Mechanisms of Salt Tolerance in Plants Relevant to Closed System Agriculture in Desert Environments

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ABSTRACT

Closed system agriculture (CSA) in arid regions provides a method for minimizing the disadvantages of arid environments such as limited supplies of fresh water, while making maximal use of the main advantages, including abundant solar radiation and long growing seasons. The greatest advantage can be obtained from CSA if it is combined with the use of the often abundant saline ground water of many arid zones. The effective use of saline water in CSA requires development of plant varieties that can be productive under saline conditions and take full advantage of the CSA environment. This study is aimed at defining physiological characteristics which might provide easily selected or engineered traits that would lead to enhanced production of C_4 plant species under CSA conditions utilizing saline water. Our findings indicate that increased carboxylation efficiency with increased salinity is a key physiological trait conferring enhanced productivity to certain species of Sporobolus under saline CSA conditions. This trait can be identified by lowered CO_2 concentrations in the intercellular spaces in response to salinity.

Keywords: Salinity, closed system agriculture, Sporobolus, salt tolerance, photosynthesis

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Many arid areas, as a result of internally drained, closed or semi-closed basins, low rainfall and high potential evaporation, have developed saline soils and/or saline water as their main water resource (Isar 1975). Salinization of agricultural lands and irrigation waters in arid zones further decreases our ability to use these arid zones for crop production. This is particularly unfortunate because arid zones offer distinct environmental advantages for agricultural development. There is an abundance of solar radiation and favorable temperatures that make growing seasons relatively long.

Closed system agriculture (CSA) in arid regions provides a method for minimizing the disadvantages of arid environments, including salinity, while making maximal use of the main advantages, including light. The general principles of CSA have been reviewed (de Bivort et al. 1978, Gale 1981a), and many possible engineering variants have been suggested (de Bivort et al. 1978, Gale 1981b, Luft and Froechtenight 1981). Although water use in CSA is low, it is not insignificant relative to the small quantities of good quality water available in arid regions. Thus, the use of saline water in CSA would be advantageous, particularly in areas like New Mexico where saline ground water is abundant.

The effective use of saline water in CSA requires advancements in two related scientific efforts. The selection of salt tolerant individual plants from which new salt tolerant variants can be developed requires a clear characterization of the basic, genetically controlled processes that confer salt tolerance. The interaction of other environmental factors in enhancing salinity tolerance and preventing other stresses must also be determined. Since environmental factors other than salinity are likely to influence various processes conferring salinity tolerance differently, the latter effort

is best undertaken with as complete of an understanding of the relevant processes as possible. For this reason a sequential approach to the two efforts seems most appropriate. Characterization of the processes conferring salinity tolerance should come first.

This characterization is most likely to identify useful characteristics and define relevant processes if the species compared: 1) are closely related phylogeneticly and thus posses similar genetic backgrounds, 2) represent a range of tolerances to saline environments, and 3) occupy otherwise similar habitats. If these criteria are met, the major differences among the species should relate to their relative abilities to tolerate salinity. Because of their high water-use-efficiency, high temperature optima for photosynthesis and growth, and ability to efficiently utilize high levels of solar radiation, plants with the C_4 photosynthetic pathway offer many advantages for arid lands agriculture in traditional irrigated, as well as closed system, agriculture.

The above considerations lead to the conclusion that the objective of characterizing basic, genetically controlled processes that confer salt tolerance that might be utilized in developing CSA in desert environments can best be met by a comparative study of C_4 species within the same genus which exhibit a range of salinity tolerance in their native habitats. Three species of C_4 eragrostoid grasses in the genus Sporobolus meet these criteria. Sporobolus airoides occurs in highly saline interior regions of the western United States. Sporobolus wrightii grows in habitats of moderate salinity and Sporobolus giganteus is found only in nonsaline habitats on well drained soils.

The research reported here evaluates several aspects of the morphological, phenological and physiological responses of these three species to various levels of salinity in an effort to define the characteristics that confer various levels of salt tolerance to each.

MATERIALS AND METHODS

Plant Material

Plants of all three species were grown concurrently from field collected seed in sand cultures on Hoagland's nutrient solution (Hoagland and Arnon 1950). The sand cultures were maintained in a temperature controlled greenhouse. Maximum and minimum air temperatures were kept at 35 $\pm$ 1 and 18 $\pm$ 1 ^{o}C. Once established, plants were adjusted to their treatment salinity at the rate of 4.2 dS m^{-1} d^{-1}, using dilutions of the final treatment salt mixtures (table 1). All salt mixtures were added to the Hoagland's nutrient solution and the pH of the composite irrigation solutions balanced at 7.2 $\pm$ 0.1. Initiation of the salinity adjustment periods was timed so that all plants received the first irrigation with their respective treatment level on the same day. Pots (PVC tubing) were watered to dripping with the appropriate solution twice daily. The final treatment levels were: control, 0.5; low salt, 14; medium salt, 28; and high salt, 42 dS m^{-1}.

Growth and Biomass Allocation

Growth and biomass allocation measurements were made on 6 replicate plants per treatment and species using a total plant destructive harvest of individuals chosen randomly from replicate blocks on the greenhouse bench. The first harvest was done on the day plants reached their treatment salinity level. The fifth and final harvest was 60 days later. Thus, a total of 360 individuals (3 species x 4 treatments x 6 replicates x 5 harvests) were measured. Plant height, root biomass, stem biomass, leaf biomass, leaf area, leaf length and leaf width were measured for each individual.

Table 1

The composition (mM of individual salts and meq l^{-1} of individual ions) of the salt treatment mixtures used in this experiment and their physical properties. Salts were added to Hoagland's solution.

	SALINITY TREATMENT		
SALT (mM)	LOW	MEDIUM	HIGH
NaCl	103.58	207.16	310.74
K_2SO_4	4.15	8.31	12.46
$MgSO_4$	19.83	39.67	59.50
Na_2SO_4	21.81	43.62	65.43
$CaCl_2$	5.45	10.91	16.36
Total	154.82	309.67	464.49
Electrical conductivity, dS m^{-1}	14.0	28.0	42.0
Water Potential, MPa	-0.59	-1.18	-2.01
ION (meq l^{-1})			
Na^+	114.49	228.97	343.46
K^+	2.08	4.15	6.23
Mg^{+2}	9.92	19.83	29.75
Ca^{+2}	2.73	5.45	8.18
Cl^-	106.31	212.61	318.92
SO_4^{-2}	22.90	45.80	68.70
Totals (cations or anions)	129.22	258.40	387.62

Carbon Dioxide and Water Vapor Exchange Rate

Simultaneous measurements of the rate of CO_2 and H_2O vapor exchange of the uppermost fully expanded leaf were made using a newly designed and constructed computer controlled open gas exchange measurement system. The system allows for precise and independent control of leaf temperature, irradiance, ambient CO_2 concentration and ambient H_2O vapor concentration. The results presented in this report were derived from measurements of gas exchange responses to varying photosynthetic photon fluxes (PPF) with all other relevant environmental variables held constant. Ambient CO_2 concentration around the leaves was held at 310 $\pm$ 0.3 μmol mol^{-1}(PPM). The mole fraction difference of water vapor between the leaf and measurement cuvette air was maintained at 20.0 $\pm$ 0.09 mmol mol^{-1}. Leaf temperature was maintained at 35°C (the previously determined optimum for all three species). All gas flow tubes in the measurement system were heated to above dew point temperatures to prevent water vapor condensation. The light source was a water cooled quartz-halogen lamp (GE Q1500/900wm Quartzline). PPF was varied by altering voltage to the lamp. Flow rates and CO_2 concentrations were controlled by two mass flow controllers (Tylan, FC-260), one for CO_2 free air and one for 2 % CO_2 in air. Flow rates were measured by a mass flow meter (Kruz 500-6, M855). Ambient cuvette CO_2 was monitored with an IRGA (Anarad). Differential CO_2 concentrations were measured to an accuracy of $\pm$0.2 mol μmol^{-1} (ADC IRGA, Model 225). Humidity was measured to an accuracy of $\pm$2 % by two sensors (Vaisala Hmp 111a), one for the ingoing and one for the outgoing air of the measurement cuvette. Gas exchange parameters were calculated using the equations developed by von Caemmerer and Farquhar (1981) programmed into a micro-computer that received data directly from a datalogger (Campbell Scientific). PPF was measured to an accuracy of $\pm$20 μmol photons m^{-2} s^{-1} by

a photodiode (NEC, PH 201A, Ser. NEPOC), measuring between 380 and 690 nm wavelength, located at leaf level within the measurement cuvette and calibrated against a standard quantum sensor (LI-COR, LI-190). Leaf temperature was monitored with a fine wire thermocouple appressed to the lower (abaxial) surface of the leaf.

