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# EFFECTS OF SOIL SALT LEVELS ON THE GROWTH AND WATER USE EFFICIENCY OF *ATRIPLEX CANESCENS* (CHENOPODIACEAE) VARIETIES IN DRYING SOIL[1]

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The effect of salt stress on the growth and water use efficiency of the xerohalophyte *Atriplex canescens* (Pursh.) Nutt. in drying soil was determined by growing plants to the wilting point in soils receiving a one-time irrigation of nutrient solution containing low, medium, and high levels of NaCl. The experiment compared three varieties of *A. canescens* that differed in salt tolerance and capacity for Na and K uptake in previous research. Contrary to expectations, we did not find that water and salt stress were strictly additive in reducing plant performance. Soil salts enhanced the growth performance of the plants in drying soil by increasing their days to wilting, ability to extract water from the soil, organic matter production, and water use efficiency. The variety with the highest salt tolerance also had the highest growth rates and water use efficiency on drying soils. We conclude that tolerances to water and salt stress are linked through a common mechanism of Na uptake for osmotic adjustment in this species.

**Key words:** *Atriplex*; Chenopodiaceae; halophytes; salt stress; water stress.

A plant in a drying, saline soil is exposed to increasing levels of both water stress and osmotic stress, because the matrix potential and the osmotic potential decrease simultaneously with decreasing soil moisture (Shalhevet, 1993). These conditions are common in halomorphic arid soils, in which salts concentrate near the surface as the soil dries between rains (McNaughton, 1991) and in cultivated arid soils, which can accumulate damaging levels of salts between irrigations (McCree, 1986; McCree and Richardson, 1987; Shalhevet, 1993). Despite their importance, relatively few studies have considered the combined effects of water and salt stress on plants (McCree, 1986; McNaughton, 1991; Richards, 1992; Shalhevet, 1993). Most studies of salt-stressed plants in drying soils have used crop plants (McCree and Richardson, 1987; Richards, 1992; Shalhevet, 1993); one study included several halophytes for comparison with crop plants (Richards, 1992), while another measured the short-term, transpiration response of the halophyte *Salsola kali* L. to drying, saline and nonsaline soils (Eshel and Waisel, 1984).

The soil matrix and osmotic potentials are additive in lowering the free energy of water in the soil (Shalhevet, 1993), and a primary physiological response of plants to both conditions is to lower the cell water potential through the accumulation of organic and inorganic solutes so that the roots can continue to extract water from the soil solution (Pitman, 1981, 1988; Flowers and Yeo, 1986). Hence, it is logical to think the two stress factors could be additive in affecting plant performance (Shalhevet, 1993). However, studies in which plants are grown in drying soils at different salinities show a more complicated response, in which soil salts actually mitigate some of the negative effects of water stress. For example, plants in drying soils usually survive longer in saline than in nonsaline soils, because salt-stressed plants grow less and therefore deplete soil moisture more slowly than non-salt-stressed plants (McCree, 1986; McCree and Richardson, 1987; Richards, 1992; Shalhevet, 1993). Furthermore, salt stress can increase leaf instantaneous water use efficiency by reducing stomatal conductance to a greater extent than photosynthesis (Guy, Reid, and Krause, 1980; Guy and Reid, 1986; Ayala and O'Leary, 1995), thereby allowing plants under salt stress to produce more dry matter than plants in nonsaline soil on the same quantity of water (Richards, 1992). Finally, salt stress can precondition plants to low soil water potential by allowing them to osmotically adjust, enhancing their ability to survive as the soil dries (Shalhevet, 1993). These generalizations appear to hold true for both $C_3$ and $C_4$ crop plants (McCree and Richardson, 1987) and halophytes (Eshel and Waisel, 1984; Richards, 1992). They have practical implications with regard to irrigation strategies for crop plants in salt-affected soils (McCree and Richardson, 1987; Richards, 1992; Shalhevet, 1993), and they may also be relevant to the growth strategies of adapted native plants in saline, desert soils (McNaughton, 1991).

We studied the effects of salt stress on the $C_4$ xerohalophytic shrub *Atriplex canescens* (Pursh.) Nutt. in drying soil. *A. canescens* is the most widespread saltbush in North America, found in saline and xeric soils from Mexico to Canada (Benson and Darrow, 1981). The species contains at least six varieties stabilized by different ploidy levels (Sanderson and Stutz, 1994). Varietal differences have been demonstrated with respect to both salt tolerance (Glenn et al., 1992, 1994, 1996) and photosynthetic water use efficiency (Senock et al., 1991), but to our knowledge the possibility of an interrelationship between these two adaptations has not been explored. We used varietal differences to probe the relationship between salt tolerance and tolerance to water stress in this species.

Previous research showed a strong, positive correlation between capacity for Na uptake and degree of salt tolerance among the different genotypes, and a negative relationship between K uptake capacity and salt tolerance

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(Glenn et al., 1996). We compared the three varieties ranked as most tolerant, intermediately tolerant, and least tolerant to salt in the previous work (Glenn et al., 1996). *Atriplex canescens* is stimulated by a moderate level of salt and inhibited by higher levels (Glenn et al., 1992); we grew the plants to the wilting point under suboptimal, optimal, and supraoptimal salinities in drying soils. Our objective was to determine whether salt tolerance and drought tolerance are linked in these plants through a common mechanism of salt uptake for osmotic adjustment (Flowers and Yeo, 1986), or, conversely, whether specialization for salt tolerance reduced a plant's ability to withstand water stress (Glenn et al., 1994, 1996).

