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Variations in Response of Two U.S. Gulf Coast Populations of *Spartina alterniflora* to Hypersalinity

S.R. Pezeshki and R.D. DeLaune

Wetland Biogeochemistry Institute
Center for Coastal, Energy and Environmental Resources
Louisiana State University
Baton Rouge, LA 70803, U.S.A.

ABSTRACT

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Two populations of *Spartina alterniflora* Lois. from Louisiana Gulf Coast marshes were studied under flooded conditions and elevated salinities of 170, 510, and 850 mol m^{-3}. The Lake Tambour population maintained greater net photosynthesis than the Leeville population under various salinity treatments. At 850 mol m^{-3} salinity, net photosynthesis was reduced significantly ($p \leq 0.05$), 28% for Lake Tambour and 52% for the Leeville population as compared to plants at 170 mol m^{-3}. Net growth of foliage and root dry weights were reduced in response to increased salinities. Statistical analyses revealed significant differences among the treatment interactions (population × treatment) on net photosynthesis and various growth parameters confirming differences in photosynthetic responses and growth traits between the study populations in response to the elevated salinities. The Lake Tambour population grew better at 850 mol m^{-3} salinity treatment as compared to the Leeville population. The observed responses are in accord with the habitat characteristics where these populations grow naturally since the Lake Tambour site is characterized by lower soil redox potentials and higher salinities than those found on the Leeville site. Results suggest that there are variations in salt-tolerance among *S. alterniflora* populations in the U.S. Gulf Coast, the potential for existence of genetic differentiation in this species and the potential for developing superior salt-tolerant planting stocks suitable for use in marsh revegetation and coastal restoration projects in salinity dominated coastal areas.

ADDITIONAL INDEX WORDS: *Spartina alterniflora, population differentiation, salinity stress, photosynthesis, stomatal conductance, smooth cordgrass.*

INTRODUCTION

The occurrence of differentiated populations in relation to a given environmental stress has been reported for numerous species (HESLOP-HARRISON, 1964; EHRLICH and RAVEN, 1969; SNAYDON, 1970; HAMRICK and ALLARD, 1972; TURKINGTON and HARPER, 1979; KEELEY, 1979, and ETHERINGTON and THOMAS, 1986) including several saltmarsh species (BOORMAN, 1967; GRAY and SCOTT, 1980, and JEFFERIES *et al.*, 1981). Genetic variation among populations of a given species is a result of interaction of several factors such as genetic recombination, mutation and natural selection (WARWICK and HALLORAN, 1991). Several marsh species show population differentiation including *Spartina alterniflora* Lois. (MOORING *et al.*, 1971, SHEA *et al.*, 1975). SILANDER (1985) reported that genotypes of *S. patens* from adjacent saltmarsh, swale and dune habitats showed evidence of genetic differentiation. Evidence for ecophenic variations in *S. patens* in Louisiana Gulf coast marshes has been reported (PEZESHKI and DELAUNE, 1991; PEZESHKI, 1991).

Spartina alterniflora is a dominant grass in the U.S. Gulf Coast salt marshes. Several height forms of this species occupy distinct zones in the saltmarshes of the U.S. Atlantic and Gulf Coast marshes (MOORING *et al.*, 1971; SHEA *et al.*, 1975; NESTLER, 1977; DELAUNE *et al.*, 1983, and PEZESHKI and DELAUNE, 1988). The existence of these height forms has prompted numerous studies to determine whether these forms are genetically distinct or are the results of phenotypic plasticity. In addition to the range of salinity tolerated by this species in its natural range, evapotranspiration in impoundments or restricted tidal exchange areas could increase soil salinity substantially. The growth of this species, however, is adversely affected by hypersaline conditions (GOSSELINK *et al.*, 1977). Field observations along the Louisiana Gulf coast indicate considerable variation in the performance of this species in response to various flooding/salinity regimes which may be attributed to genetic differentiation of

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populations or the result of phenotypic plasticity of individuals.