Germination

Germination percentages of 100 seeds of each species were determined for each of the salt solutions (table 1). Twenty seeds were placed in petri dishes containing filter paper disks wetted with the appropriate solution. The seeds were maintained in a controlled environment chamber with 500 μmol m^{-2} s^{-1} PPF, a 16/8 h d/n photoperiod and 35/18 ^{o}C d/n thermoperiod of the same length. The number of germinated seeds was counted after 19 d. All seeds were rewet with the control solution and germinates counted again after 31 d of combined treatment (19 d with treatment solution, plus 12 d with control solution).

RESULTS AND DISCUSSION

Plant Growth

After 60 d of growth under the treatment conditions, individuals of both S. airoides and S. wrightii had obtained as much growth in overall plant height in both the low and medium salt treatments as they did in the Hoagland's solution control. Only under the high salt conditions was height growth adversely affected in these species (table 2). Although S. giganteus grew taller than the other species under the control conditions, as it does in its native habitat, even the low salinity treatment reduced its height growth to a level comparable to the other two species under the same conditions. The medium and high salinities caused comparable decrements in height growth in all species with very little or no difference between the low and medium

Table 2

Height (cm) above ground after 60 d of growth in the greenhouse at the treatment salinity level. Mean of 6 replicates ±1 standard deviation. Values in a column with the same superscript are not significantly different ($P \leq .05$).

Salinity	Species		
	S. airoides	*S. wrightii*	*S. giganteus*
Control	74± 7[a]	71± 10[a]	97± 6[a]
Low	64± 8[a]	60± 10[ab]	78± 7[b]
Medium	64± 6[a]	57± 7[ab]	67± 5[b]
High	48± 8[b]	43± 9[b]	46± 5[c]

treatments, but a marked reduction in height in the high salinity compared to the medium salinity. Growth in height can be taken as a measure of a plant's ability to intercept and effectively compete for the light energy resource in its environment. The reduction in height growth of S. giganteus even at the low salinity level may result in a reduction in its ability to capture light and, thus, reduce its overall production and competitive ability. A similar fate would befall the other species only at much higher levels of salinity.

Total dry mass accumulation over the 60 d growth period of the experiment shows a similar pattern to height growth with a few significant exceptions (table 3). All three species exhibited an apparent decline in mean total dry mass accumulated with increasing salinity. The gradual nature of this trend is apparent only in the means. In fact, the only statistically significant decrement for S. airoides was between the low and medium salinity treatments. For the other two species the statistically significant decrement occurred between the medium and high salinity treatments. On the basis of these data it would appear that S. wrightii and S. giganteus are more salt tolerant than S. airoides even though their natural distributions suggest otherwise, as do other results reported here.

The mean relative growth rates (mg g^{-1} d^{-1}) declined with time for all three species under each salinity treatment. In S. airoides the initial relative growth rates although lower for salinity treatments were more comparable to the control than in the other two species (figure 1.) The control, medium and high salt treatments resulted in comparable rates of decline in the relative growth rate of S. airoides over time. The low salt treatment resulted in a lower rate of decline and thus, these plants maintained higher growth rates at the end of the 60 d experimental growth period. S. wrightii showed an initial depression in relative growth rates, in

Table 3

Total dry mass (g) after 60 d of growth in the greenhouse at the treatment salinity level. Mean of 6 replicates ± 1 standard deviation. Values in a column with the same superscript are not significantly different ($P \leq 0.05$).

Salinity	Species		
	S. airoides	*S. wrightii*	*S. giganteus*
Control	3.35 ± 0.54^{a}	3.58 ± 0.47^{a}	5.49 ± 1.14^{a}
Low	3.29 ± 0.61^{a}	3.25 ± 0.59^{ab}	4.33 ± 1.00^{ab}
Medium	1.83 ± 0.37^{b}	2.43 ± 0.27^{b}	2.59 ± 0.78^{b}
High	1.30 ± 0.41^{b}	1.05 ± 0.26^{c}	1.20 ± 0.48^{c}

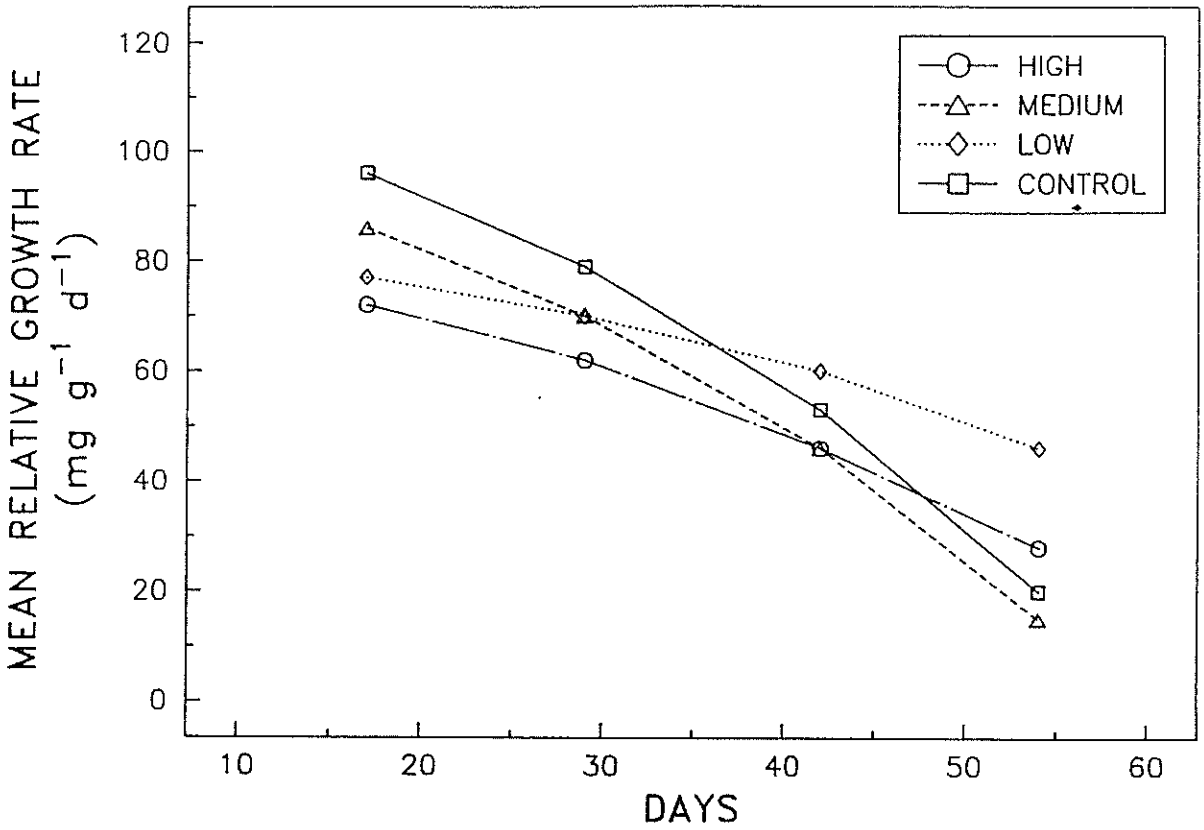

Figure 1. Growth Rate of S. airoides as a Function of Time at Each of the Treatment Salinity Levels

comparison to the control, for each of the salinity treatment levels. The rates of decline in relative growth rates were comparable for the control and the high salinity treatment. However, higher relative growth rates were maintained with time in both the low and medium salt treatment (figure 2). Initial relative growth rates were incrementally decreased by each successively higher level of salinity in S. giganteus. Higher levels of salinity resulted in lower rates of decline in relative growth rate with time such that all treatments exhibited comparable rates by the end of the 60 d experimental growth period (figure 3). The general pattern for all three species seems to be that salinity has its most detrimental effects on relative growth rate immediately after application or in the earlier stages of growth and may, in fact, delay the decline in growth rate with time. This may be a result of delayed senescence caused by salinity. Most of the detrimental effect of salinity on total biomass accumulation in S. giganteus seems to have resulted from reduced growth early, rather than late, in the experimental growth period. This early detrimental effect was less in S. wrightii and almost nonexistent in S. airoides. These differences may indicate a difference in the rate of acclimation to salinity that might account for the differences in salinity tolerance among the species.