## MATERIALS AND METHODS

***General***—We modified the experimental design of Richards (1992) to compare *A. canescens* varieties *linearis* (S. Wats.) Munz, *grandidentatum* Stutz & Sanderson and *occidentalis* (Torr. & Frem.) Welsh & Stutz (nomenclature follows Sanderson and Stutz, 1994) in drying, saline soils. They ranked *linearis* > *grandidentatum* > *occidentalis* in salt tolerance and capacity for Na uptake in previous studies (Glenn et al., 1994, 1996). The experimental method involved growing seedlings in closed pots containing moistened soil. The plants were allowed to grow up to their wilting point, at which point they were harvested for determination of dry matter production, water use efficiency, and transport of Na and K over the experiment. The ratio of soil to starting plant mass was large so that plants grew 40–100 d before wilting, allowing time for plants to adjust as the soil dried (McNaughton, 1991).

***Plant materials***—Seeds of var. *linearis* and *grandidentatum* were collected in 1990 from intertidal and foredune habitats, respectively, in a coastal desert location at Puerto Penasco, Sonora, Mexico (Glenn et al., 1992, 1994, 1996). Seeds of var. *occidentalis* were collected in 1995 from an inland, disturbed dune habitat in the Navajoan desert near Tuba City, Arizona. Var. *occidentalis* occurred with var. *angustifolia* at this location but was distinguished by its smaller fruit and wider leaves (length:width ratio <6 for var. *occidentalis* vs. >10 for var. *angustifolia*)(Sanderson and Stutz, 1994). Seeds and living specimens are maintained at Environmental Research Laboratory.

***Experimental design and procedures***—Seeds of each variety were sown in germinating trays and allowed to grow to 2 cm height prior to transfer to experimental treatments. Seedlings selected for uniform height were transplanted to prepared, 2.65-L capacity pots with bottom drain holes to allow for the initial draining of excess solution from pots before they were sealed. One seedling was planted per pot for a total of 27 pots with seedlings in three salinity treatments with three replications per treatment. Ten additional seedlings from each variety were harvested to determine initial plant mass and organic matter content, used in the calculation of relative growth rates (RGR).

Each pot contained 1700 g of a dry mixture of washed river sand and peat-based potting mix (85:15, mass/mass). The soil was chosen to represent the sandy soils in which the plants grow naturally, while the potting mix was added to increase the water-holding capacity of the soil and thereby the growth period before water was depleted. Each pot was soaked in 3 L of treatment solution to saturate the soil and then allowed to stand for several minutes until no more solution drained out, at which point the initial water content of each pot was determined by the difference between the volume added and the volume collected as drainage (mean initial water content = 0.899 L/pot, SE = 0.002 L).

A 2-cm layer of white perlite was placed on the soil surface of each pot as a vapor barrier, and each pot was wrapped tightly with a plastic film to prevent further water loss through drainage. The plastic was brought tightly over the top of the pot and the seedling was planted in the center of the pot through a hole punctured in the plastic. Additional perlite was added around the puncture to slow water loss through evaporation; the seedling emerged 1 cm above the vapor barrier. Richards (1992) assumed that the vapor barrier prevented bare-soil evaporation. However, we prepared three blank pots, one at each salinity, exactly the same as experimental pots but without seedlings, to correct for water loss from pots in the absence of plants. Differences in water loss among the three blank pots were small (see Fig. 2) and their mean value was used as the estimate of bare-soil evaporation among treatment levels of NaCl. The starting mass of all pots was recorded.

All pots were placed in a random design on a bench in a high insolation greenhouse at Tucson, Arizona (Glenn et al., 1996). The pots were placed in a single block with adjacent pots touching to minimize radiant heating of the sides of the pots, and the position of the pots was rotated weekly within the block during the experiment. Day temperatures ranged from 25° to 35°C; light transmission was 65% of ambient and midday values ranged from 400 to 1300 $\mu mol \cdot m^{-2} \cdot s^{-1}$; relative humidity was 60–70% (the greenhouse was evaporatively cooled) (Khan and Glenn, 1996). The experiment was conducted from February to May 1996.

***Harvest of plants***—Richards (1992) allowed plants to remain in pots until they were completely dead, but in our experience *Atriplex* plants can retain some living tissue even after the plant can no longer extract water from the soil, hence we used the permanent wilting point as the criterion for ending the experiment. Plants were allowed to grow until 80% or more of the fully expanded leaves were wilted for at least 2 d without morning recovery of turgor (see Slayter, 1957), at which point the plant was harvested. At harvest, pots had depleted the initial soil moisture to a mean value of 0.115 L. The residual moisture in each pot at harvest was determined gravimetrically by oven drying soils at 100°C to constant mass.

***Treatment solutions***—Treatment solutions were made up in distilled water containing half-strength, Na-free, Hoagland's nutrient solution (2 $mol/m^3$ K) plus NaCl to produce salinity levels of 0, 85, and 520 $mol/m^3$). The three treatments were chosen to represent suboptimal, optimal, and supraoptimal NaCl levels with respect to growth (Glenn et al., 1992; Ayala and O'Leary, 1995). While there was no Na in the 0 $mol/m^3$ treatment solution, we found there was a small amount of Na present in the dry soil mixture, which contributed Na to the soil solution. A composite sample of soil solution was extracted from all pots in the 0 $mol/m^3$ treatment to estimate the initial Na level (0.74 $mol/m^3$). Na:K ratios in soil solutions of the 0, 85, and 520 $mol/m^3$ treatments were 0.37, 43, and 258, respectively.