The present study was conducted to test the hypothesis that there is a potential population differentiation among the Gulf Coast *S. alterniflora* sources and that the differences can be evaluated by examining the salinity responses of individuals using physiological and growth analysis techniques. Evaluation of variation in salt-tolerance at subspecies level is needed to assess the threshold of salinity tolerance among individuals from these populations. Leaf gas exchange characteristics, growth parameters, and biomass partitioning were used as markers to identify differences in salinity tolerance among the individuals from the study populations.

MATERIALS AND METHODS

Population samples of *S. alterniflora* were collected from two sites, Leeville and Lake Tambour, in coastal Louisiana. The Leeville population grows in a saltmarsh (29° 15′ N, 90° 10′ W), and the Lake Tambour population site is also located in a saltmarsh (29° 20′N, 90° 40′W). The predominant salinity concentrations in sediment water range for the Leeville site is 136–187 mol m^{-3}, while the Lake Tambour population grows under a salinity range of 221–323 mol m^{-3}. The sites are approximately 40 km apart. Approximately 100 tillers per population were collected, transplanted in a greenhouse and cloned. Newly emerged culms and associated roots were planted in nursery pots filled with potting soil (commercial potting soil) in a greenhouse. The greenhouse was ventilated but not air conditioned. Study pots were watered to excess and fertilized (0.05 g pot^{-1}) with a commercial water soluble fertilizer (23-19-17, N, P, K, respective percentages) once per week. Three weeks after transplanting, salinity treatments were initiated (May 14, 1991).

Salt solutions were prepared using Instant Ocean Synthetic Sea Salt (Aquarium Systems, Inc., Mentor, Ohio, U.S.A.), with major ionic components of 47% Cl, 26% Mn, 6% SO_4, 3% Mg, 1% Ca, and 1% K (percentage of dry weight). Treatments began by flooding the pots with 50 mol m^{-3} (17 mol m^{-3} equals 1 ppt) salt on the first day. The salinity concentration of the first treatment was then increased to 120 mol m^{-3} on the 3rd day and to 170 mol m^{-3} on the 5th day of the experiment. The second treatment consisted of salt solutions which were added at the same rate as in the first treatment except that salinity was increased to 225 mol m^{-3} on day 10, 340 mol m^{-3} on day 12, and 510 mol m^{-3} on day 15. In the third treatment, plants were subjected to salinity levels in the sequences described except that salinity increased to 510 mol m^{-3} on day 10, 680 mol m^{-3} on day 12, and 850 mol m^{-3} on day 15. A YSI model 33 meter (Yellow Springs Instrument Co., Yellow Springs, Ohio, U.S.A.) was used to measure salt concentration in all pots throughout the experiment. Throughout the study, pots were drained once every two weeks and freshly made salt solution (at the respective concentrations) and fertilizer were reapplied. The 170 mol m^{-3} and 510 mol m^{-3} treatments represent the range of salinity encountered by these populations in the environments from which they were collected. The highest salinity treatment (850 mol m^{-3}) allowed the evaluation of both populations under hypersaline condition. The experimental design was a completely randomized block design with two populations, three salinity treatments and 54 replications (pots) per population/salinity combination (total of 324 pots). Each pot consisted of one plantlet which subsequently reproduced new culms.

Measurements of temperature, relative humidity, photosynthetic photon flux, leaf temperature, leaf conductance and net photosynthesis were made on 5 sample leaves per treatment (per population) every 3 hr beginning at 0900 until 1800 hr on each sample day. Well-developed leaf blades, 3rd or 4th blade, were used for gas exchange measurements. There were 8 sample days during the experiment, on days #9, 12, 25, 35, 39, 45, 55, and 60. Leaf conductance was measured using a steady-state porometer (LI-1600, LiCor, Inc., Lincoln, Nebraska, U.S.A.). After recording leaf conductance, the same leaf was used for net photosynthesis measurement. A portable gas-exchange system (Model A120, ADC, Field Analytical System, Analytical Development Co., England) was used to provide rapid measurement of net photosynthesis. Stomatal conductance and net photosynthesis values were calculated per unit leaf area (single surface) determined with a surface area meter (Model SI701, SKYE Instrument, Inc., Buckingham, Pennsylvania, U.S.A.).

