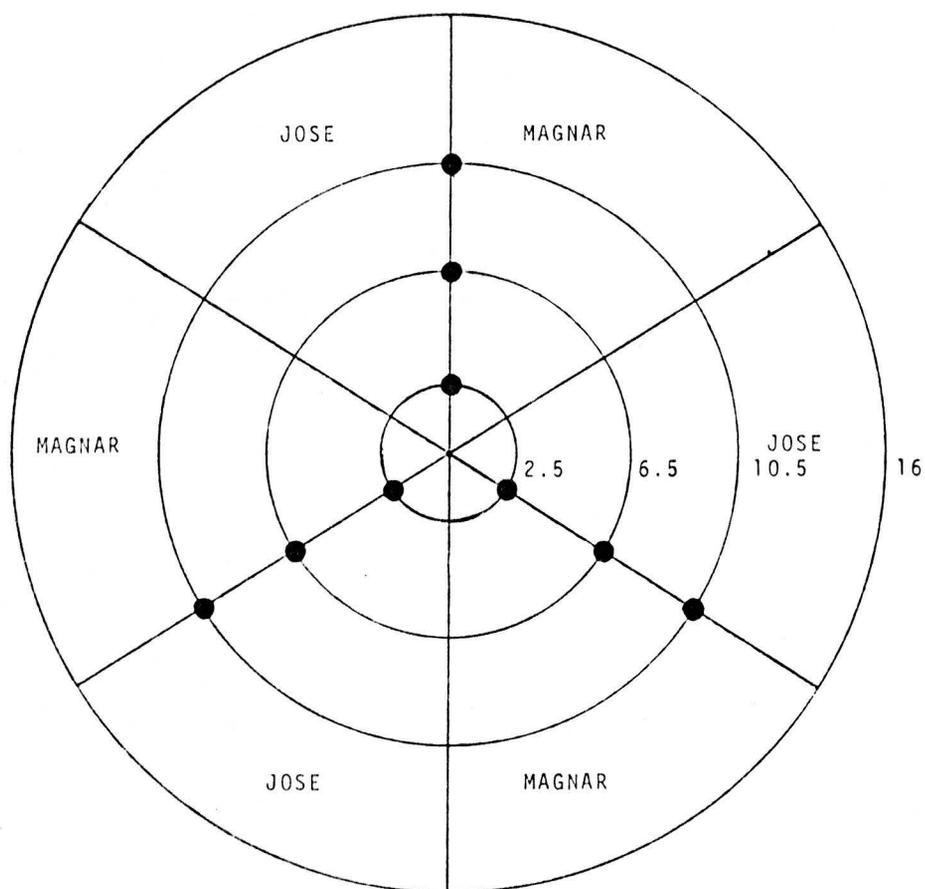


Figure 29. Diagram of circular plots seeded on nonsaline and saline soil to Jose tall wheatgrass and Magnar basin wildrye in the fall of 1981. Black dots indicate location of irrigation measurement cans and numbers indicate distance in m from plot center at which soil and seedlings were sampled.

Table 18. Slopes (b), intercepts (a), and correlation coefficients (r) for regressions of Figure 18 for Jose tall wheatgrass and Magnar basin wildrye seedling shoot and root weights on soil osmotic potential of the form: weight (g) = a + b x ln (soil osmotic potential [-bars])*.

| <u>Treatment</u> | Shoots | | | Roots | | |
|--|----------|----------|-----------------------|----------|----------|-----------------------|
| | <u>b</u> | <u>a</u> | <u>r</u> ⁺ | <u>b</u> | <u>a</u> | <u>r</u> ⁺ |
| <u>Jose</u> | | | | | | |
| CaCl ₂ | 0.23a | 0.85c | 0.88 | 0.13a | 0.42a | 0.78 |
| NaCl | 0.23a | 0.92b | 0.90 | 0.12a | 0.43a | 0.79 |
| Na ₂ SO ₄ | 0.19b | 0.93a | 0.84 | 0.12a | 0.43a | 0.75 |
| CaCl ₂ + NaCl | 0.24a | 0.91b | 0.90 | 0.12a | 0.41a | 0.76 |
| Na ₂ SO ₄ + NaCl | 0.22ab | 0.93a | 0.89 | 0.13a | 0.43a | 0.77 |
| <u>Magnar</u> | | | | | | |
| CaCl ₂ | 0.19a | 0.61b | 0.87 | 0.09a | 0.28b | 0.72 |
| NaCl | 0.19a | 0.64ab | 0.90 | 0.08a | 0.29ab | 0.70 |
| Na ₂ SO ₄ | 0.19a | 0.67a | 0.87 | 0.08a | 0.29ab | 0.61 |
| CaCl ₂ + NaCl | 0.20a | 0.66ab | 0.90 | 0.08a | 0.29ab | 0.69 |
| Na ₂ SO ₄ + NaCl | 0.19a | 0.66ab | 0.91 | 0.08a | 0.30a | 0.64 |
| <u>Salts Combined</u> | | | | | | |
| Jose | 0.87a | 0.21a | 0.80 | 0.12a | 0.43a | 0.77 |
| Magnar | 0.54b | 0.16b | 0.81 | 0.08b | 0.29b | 0.82 |

* Values followed by the same letter within a column and among salts for each species or between species with salts combined are not significantly different at the 0.05 probability level according to slope and interception comparison tests of Snedecor and Cochran (1971).

VITA

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