***Measurement of growth, cation content, and water use efficiency***—Water loss through evapotranspiration was estimated during the experiment by measuring the weekly mass loss of each pot (the weekly increment of plant mass increase was small in comparison to water loss and was not taken into account in the estimate). Plant growth was estimated by measuring plant height once a week. After harvest, evapotranspiration over the growth period was measured with more accuracy by subtracting the final mass of the pot (minus the plant fresh mass at harvest) from the initial mass. Transpiration was estimated by subtracting the water loss from the blank pots up to the day of harvest from the water loss from planted pots. Plants were separated into shoots (stems + leaves) and roots and measured for oven-dry mass (60°C). The mineral content of plant shoots was determined by combusting samples at 500°C. Na and K contents of shoots and soil extracts were determined by flame emission spectrophotometry at a commercial laboratory (Laboratory Consultants, Inc., Tempe, Arizona).

Water use efficiency was calculated by dividing the mineral-free dry mass of shoots (= shoot organic matter production) by the amount of water transpired over the experiment (Hsiao, 1993). Relative growth rate was calculated from the initial and final mineral-free shoot masses of plants, using the formula: RGR = (ln final mass − ln initial mass)/days of growth. The concentration of Na, K, or Na + K in the transpi-

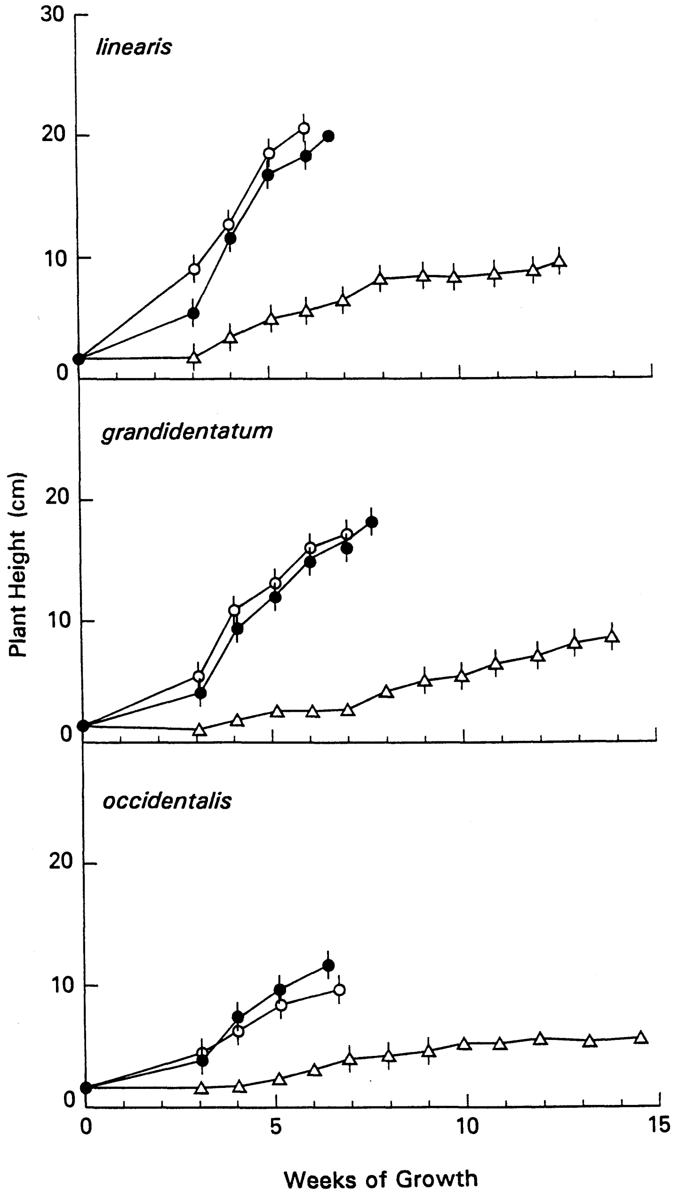

Fig. 1. Increase in plant height of *A. canescens* varieties grown to the wilt point in soils moistened with nutrient solution containing 0 (open circles), 85 (closed circles), or 520 (open triangles) $mol/m^3$ NaCl. Bars show ±1 SE.