The total biomass accumulation of a plant over time can be viewed as consisting of several components: 1) the rate of carbon gain per unit of leaf area, 2) the translation of that carbon gain into biomass per unit leaf area per unit time, 3) the allocation of biomass to new leaf, and 4) the length of time the new leaf biomass remains on the plant. Each of these components could potentially vary with species and level of salinity in the growth medium. The rate of carbon gain per unit leaf area will be addressed in the next section of the results. Here, the other three components are addressed

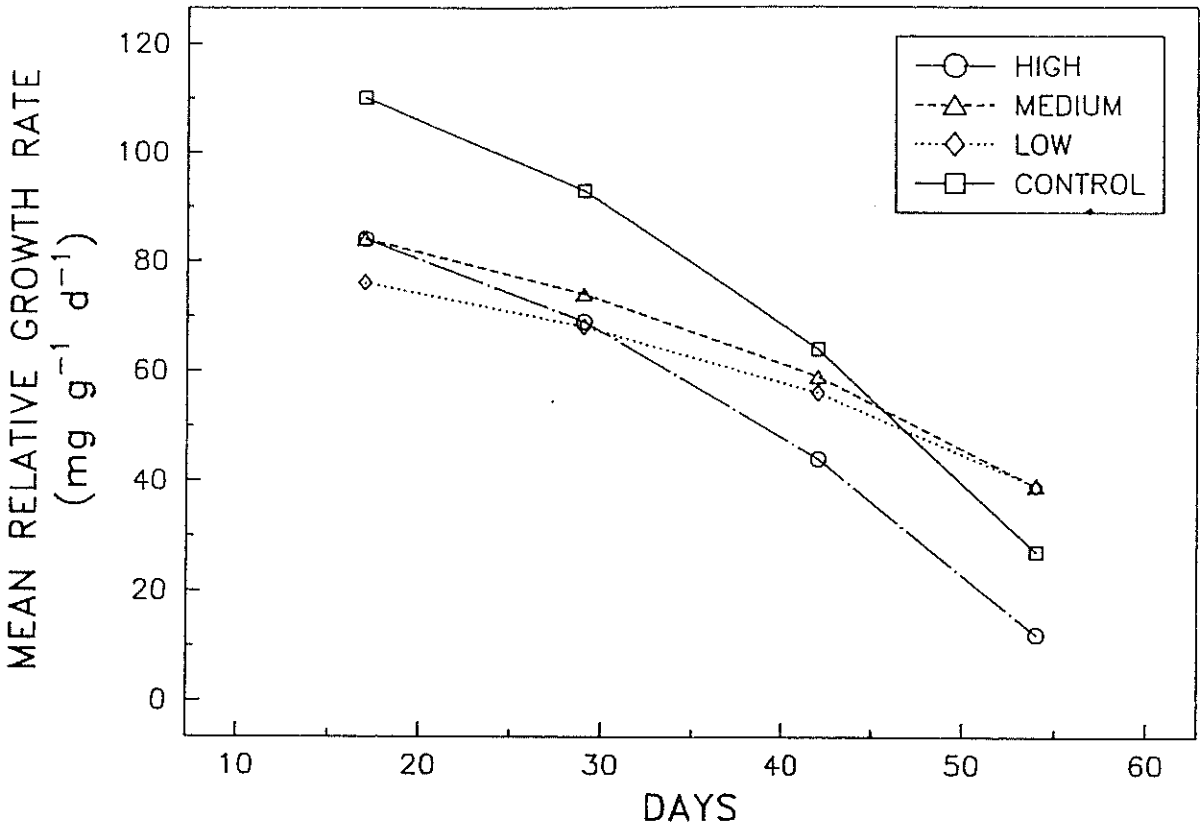

Figure 2. Growth Rate of S. wrightii as a Function of Time at Each of the Treatment Salinity Levels

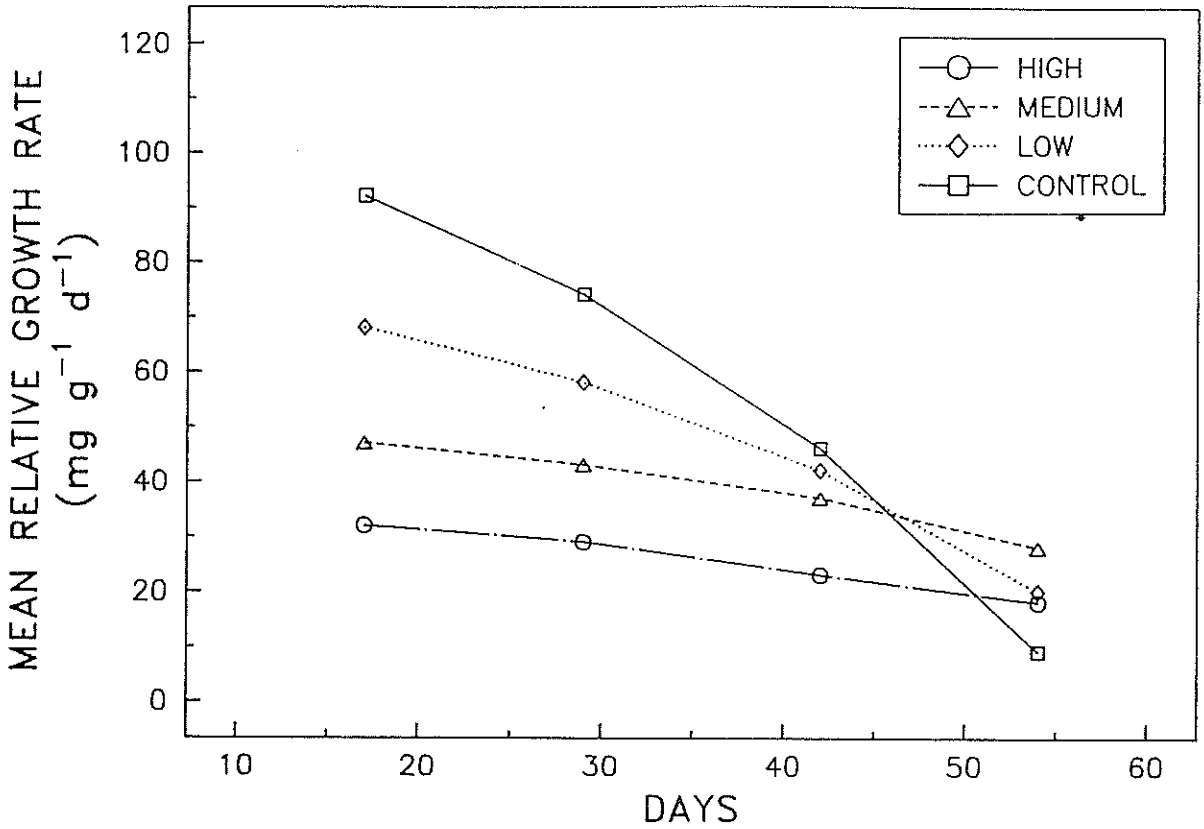

Figure 3. Growth Rate of S. giganteus as a Function of Time at Each of the Treatment Salinity Levels

relative to their dynamics as revealed by the harvest data from the growth experiments.

From the harvest data the rate of total biomass accumulation per unit leaf area per day was calculated. For S. airoides this unit leaf rate of biomass accumulation was identical for the control and medium salinity treatment through the entire experimental growth period (figure 4). The high salinity treatment actually had a higher mean unit leaf rate at the end of the growth period than did the low salinity treatment. Although the high salinity plants started with a lower rate, they maintained that rate throughout the 60 d period. The salinity treatments caused some reduction in mean unit leaf rates in S. wrightii, but the low and medium salinity plants maintained their rates quite well during the 60 d period (figure 5). Salinity had the greatest effect on the mean unit leaf rate of S. giganteus (figure 6). Although the rate dropped to its lowest level in the control plants at the end of the growth period, for most of the experiment the control plants had much higher mean unit leaf rates. These results indicate that biomass gain per unit leaf area is a significant component of the ability of S. airoides and to some extent S. wrightii to maintain higher growth rates under saline conditions.