Initial data on height, fresh weight and dry weight of root and shoot were measured on 12 additional plants per population selected randomly for the initial biomass sampling. Dry weights of each component were then estimated based on the models developed which estimated

root or shoot dry weight based on height and total plant fresh weight. At the conclusion of the study, biomass partitioning was determined by separating each sample plant into shoot and root components and drying them at 80 °C to a constant weight. The net growth of shoot and root were calculated based on the increment in dry weight of each component during the experimental period. Initial dry weights were based on regression models developed which correlated dry weight of each component to height and total fresh weight from the initial destructive samples obtained at the beginning of the experiment. Changes in biomass of shoots and roots were evaluated from replicated destructive samples taken from each population-treatment combination during the 10th week of the study. Leaf surface area (LA) was determined using a Leaf Area Analysis System (SI-701, SKYE Instrument, Inc., Buckingham, Pennsylvania).

The General Linear Models (GLM) procedure of the SAS System (SAS Institute, Cary, North Carolina) was used to test for differences in leaf conductance and net photosynthesis among the treatment means, by using a repeated-measures design which included the day and the hour of measurement (MOSER *et al.*, 1990). Mean values of growth parameters were compared within each treatment using multiple comparison procedures of the same statistical system. GLM and Least Significant Difference (LSD) procedures were used where appropriate to compare means for each population among the salinity treatments.

RESULTS

Mean values of net photosynthesis measured over the study period in both populations were adversely affected at the highest salinity (Table 1). Salinity increase from 170 to 850 mol m^{-3} reduced net photosynthesis by 28% in Lake Tambour population and by 52% in Leeville population. Both populations had comparable photosynthetic rates under 170 and 510 mol m^{-3} salinity treatments; however, at 850 mol m^{-3} salinity, Lake Tambour plants showed significantly greater photosynthesis as compared to the Leeville plants. ANOVA also revealed significant differences among the treatment interactions (population × treatments) further confirming differences in photosynthetic responses between the study populations to the elevated salinities (Table 1).

Table 1. *Mean values of stomatal conductance and net photosynthesis for two populations of* Spartina alterniflora *in response to elevated salinities. The experiment was conducted under greenhouse conditions where plants were exposed to the treatments by gradual addition of salinity to floodwater over 15 days followed by periodic measurements. (*) dneotes significant differences ($p \leq 0.05$) between populations for the designated treatment using multiple comparison (Scheffe options). See text for details. Values (for each population) within each column not followed by the same letter are significantly different at $p < 0.05$ level. Analysis of variance (p-values), for the effects of populations, salinity levels and interaction are also presented.*

Sea Salt Concentration	Population	Stomatal Conductance	Net Photosynthesis
170 mol m^{-3}	Leeville	89 ± 10a	14.8 ± 1.4a
	Lake Tambour	97 ± 9a	18.1 ± 1.5a
510 mol m^{-3}	Leeville	96 ± 10a	15.8 ± 1.5a
	Lake Tambour	88 ± 10a	15.7 ± 1.8ab
850 mol m^{-3}	Leeville	87 ± 11a	*7.1 ± 1.0b
	Lake Tambour	92 ± 12a	13.1 ± 1.2b
Source			
Population		0.7625	0.0009
Treatment		0.8915	0.0001
Interaction		0.9075	0.0003

Leaf conductance values were not affected by the treatment in both populations (Table 1). Furthermore, both populations had comparable conductance values at various treatments. There was no significant effects of population, treatment and interaction (population × treatment) on leaf conductance (Table 1).