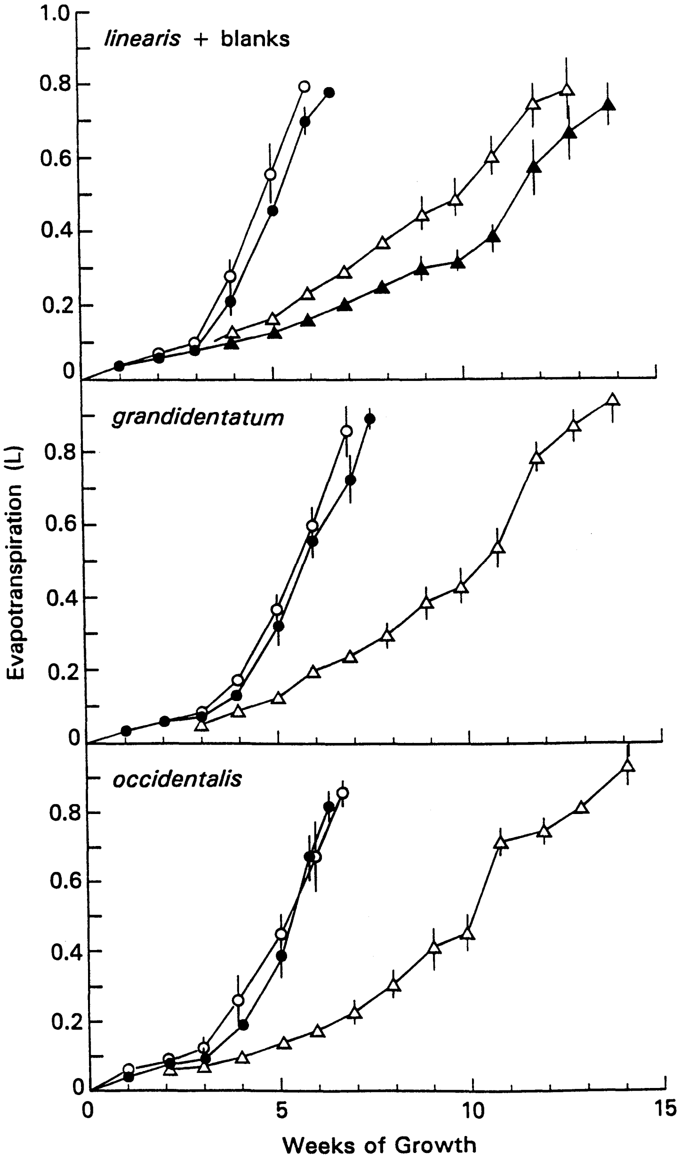

Fig. 2. Cumulative evapotranspiration from pots containing seedlings of *A. canescens* varieties grown to the wilt point in soils moistened with nutrient solution containing 0 (open circles), 85 (closed circles), or 520 (open triangles) $mol/m^3$ NaCl. The top graph also shows evaporation from blank pots without plants (closed triangles). Bars show ±1 SE.

ration stream was estimated by multiplying the concentration of each cation in the shoot tissue by the dry mass of shoot tissue divided by the volume of water transpired over the experiment (Glenn et al., 1994). The osmolarity of the shoot sap attributed to Na and K was calculated from the tissue cation levels and water content using the formula Osm ($mol/m^3$) = $[(Na+K)x2/H_2O]$, which assumes a balancing anion such as Cl and does not make a correction for activity coefficients (Glenn et al., 1994). Greater than 90% of measured leaf sap osmotic pressure in these varieties can be accounted for by Na and K (Glenn et al., 1992).

***Statistical methods***—The experiment was analyzed as a randomized design using a two-way analysis of variance (ANOVA) with salt level (*S*) and plant variety (*V*) as independent, categorical variables. Significance levels in tables are reported as not significant (ns), $P < 0.05$ (*), $P < 0.01$ (**), or $P < 0.001$ (***). If the ANOVA was significant at $P < 0.05$, individual means were separated using Duncan's multiple mean test at $P < 0.05$. The ANOVA also provided a comparison of pooled means across salt levels and varieties when the main effects were significant ($P < 0.05$). Experimental design and statistical analyses were based on discussions in Kuehl (1994) using computer software (CoStat) to carry out the calculations.

## RESULTS

***Overall growth and water use***—All three varieties showed similar trends with respect to growth (Fig. 1) and water use (Fig. 2). After a lag of 3 wk, plants at 0 and 85 $mol/m^3$ NaCl grew and consumed water rapidly up to their wilting points, whereas plants at 520 $mol/m^3$ NaCl grew and consumed water much more slowly and over a longer

TABLE 1. Mean and standard errors of days to wilt, shoot ash-free dry mass (AFDM), shoot ash content, shoot water content, and shoot relative growth rate of *A. canescens* varieties *linearis, grandidentatum,* and *occidentalis* grown in drying, saline soils. Ash and water content are expressed as grams per grams of dry matter. The ANOVA results indicate the significance level of treatment effects. Within a salt level, means followed by the same letter are not significantly different at $P < 0.05$. Significant differences between salt levels across varieties ($P < 0.05$) are indicated by different underlined letters in the table row denoting salt level.