The allocation of biomass to leaves, shoots and roots in S. airoides and S. wrightii was affected similarly by the salinity treatments. Salinity level did not affect the allocation to new leaf material in either of these species. The only effect of increased substrate salinity was to increase the allocation of biomass to shoots at the expense of roots (figures 7 and 8). Salinity also caused a reduction in biomass allocation to roots in S. giganteus. In this species, however, the biomass not allocated to roots was utilized in the construction of both new shoot and new leaf biomass (figure 9). S. giganteus, unlike the other two species, thus shows some ability to compensate for its

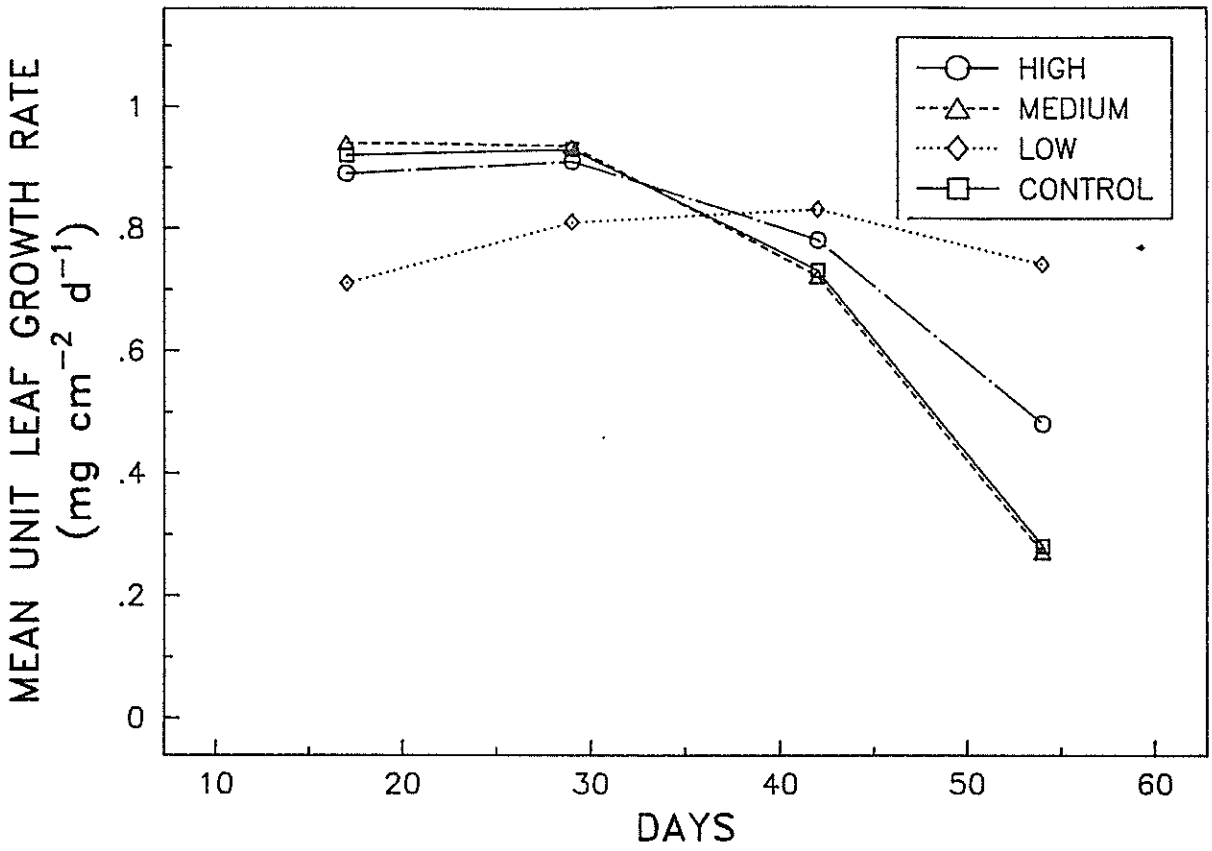

Figure 4. Growth Rate Per Unit Leaf Area of S. airoides as a Function of Time at Each of the Treatment Salinity Levels

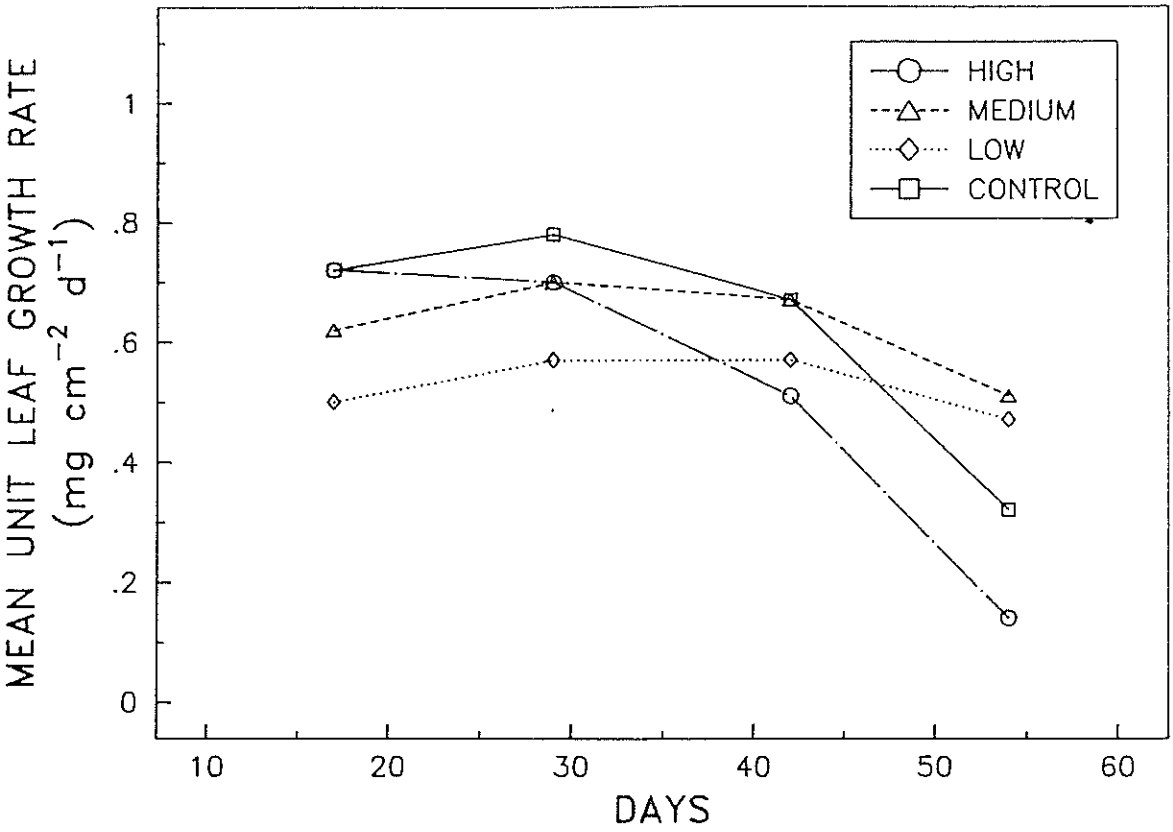

Figure 5. Growth Rate Per Unit Leaf Area of S. wrightii as a Function of Time at Each of the Treatment Salinity Levels