| Salt level and variety | | Wilt (d) | Shoot AFDM (g) | Ash (g/g) | Water (g/g) | RGR ($g \cdot g^{-1} \cdot d^{-1}$) |
|---|---|---|---|---|---|---|
| 0 mol/m$^3$ | | a | a | a | a | a |
| *lin.* | Mean | 43 a | 1.58 a | 0.196 a | 2.06 a | 0.126 a |
| | SE | 0 | 0.10 | 0.007 | 0.27 | 0.002 |
| *grand.* | Mean | 49 b | 1.47 a | 0.185 a | 2.64 b | 0.110 b |
| | SE | 0 | 0.13 | 0.007 | 0.07 | 0.002 |
| *occid.* | Mean | 47 b | 0.95 b | 0.235 a | 2.14 a | 0.092 c |
| | SE | 2 | 0.18 | 0.010 | 0.07 | 0.004 |
| 85 mol/m$^3$ | | a | b | b | b | a |
| *lin.* | Mean | 46 a | 1.78 a | 0.298 a | 2.61 a | 0.120 a |
| | SE | 1 | 0.07 | 0.018 | 0.13 | 0.001 |
| *grand.* | Mean | 53 b | 1.66 ab | 0.261 a | 3.26 b | 0.106 b |
| | SE | 4 | 0.12 | 0.035 | 0.33 | 0.008 |
| *occid.* | Mean | 44 a | 1.55 b | 0.265 a | 2.40 a | 0.109 b |
| | SE | 2 | 0.08 | 0.10 | 0.10 | 0.004 |
| 520 mol/m$^3$ | | b | c | c | c | b |
| *lin.* | Mean | 92 a | 0.36 a | 0.356 a | 0.41 a | 0.042 a |
| | SE | 3 | 0.09 | 0.017 | 0.18 | 0.004 |
| *grand.* | Mean | 98 b | 0.39 a | 0.310 a | 1.22 b | 0.042 a |
| | SE | 4 | 0.12 | 0.021 | 0.13 | 0.002 |
| *occid.* | Mean | 100 b | 0.52 a | 0.320 a | 0.45 a | 0.037 a |
| | SE | 2 | 0.06 | 0.002 | 0.10 | 0.002 |
| ANOVA results | | | | | | |
| Salt level (S) | | *** | *** | *** | *** | *** |
| Variety (V) | | * | * | ns | *** | *** |
| S × V | | ns | * | ns | ns | * |

time period. Despite the vapor barrier, the loss of water from blank pots was substantial, especially towards the end of the experiment as the greenhouse warmed in spring.

***Comparative growth performance***—Significant differences were found for salt levels and varieties with respect to days to wilt, shoot organic matter production, shoot RGR, and shoot water content but only salt level affected shoot ash content; the interaction of salt level and variety was significant for shoot organic matter production and RGR (Table 1). Plants at 0 and 85 mol/m$^3$ NaCl wilted within 43–58 d, whereas plants at 520 mol/m$^3$ NaCl survived nearly 100 d. Var. *linearis* wilted 7 d sooner than var. *grandidentaum* across salinity treatments (60 vs. 67 d), while var. *occidentalis* was intermediate (64 d). Organic matter production was highest at 85 mol/m$^3$ NaCl and was very low at 520 mol/m$^3$ NaCl for all varieties. Var. *occidentalis* was less productive ($P < 0.05$) than the other varieties at all salt levels (see also plant heights, Fig. 2). The ash contents of all varieties were high (18.5–36.5% of dry mass) and increased with salt level. Shoot water contents were highest at 85 mol/m$^3$ NaCl and were very low at 520 mol/m$^3$ NaCl, following the same trend as the growth curve. Var. *grandidentatum* had 50% higher water content ($P < 0.05$) than the other varieties at all salt levels. Var. *linearis* had 10–20% higher RGRs ($P < 0.05$) than the other varieties in the first two salt treatments, whereas all had low RGRs in the highest salt level.

Root tissues were difficult to recover completely and tended to be contaminated with adhering soil particles so mineral contents were not determined. Fine roots penetrated throughout the soil of all pots, but it was mainly the larger, fibrous roots that were recovered. Root dry masses were significantly reduced at 520 mol/m$^3$ NaCl ($P < 0.001$) but did not differ by variety; roots accounted for 15.6% (SE = 0.6%) of total plant masses.

***Comparative water use and cation uptake***—Significant differences were found for salt levels and varieties with respect to residual water left in the pots, shoot Na content, and shoot Na:K ratios. Significant differences were found for varieties but not salt levels for evapotranspiration while only salt level was significant for transpiration. Shoot K did not differ significantly by salt level or variety (Table 2). Evapotranspiration was similar at all salt levels but var. *linearis* used 10–15% less water ($P < 0.05$) than the other varieties. Since it wilted sooner than the other varieties, it had fewer days for water to evaporate from pots. By contrast, transpiration (evapotranspiration minus the blank pot evaporation rate) did not differ significantly among varieties or at 0 and 85 mol/m$^3$ NaCl ($P > 0.05$), but it was only 17% as high on 520 mol/m$^3$ NaCl as on the lower salt levels. The transpiration estimates on 520 mol/m$^3$ NaCl had large measurement errors because they were only 10–15% higher than the blank pot evaporation rates (Fig. 2).

Residual water content in pots differed significantly by salt level ($P < 0.05$) and variety ($P < 0.01$), but the interaction term was the most significant factor ($P < 0.001$). Plants left more residual water in the pots at 0 mol/m$^3$ NaCl (mean = 0.147 L) than at 85 or 520 mol/m$^3$ NaCl (means = 0.111 L and 0.087 L, $P < 0.05$), but the trend was especially pronounced for var. *linearis,* which left 22% of the water unused at 0 mol/m$^3$ NaCl but only 7% on the two higher salt levels. Variety *occidentalis* used significantly more of the soil water than var. *grandidentatum* at all salt levels ($P < 0.05$).

Na in the shoots increased sharply across salt levels and var. *linearis* had 25% higher levels across salinities ($P < 0.05$), whereas K did not differ significantly ($P < 0.05$) among salt levels or varieties. Assuming Cl as the balancing anion, Na, K, and Cl could account for 83.7% (SE = 2.8%) of the mean ash content in the shoots.