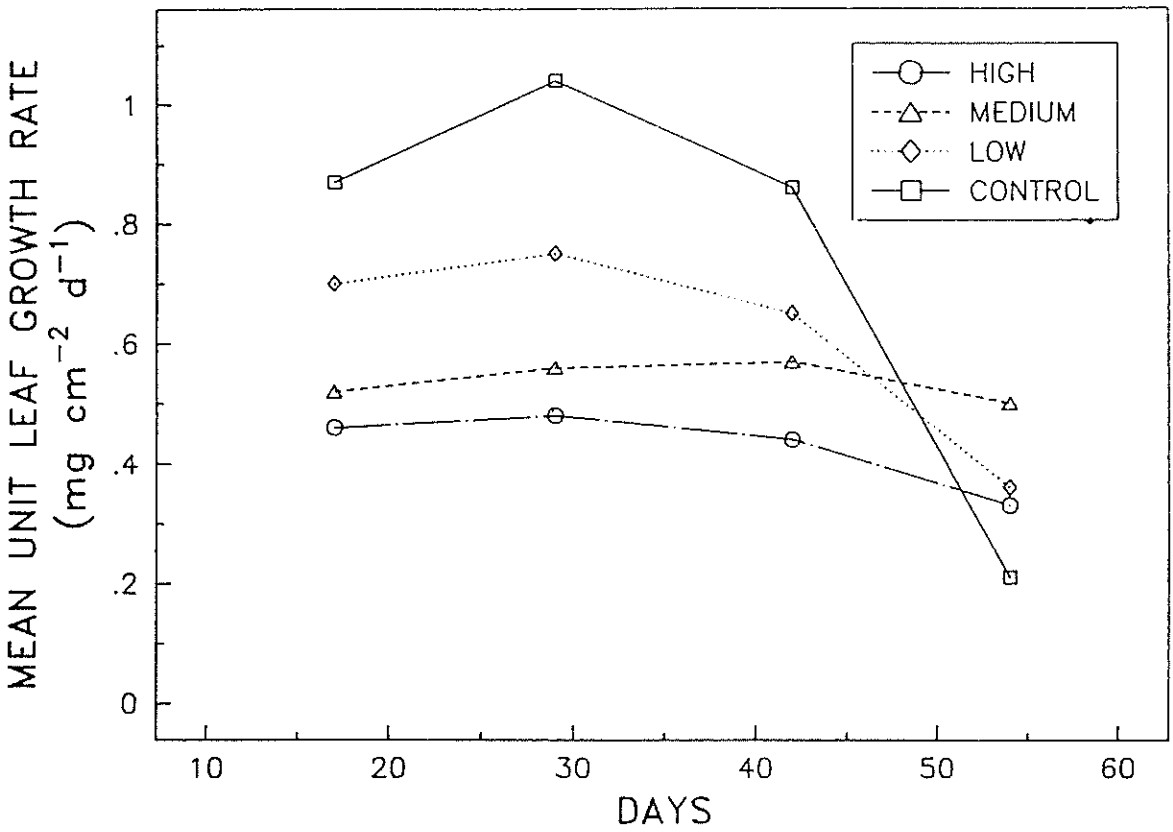

Figure 6. Growth Rate Per Unit Leaf Area of S. giganteus as a Function of Time at Each of the Treatment Salinity Levels

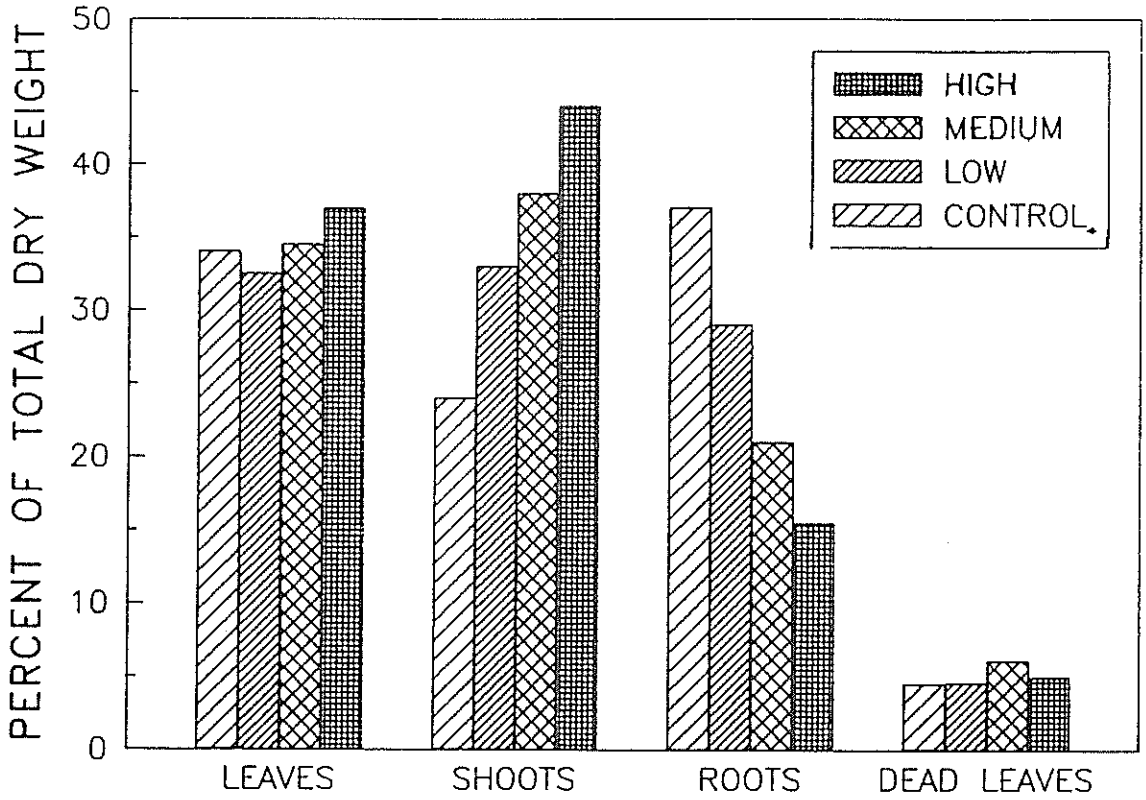

Figure 7. Percent of Total Dry Weight Allocated to Various Vegetative Plant Parts by S. airoides at Each of the Treatment Salinity Levels

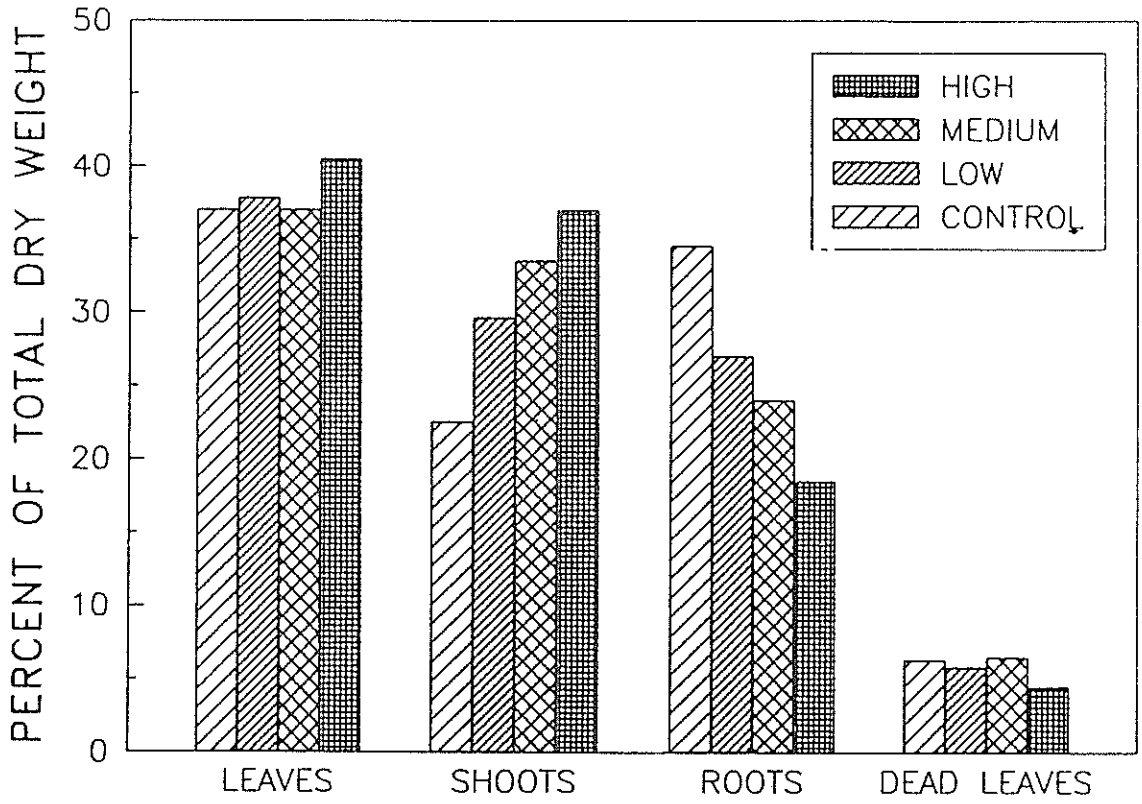

Figure 8. Percent of Total Dry Weight Allocated to Various Vegetative Plant Parts by S. wrightii at Each of the Treatment Salinity Levels

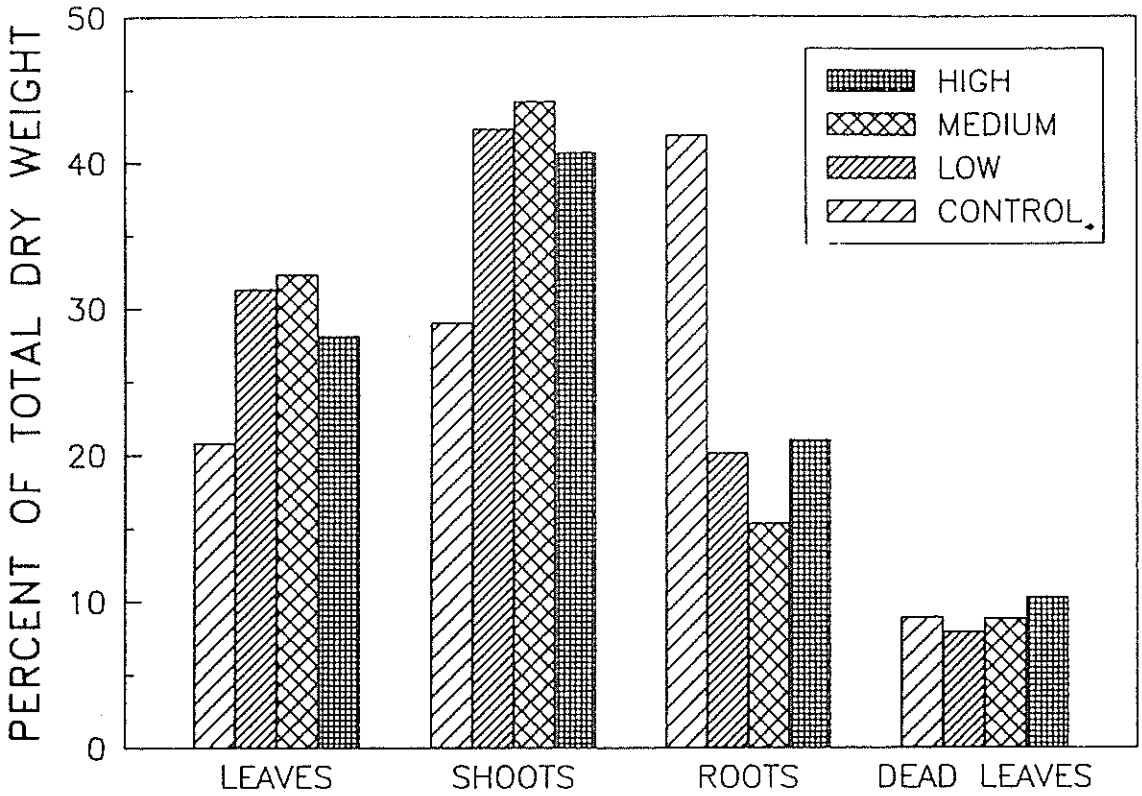

Figure 9. Percent of Total Dry Weight Allocated to Various Vegetative Plant Parts by S. giganteus at Each of the Treatment Salinity Levels

reduced unit leaf biomass accumulation rate by allocating more of its available material to photosynthetic tissue. Although S. giganteus does allocate more of its biomass to new leaves, the individual leaves are smaller (table 4). This is not the case with the other two species.

The ability of all three species to maintain photosynthetic leaf area over time was greatly reduced by salinity (figures 10, 11, and 12). This reduction was less for S. airoides than for the other two species. This could be an important factor in this species' ability to maintain growth rates under saline conditions.

Carbon Dioxide and Water Vapor Exchange

The net CO_2 exchange rates as a function of photosynthetic photon flux (PPF) for each of four replicate samples of each species and salinity treatment were fit to a Michaelis-Menton type equation using least squares regression techniques:

$$P = \frac{Pm * (I-L)}{Km + I - L}$$

where; P = net CO_2 exchange rate (μmol m^{-2} s^{-1})

Pm = maximum rate of net CO_2 exchange with unlimited light (μmol m^{-2} s^{-1})

I = PPF (μmol m^{-2} s^{-1})

L = light compensation point (μmol m^{-2} s^{-1}

Km = photosynthetic photon flux which yields one half the value of Pm (μmol m^{-2} s^{-1})

This procedure allowed the estimation of a theoretical maximum rate of net CO_2 uptake without light limitation (Pm). Increased substrate salinity did not have a statistically significant effect on Pm of S. airoides, and only the medium salinity treatment resulted in a decrease of Pm for S. wrightii

Table 4

Length (cm) of longest leaf on the plant. Mean ± 1 standard deviation for 10 replicate samples of each species and treatment. Values in a column with the same superscript are not significantly different ($P \leq 0.05$).

	Species		
Salinity	*S. airoides*	*S. wrightii*	*S. giganteus*
Control	54 ± 6^{a}	62 ± 6^{a}	74 ± 7^{a}
Low	56 ± 5^{a}	67 ± 6^{a}	72 ± 8^{a}
Medium	53 ± 5^{a}	67 ± 6^{a}	40 ± 4^{b}
High	45 ± 4^{a}	62 ± 6^{a}	40 ± 5^{b}

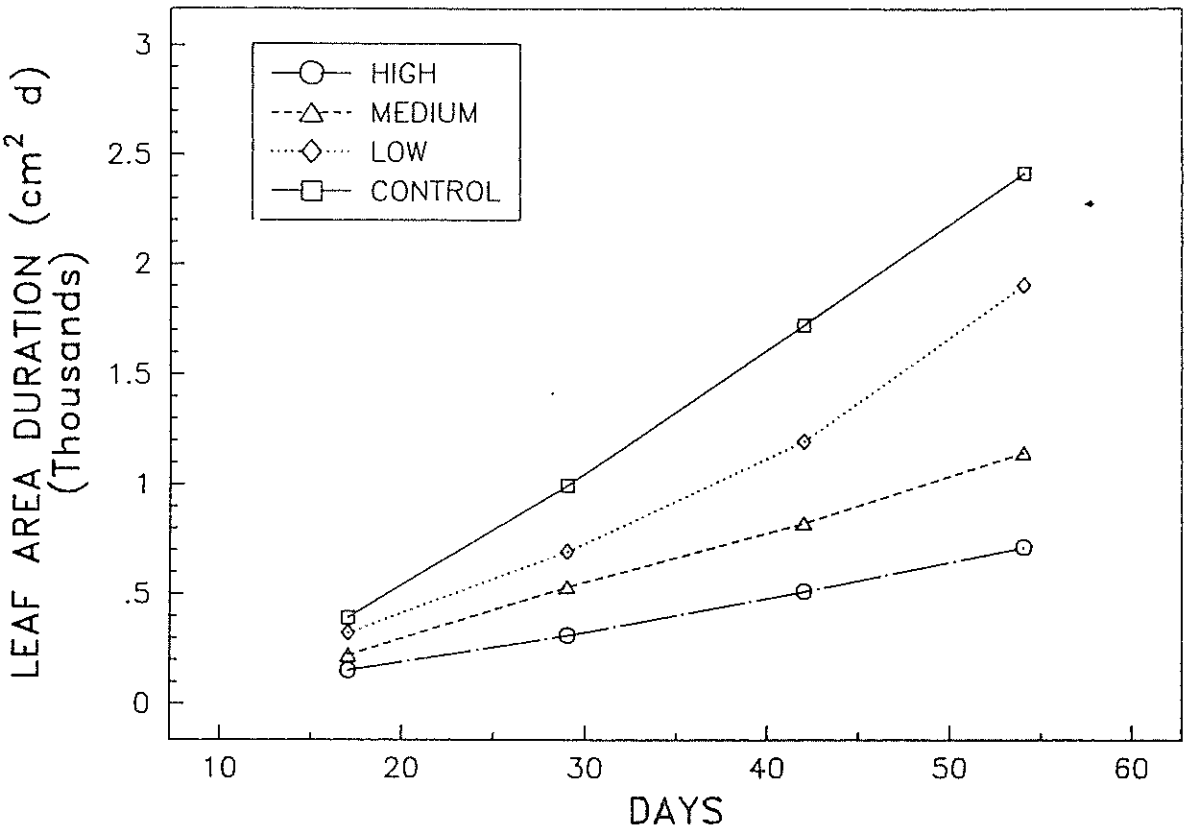

Figure 10. Leaf Area Duration of S. airoides as a Function of Time at Each of the Treatment Salinity Levels