Water use efficiency and calculated concentrations of Na and K in the transpiration stream are in Table 3. These calculations required an accurate estimate of transpiration, which was not available for the highest salt level. Hence, the 520 mol/m$^3$ treatment was omitted. Significant differences were found for salt level and varieties with respect to Na and Na + K in the transpiration stream for water use efficiency, while K concentration in the transpiration stream was not significantly affected by either salt level or variety. Water use efficiency was 20% higher at 85 mol/m$^3$ NaCl than at 0 mol/m$^3$ NaCl ($P < 0.05$) in all varieties and var. *linearis* was 20% higher than the other varieties at both salt levels ($P < 0.05$). Concentrations of Na in the transpiration stream were 50–70% higher ($P < 0.05$) in var. *linearis* than the other varieties and the concentrations increased more than fivefold going from 0 to 85 mol/m$^3$ NaCl in all vari-

TABLE 2. Mean and standard errors of evapotranspiration (ET), transpiration (T), residual water content in pots at wilt, shoot levels of Na and K, and shoot Na:K ratios of *A. canescens* varieties *linearis, grandidentatum,* and *occidentalis* grown in drying, saline soils. Na and K are expressed per gram of dry matter. The ANOVA results indicate the significance level of treatment effects. Within a salt level, means followed by the same letter are not significantly different at $P < 0.05$. Significant differences between salt levels across varieties ($P < 0.05$) are indicated by different underlined letters in the table row denoting salt level.

| Salt level and variety | | ET (L) | T (L) | Residual (L) | Na (mol/kg) | K (mol/kg) | Na:K |
|---|---|---|---|---|---|---|---|
| 0 mol/m$^3$ | | | a | a | a | | a |
| *lin.* | Mean | 0.794 a | 0.571 a | 0.233 a | 0.71 a | 1.32 | 0.54 a |
| | SE | 0.013 | 0.010 | 0.041 | 0.06 | 0.04 | 0.04 |
| *grand.* | Mean | 0.850 a | 0.603 a | 0.168 b | 0.41 a | 1.39 | 0.30 a |
| | SE | 0.077 | 0.075 | 0.011 | 0.02 | 0.14 | 0.02 |
| *occid.* | Mean | 0.868 a | 0.600 a | 0.040 c | 0.60 a | 1.85 | 0.32 a |
| | SE | 0.030 | 0.024 | 0.018 | 0.07 | 0.57 | 0.05 |
| 85 mol/m$^3$ | | | a | ab | b | | b |
| *lin.* | Mean | 0.789 a | 0.549 a | 0.061 a | 2.57 a | 1.26 | 2.08 a |
| | SE | 0.014 | 0.015 | 0.016 | 0.11 | 0.13 | 0.18 |
| *grand.* | Mean | 0.884 b | 0.605 a | 0.171 b | 2.31 ab | 1.40 | 1.87 a |
| | SE | 0.021 | 0.002 | 0.022 | 0.26 | 0.25 | 0.64 |
| *occid.* | Mean | 0.849 ab | 0.616 a | 0.101 c | 2.08 b | 1.42 | 1.50 a |
| | SE | 0.027 | 0.036 | 0.015 | 0.43 | 0.16 | 0.18 |
| 520 mol/m$^3$ | | | b | b | c | | c |
| *lin.* | Mean | 0.774 a | 0.054 a | 0.061 a | 4.32 a | 0.82 | 5.81 a |
| | SE | 0.099 | 0.049 | 0.023 | 0.38 | 0.02 | 1.19 |
| *grand.* | Mean | 0.937 b | 0.147 a | 0.122 b | 3.23 b | 1.29 | 3.16 b |
| | SE | 0.064 | 0.036 | 0.024 | 0.31 | 0.40 | 1.06 |
| *occid.* | Mean | 0.948 b | 0.108 a | 0.078 a | 3.24 b | 1.31 | 2.50 b |
| | SE | 0.047 | 0.067 | 0.007 | 0.16 | 0.08 | 0.26 |
| ANOVA results | | | | | | | |
| Salt level (S) | | ns | *** | * | *** | ns | *** |
| Variety (V) | | * | ns | ** | ** | ns | * |
| S × V | | ns | ns | *** | ns | ns | ns |

TABLE 3. Mean and standard errors of water use efficiency (WUE), concentration (C) of Na, K, and Na + K in the transpiration stream, and Na + K osmolality of the cell sap in shoots of *A. canescens* varieties *linearis, grandidentatum,* and *occidentalis* grown in drying, saline soils. Cation concentrations are expressed as mmol/L of water transpired over the experiment; osmolality is expressed as mOsmole based on Na + K in the shoot sap and assuming an equal contribution from a balancing anion. The ANOVA results indicate the significance level of treatment effects. Within a salt level, means followed by the same letter are not significantly different at $P < 0.05$. Significant differences between salt levels across varieties ($P < 0.05$) are indicated by different underlined letters in the table row denoting salt level. The 520 mol/m$^3$ treatment was omitted due to the large errors in estimating transpiration at that salinity.