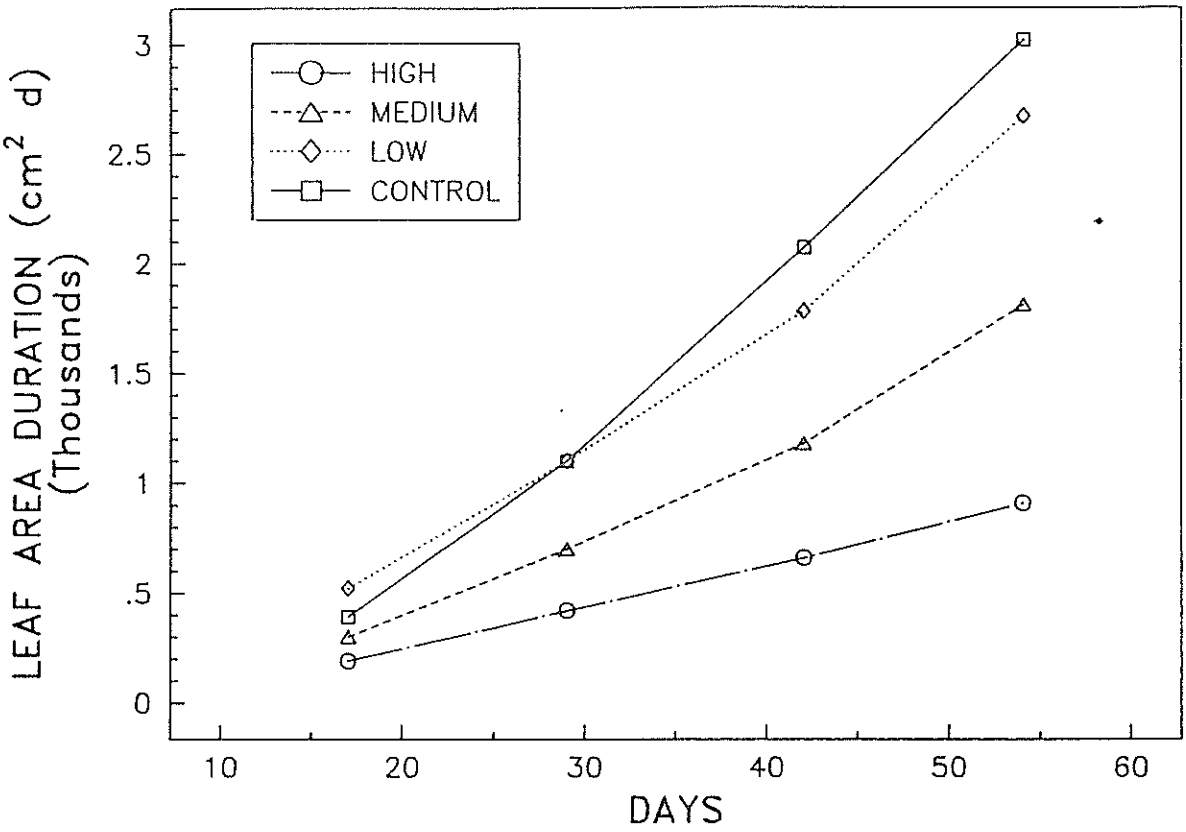

Figure 11. Leaf Area Duration of S. wrightii as a Function of Time at Each of the Treatment Salinity Levels

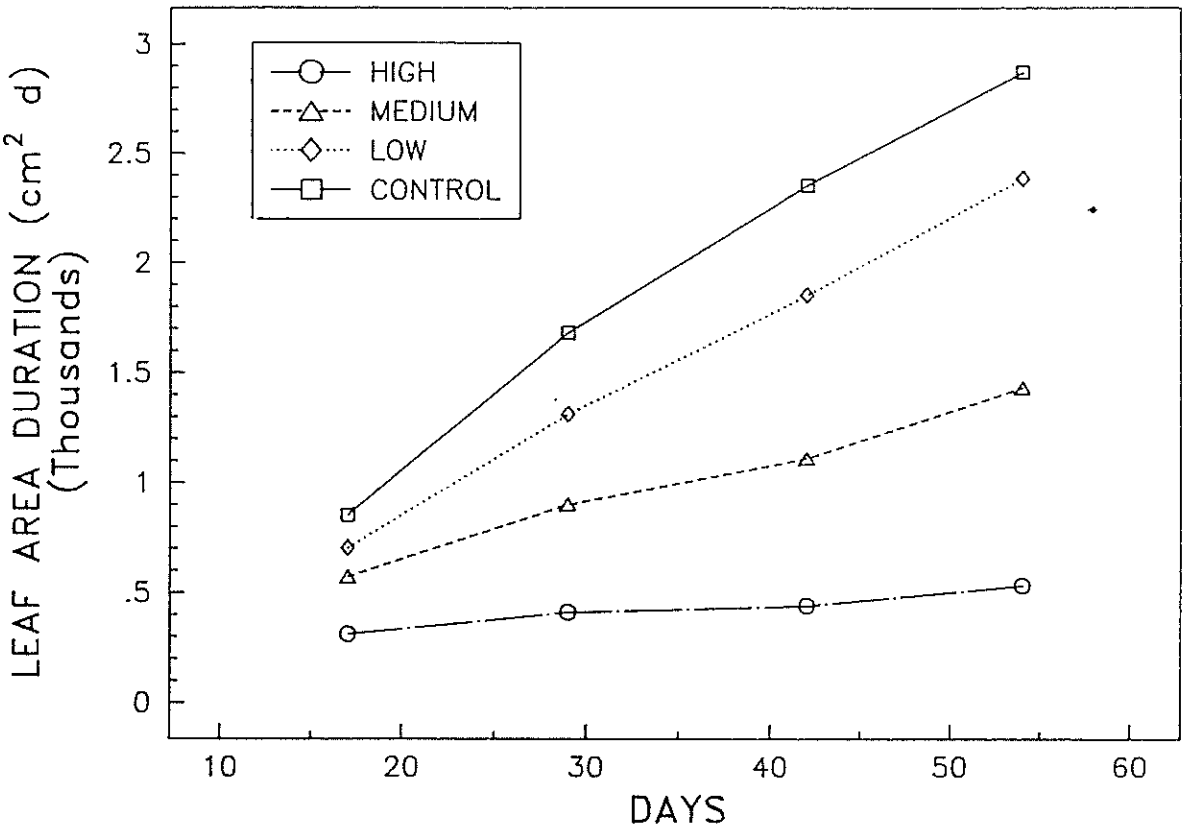

Figure 12. Leaf Area Duration of S. giganteus as a Function of Time at Each of the Treatment Salinity Levels

Table 5

Calculated maximum rate of net CO_2 exchange (μmol CO_2 m^{-2} s^{-1}) with unlimited light, ambient CO_2 of 310 μmol mol^{-1}, leaf temperature 35°C. Mean $\pm$ 1 standard deviation for 4 replicate samples. Values in a column with the same superscript are not significantly different ($P \leq 0.05$).

	Species		
Salinity	S. airoides	S. wrightii	S. giganteus
Control	45±6[a]	28±2[a]	50±10[a]
Low	36±13[a]	28±3[a]	46±6[a]
Medium	37±12[a]	20±2[b]	24±13[b]
High	31±9[a]	24±6[a]	–

(table 5). Pm was also reduced in S. giganteus by the medium salinity. No gas exchange data were obtained for S. giganteus at the high salinity because all plants in this treatment died before measurements were made at the end of the growth experiment. The photosynthetic system of S. airoides appears most resistant to salinity, but S. wrightii is only slightly less resistant. In fact, under normal greenhouse light conditions of 2200 μmol m^{-2} s^{-1} PPF and leaf temperatures of 35°C, the net CO_2 exchange rate of neither of these two species was significantly reduced by the salinity treatments (table 6).