| Salt level and variety | | WUE (g/L) | $C_{Na}$ (mol/m$^3$) | $C_K$ (mol/m$^3$) | $C_{Na+K}$ (mol/m$^3$) | Osmolality (Osmol/m$^3$) |
|---|---|---|---|---|---|---|
| 0 mol/m$^3$ | | a | a | | a | a |
| *lin.* | Mean | 2.76 a | 2.44 a | 4.51 a | 6.94 a | 2008 a |
| | SE | 0.22 | 0.28 | 0.22 | 0.48 | 181 |
| *grand.* | Mean | 2.43 a | 1.21 b | 4.16 a | 5.37 a | 1358 b |
| | SE | 0.08 | 0.09 | 0.50 | 0.59 | 87 |
| *occid.* | Mean | 1.62 b | 1.20 b | 4.28 a | 5.38 a | 2294 a |
| | SE | 0.38 | 0.12 | 0.89 | 0.90 | 206 |
| 85 mol/m$^3$ | | b | b | | b | b |
| *lin.* | Mean | 3.24 a | 11.94 a | 5.86 a | 17.80 a | 2962 a |
| | SE | 0.10 | 0.86 | 0.86 | 1.71 | 302 |
| *grand.* | Mean | 2.62 b | 8.43 b | 5.32 a | 13.75 ab | 2327 b |
| | SE | 0.17 | 0.69 | 1.20 | 1.00 | 240 |
| *occid.* | Mean | 2.53 b | 7.15 c | 4.53 a | 11.68 b | 2928 a |
| | SE | 0.20 | 0.55 | 0.49 | 1.04 | 226 |
| ANOVA results | | | | | | |
| Salt level (S) | | * | *** | ns | *** | *** |
| Variety (V) | | ** | *** | ns | * | ** |
| S × V | | ns | * | ns | * | ns |

eties. K did not vary significantly among salt levels or varieties, hence the sum of Na and K followed the same trend as Na.

Table 3 also contains an estimate of the osmolarity of the cell sap in the shoots, based on their Na, K, and water contents. These calculations are normally made from measurements taken from fully expanded, unwilted leaves (Glenn et al., 1992), whereas in this experiment they were made using data from whole shoots after the leaves had wilted. They provide a rough measure of the osmotic pressure in the shoots at the wilting point. Significant differences were found for salt levels but not varieties. Osmolarity increased from 1900 to 2740 Osm/m$^3$ in going from the 0 to 85 mol/m$^3$ NaCl, similar to previous data (Glenn et al., 1992). Var. *grandidentatum* maintained 25–30% lower osmolarity than the other varieties, which can be attributed to its higher shoot water content. Osmolarities calculated for the 520 mol/m$^3$ exceeded the saturation concentration of NaCl in water, and much of the salt was assumed to have been excreted onto the leaf surfaces through salt bladders.

## DISCUSSION

Xerohalophytes are often regarded as being adapted to a doubly harsh environment (Osmond, Bjorkman, and Anderson, 1980), but we found that soil salts enhanced the performance of seedlings in drying soil, contrary to the initial expectation that it would be an additive stress factor. Richards (1992) also reported a beneficial effect of salts on plants grown to the wilting point in drying soils. His experiments included crop plants such as wheat, barley, and sunflower as well as halophytes, and even the nonhalophytes generally reached a higher final mass on saline than nonsaline soil, although they grew more slowly. Wheat and barley were able to produce viable seed on the saline but not the nonsaline treatments. His results led him to question the usefulness of experiments that present salt as a single stress in determining the salt tolerance of different genotypes and the factors responsible for increasing salt tolerance, since those experiments invariably show only a negative effect of salt on plant growth (Richards, 1992). The present study, using different varieties of a wild plant, generally support Richards' conclusion regardless of variety.

One way soil salts can enhance plant performance is by lowering the leaf area and growth rate of plants, thereby decreasing the rate at which soil water is depleted and enhancing the longevity of the plants (McCree and Richardson, 1987; Richards, 1992; Shalhevet, 1993). Eshel and Waisel (1984) found that similar-sized *Salsola kali* plants took twice as long to reach the wilting point on saline compared to nonsaline medium. *A. canescens* seedlings grew much more slowly at 520 mol/m$^3$ NaCl than at lower salinities but lasted nearly 100 d before wilting. This increased longevity could aid the survival of *A. canescens* seedings establishing in saline soil between widely scattered rains. That the soil gets saltier as it dries would be beneficial to survival.

Var. *linearis,* which had the highest growth rate, also reached the wilting point sooner than the other varieties, although the differences tended to be small. In the terminology of Levitt (1980), var. *linearis* is a "water spender," whereas the slower growing var. *occidentalis* is a "water saver," while var. *grandidentatum* is intermediate. These water use strategies can be matched to the varieties' natural habitats; var. *linearis* seeds were collected from the permanently moist, but highly saline intertidal zone of a coastal desert estuary, whereas var. *occidentalis* and *grandidentatum* seeds were collected from presumably drier, inland and coastal dune habitats, respectively (Sanderson and Stutz, 1994). Even though var. *linearis* reached the wilting point soonest, however, it did not actually "spend" more water than the other varieties and it had the highest water use efficiency across the first and second salt levels.

A second way salts enhanced plant performance was by allowing them to reduce the soil moisture content to a lower level before wilting than was possible under nonsaline conditions. Variety *linearis* wilted while there was still a remarkably high level of soil water available on the nonsaline treatment. Pots on that treatment contained an estimated 0.8 mmol of Na in the original soil solution (0.74 mol/m$^3$ Na in the soil solution × 1.03 L of solution per pot), whereas the plants contained an estimated 1.1 mmol in shoots at harvest (1.58 g per plant × 0.71 mmol per g); it appears that the plants may have used all the available Na in the pot and that wilting was due to lack of Na rather than lack of water. This effect could also be of ecological significance, because heavy rains on sandy soils can wash the salts to deeper layers, exposing seedlings to nonsaline conditions during early establishment.

A third way salts way can enhance plant performance in drying soil is by increasing their water use efficiency. Both halophytes (Guy, Reid, and Krause, 1980; Guy and Reid, 1986; Ayala and O'Leary, 1995) and nonhalophytes (Brugnoli and Lauteri, 1991) can have higher photosynthetic water efficiency when grown in the presence of salt, which can lead to higher biomass production under water-limiting growth conditions (Richards, 1992). *A. canescens* seedlings had 20% greater water use·efficiency and greater organic matter production on the optimal compared to the suboptimal salt level. Richards (1992) found that water use efficiency increased with salinity up to 150 mol/m$^3$ NaCl, then it decreased. However, he did not use blank pots to correct for soil evaporation, which our experiment showed is substantial even with a vapor barrier over the soil surface. On high salt levels, transpiration is low compared to soil evaporation and the water use efficiency calculated from evapotranspiration will be misleadingly low. Our transpiration estimates were not accurate for the highest salinity treatment, but Ayala and O'Leary (1995) found that instantaneous and long-term water use efficiency of *Salicornia bigelovii* Torr., measured by gas exchange and $^{13}$C ratios, respectively, both increased with salinity up to 600 mol/m$^3$, the highest level they tested.

The enhanced water use efficiency of nonhalophytes under salt stress is generally regarded as a Na-avoidance mechanism (Greenway and Munns, 1980; Brugnoli and Bjorkman, 1992). Na enters plants in proportion to the transpiration rate (Pitman, 1981, 1988), so by lowering stomatal conductance plants can reduce the rate of Na entry into leaves. Photosynthesis and growth are also lowered at lower stomatal conductance but not in direct proportion, so water efficiency increases, though net primary production decreases (Brugnoli and Lauteri, 1991; Brugnoli and Bjorkman, 1992). This may be a plausible explanation for nonhalophytes, but our results suggest a different explanation for halophytes.

The RGRs of *A. canescens* seedlings were nearly the same at 0 and 85 mol/m$^3$ NaCl so the enhanced water use efficiency was not associated with a decrease in growth. In this experiment, higher water use efficiencies were associated with treatments with increased rates of Na uptake. This was true whether comparisons were made between salt levels (water use efficiency was higher on 85 than 0 mol/m$^3$ NaCl) or among varieties (water use efficiency was highest for var. *linearis,* which had the highest level of Na in the transpiration stream). The osmolarity in the shoot sap was high even on the nonsaline treatment and required high uptake rates of cations to support growth, a distinguishing feature of dicotyledonous euhalophytes (Osmond, Bjorkman, and Anderson, 1980; Glenn and O'Leary, 1984; Yeo and Flowers, 1986; Glenn et al., 1992, 1994, 1996). On the nonsaline solution, presumably, water use efficiency was not limited by photosynthetic carbon demands but by the transport requirements for Na for growth. Similar to plants under drought conditions (Flowers and Yeo, 1986), osmotic potential in the shoot sap was increased not only by the seedlings taking up ions but also by a reduction in shoot water content, which was highest at 85 mol/m$^3$ NaCl. The very high degree of apparent osmotic adjustment of seedlings at 520 mol/m$^3$ may have delayed their wilting even after growth and water extraction from the soil had ceased (Slayter, 1957).

Since Na and K uptake can be competitive processes in higher plants (Epstein, Rains, and Elzam, 1963; Pitman, 1981, 1988), and since K is generally the cation most associated with osmotic adjustment to water stress (Flowers and Yeo, 1986), we originally hypothesized that the *A. canescens* genotypes most specialized for Na uptake and salt tolerance might be at a disadvantage under water stress. However, var. *linearis* not only had the highest salt tolerance in previous experiments (Glenn et al., 1994, 1996), but it had the highest RGR, organic matter production, and water use efficiency on drying soils in the present experiment. Although the Na:K ratios increased with salinity for all varieties, this was mainly due to increased Na uptake rather than decreased K. Potassium levels in the shoots and transpiration stream were remarkably constant across salt treatments and varieties, and did not seem to be affected by Na levels in the plant tissues or the external solution. We conclude that Na is the cation most responsible for osmotic adjustment to both water and salt stress of xerohalophytes on saline soils.

Dicotyledonous halophytes typically have maximum growth at salt levels ranging from 50 to 150 mol/m$^3$ NaCl, and the reason for the growth depression at suboptimal salinity has not been resolved (Ayala and O'Leary, 1995). Flowers and Yeo (1986) hypothesized that the rate of transport of Na from the roots to shoots could be the limiting factor for the growth of *Suaeda maritima* at suboptimal salinity. They found concentrations of Na in the transpiration stream no higher than 46 mmol/L, which they regarded as too low to support maximum growth, given the high Na content of the leaf tissues. Our estimates of Na + K in the transpiration stream were even lower: <20 mmol/L on the optimal salt level and <10 mmol/L on the suboptimal level. Therefore, our results support the conclusion that Na and K uptake are growth limiting for *A. canescens* seedlings under suboptimal external salt levels. In a drying soil, the absence of salts would exacerbate rather than alleviate the stress load on this species.

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