Stomatal conductance under the above conditions was reduced by increased salinity that did not affect the rate of net CO_2 uptake (table 7). The stomatal conductance of S. airoides was reduced relative to the control by all three salinity treatments. The low salinity treatment did not reduce the stomatal conductances of either S. wrightii or S. giganteus.

A reduction in stomatal conductance without a concomitant reduction in the rate of net CO_2 uptake implies an increase in both water-use-efficiency and carboxylation efficiency. S. airoides did show an increase in water-use efficiency in the salt treatments relative to the control (table 8). This increase was at least partially the result of an increase in carboxylation efficiency as indicated by the lower intercellular space CO_2 concentrations under the medium and high salinity treatments in comparison with the control (table 9). The low salinity treatment did not have a statistically significant effect on the intercellular space CO_2 concentration although it did result in a lower stomatal conductance and an increased water-use efficiency.

The interrelationships of these gas exchange parameters are more complex and difficult to interpret for the other two species. S. wrightii like S. airoides did not show a significant reduction in net CO_2 uptake with increased

Table 6

Net CO_2 exchange rate ($\mu mol\ m^{-2}\ s^{-1}$) at 2200 $\mu mol\ m^{-2}\ s^{-1}$ PPF, 35°C leaf temperature and 310 $\mu mol\ mol^{-1}$ ambiant CO_2. Mean ± 1 standard deviation for 4 replicate samples. Values in a column with the same superscript are not significantly different ($P \leq 0.05$).

	Species		
Salinity	S. airoides	S. wrightii	S. giganteus
Control	31±3[a]	21±3[a]	35±6[a]
Low	28±9[a]	21±1[a]	36±5[a]
Medium	29±6[a]	18±2[b]	19±9[b]
High	26±7[a]	18±9[a]	-

Table 7

Stomatal conductance (mmol H_2O m^{-2} s^{-1}) at 2200 µmol photons m^{-2} s^{-1} PPF, 35°C leaf temperature and 310 µmol mol^{-1} ambient CO_2. Mean ± 1 standard deviation of 4 replicate samples. Values in a column with the same superscript are not significantly different ($P \leq 0.05$).

	Species		
Salinity	S. airoides	S. wrightii	S. giganteus
Control	427±71[a]	222±68[a]	362±109[a]
Low	275±61[b]	281±51[a]	416±65[a]
Medium	230±68[b]	147±33[b]	196±118[b]
High	219±72[b]	152±64[b]	-

Table 8

Water use efficiency (mmol CO_2 (mol H_2O)$^{-1}$) at 2200 μmol photons m^{-2} s^{-1} PPF, 35°C leaf temperature and 310 μmol mol^{-1} ambient CO_2. Mean ± 1 standard deviation of 4 replicate samples. Values in a column with the same superscript are not significantly different ($P \leq 0.05$).

	Species		
Salinity	S. airoides	S. wrightii	S. giganteus
Control	3.71±4.3[a]	5.42±6.7[a]	3.59±5.1[a]
Low	4.79±4.4[b]	4.63±3.6[b]	5.02±5.7[b]
Medium	5.77±5.0[c]	5.90±9.8[a]	4.77±6.7[b]
High	4.73±2.1[b]	5.09±5.2[a]	-

Table 9

Intercellar space CO_2 concentration (μmol mol^{-1}) at 2200 μmol m^{-2} s^{-1} PPF, 35°C leaf temperature and 310 μmol mol^{-1} ambient CO_2. Mean ± 1 standard deviation of 4 replicate samples. Values in a column with the same superscript are not significantly different ($P \leq 0.05$).

	Species		
Salinity	S. airoides	S. wrightii	S. giganteus
Control	180±15[a]	122±23[ab]	95±58[a]
Low	137±58[ab]	177±30[a]	135±62[a]
Medium	58±39[c]	46±35[c]	107±58[a]
High	107±16[cb]	81±64[bc]	-

salinity, and stomatal conductance was lower, at least at the medium and high salinities. Carboxylation efficiency was greater in the medium salinity treatment than in the control, but the control was not different in this respect from the high salinity treatment (table 9). The low salinity treatment had the lowest water-use-efficiency and a much lower carboxylation efficiency (high intercellar CO_2 concentration) than the other salt treatments (tables 8 and 9).

In the case of S. giganteus water-use-efficiency was increased by both the low and medium salinity treatments (table 8). In this species, however, this was not a result of increased carboxylation efficiency (table 9). In S. giganteus stomatal conductance and net CO_2 exchange rate change concomitantly with salinity treatments and carboxylation efficiency remains constant.

S. airoides and S. wrightii both appear to have a capacity for increasing their carboxylation efficiency in response to salt stress. This allows net CO_2 uptake rates to remain high as stomatal conductance and thus transpiration decrease. As a result, these species would take up less water and presumably salt for each increment of carbon gained in photosynthesis than would S. giganteus. Although the data are not conclusive on this point, they do suggest that S. airoides may have a greater ability to adjust its carboxylation efficiency under salt stress than does S. wrightii.

Germination

Seeds of all three species germinated well under the control conditions and no additional seeds germinated after the first 19 days. Seeds of S. airoides germinated in all three salinity treatments, salinity only slightly reduced the percent germination, and no additional seeds germinated after being transferred to the control solutions. The medium and high salinities prevented germination of S. wrightii seeds but these seeds retained their

ability to germinate when transferred to the control solution. All three salinity treatment levels prevented the germination of S. giganteus seeds and treatment with salt prevented their germination upon transfer to the control solution (table 10). It would appear that the natural distributions of these species might be explained simply on the basis of the effects of salinity on their germination.

SUMMARY AND CONCLUSIONS

The three species of Sporobolus used in this study were chosen because their natural distributions in habitats of different soil salinities indicated that they might show marked qualitative differences in their responses to salinity which would provide a key to developing more salt tolerant genotypes for use in CSA with saline or brackish water irrigation. In general, however, it appears that the differences that do exist are of a more quantitative rather than qualitative nature. This indicates that genetic engineering or breeding for salt tolerance among these and perhaps other C_4 graminoides is likely to be difficult. In fact, the clearest qualitative difference found among these species was in their germination responses to salinity. It is not unlikely that this characteristic is largely responsible for their natural distributions.

The growth studies did show, however, that the presumed differences in salt tolerance were reflected in differential growth rate responses to salinity under CSA conditions. S. airoides maintained relatively higher levels of production with increased salinity than did S. wrightii. S. giganteus was most affected by salinity. These growth rate differences among the species corresponded to differences in carboxylation efficiency in response to salinity, as measured by intercellular CO_2 concentrations. The ability of S. airoides and to some extent S. wrightii to increase carboxylation efficiency with increased salinity causes their net

Table 10

Percent germination at 19 days (in the indicated treatment solution) and at 31 days after transfer at day 19 to the control half-strength Hoagland's solution.

	S. airoides		*S. wrightii*		*S. giganteus*	
Days	19	31	19	31	19	31
Control	88	88	86	86	48	48
Low salinity	87	85	85	85	0	0
Medium salinity	71	71	0	80	0	0
High salinity	60	60	0	82	0	0

photosynthesis rates to remain relatively high and increases their water-use-efficiency.

Perhaps an equally important finding relates to the high degree of intraspecific variation observed in the response to salinity in both S. airoides and S. wrightii. In many of the measurements made in this study mean values showed trends that could not be declared statistically significant. This is a reflection of the high intraspecific variability in the measured characteristics. This variation indicates that selection for enhancement of specific traits could be valuable in obtaining genotypes particularly suited for utilization of saline water in CSA environments.

A particularly useful strategy might be to establish a breeding program using the level of increase in carboxylation efficiency of an individual with an increase in salinity as a selection criterion. More salt tolerant genotypes well suited to CSA and saline water irrigation might be readily obtained in this way.

An even more productive extension of these findings might be an investigation of the mechanism by which salt increases the carboxylation efficiency. Perhaps increased salinity is a general stimulator of protein synthesis, and the resulting higher levels of enzyme activity lead to an increase in the rates of ribulose-bis-phosphate and/or phosphoenol pyruvate regeneration. If this is the case the results of this study could have important implications for many potential CSA crops.

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