Biomass production was reduced in response to elevated salinity treatments in both populations. However, with progression of the study, the Lake Tambour population maintained greater biomass compared to the Leeville population. Increased salinity to 850 mol m^{-3} reduced foliage dry weight, root dry weight, leaf area, and number of culms in both populations (Table 2). For example, in the Leeville population, foliage dry weight was reduced by 32% and 95% in 510 and 850 mol m^{-3} treatment compared to 170 mol m^{-3} treatment, respectively. Root dry weight was not reduced at 510 mol m^{-3} treatment but reduced by 83% in 850 mol m^{-3} plants. Similarly, in the Lake Tambour population, foliage dry weight was reduced by 45% and 73% in response to 510 mol m^{-3} and 850 mol m^{-3} salinity treatments, respectively. Similar trends were found in leaf area and number of culms under increasing salinity in the Lake Tambour population.

Table 2. *Mean values of several growth parameters for two populations of* Spartina alterniflora *in response to elevated salinities. Analysis of variance (p-values) for the effects of population, salinity treatment and interaction are also presented. Data were collected during the 10th week of the experiment (final values). Data of initial harvest were used for calculation of growth (final values minus initial values) for the respective population-treatment means. (*) denotes significant differences ($p \leq 0.05$) between the populations within a given treatment. Values (for each population) within each column not followed by the same letter are significantly different at the $p < 0.05$ level. Analysis of variance (p-values) for the effects of population, salinity levels and interaction are also presented.*

Sea Salt Concentration	Population	No. Of Culm (per pot)	Foliage DW (g/pot)	Leaf Area (cm^2/pot)	Root DW (g/pot)
170 mol m^{-3}	Leeville	5.4 ± 1.2*a	9.3 ± 1.4*a	500 ± 130*a	1.8 ± 0.8*a
	Lake Tambour	18.2 ± 2.1a	26.7 ± 3.2a	1,300 ± 180a	8.0 ± 1.7a
510 mol m^{-3}	Leeville	4.7 ± 1.3*a	6.3 ± 1.5*a	300 ± 80*a	1.8 ± 0.9*a
	Lake Tambour	12.6 ± 2.7ab	14.6 ± 2.4b	700 ± 90b	5.0 ± 1.2a
850 mol m^{-3}	Leeville	0.7 ± 0.2*b	0.5 ± 0.2*b	20 ± 10*b	0.3 ± 0.1*b
	Lake Tambour	9.1 ± 1.4b	7.1 ± 1.3c	350 ± 70c	2.5 ± 0.3b
Source					
Population		0.0001	0.0001	0.0001	0.0001
Treatment		0.0001	0.0001	0.0001	0.0001
Interaction		0.0321	0.0065	0.0065	0.0018

Changes in biomass parameters (final value minus estimated initial value) for both populations in response to the treatments revealed that at 850 mol m^{-3} treatments, leaf dry weight, root dry weight, leaf area and number of culms decreased in both populations (Figure 1). The statistical significance of changes in these variables is shown in Table 2. The Lake Tambour population grew larger in all treatments as compared to plants from the Leeville population. The net increment in biomass parameters was significantly ($p < 0.05$) greater in the Lake Tambour population as compared to the Leeville population in 510 mol m^{-3} and 850 mol m^{-3} treatments. Further analyses showed significant population, treatment, and interaction effects for number of culms, leaf dry weight, leaf area, root dry weight and total dry weight indicating significant differences in growth traits between the two populations in response to elevated salinities.

DISCUSSION

Salinity increases in the rhizosphere coupled with soil flooding resulted in reduction of net carbon assimilation in both populations of *S. alterniflora* at 850 mol m^{-3}. The decrease in net photosynthesis was not significant at medium salinity but was significant at the highest salinity treatment. Such response may be attributed primarily to non-stomatal (metabolic) factors. In the present study, there was no evidence of significant stomatal limitations of gas exchange in response to the treatments as was evident by the stomatal conductance (Table 1). Thus, the decrease in capacity of chloroplasts for CO_2 fixation is likely to have been associated with adverse metabolic effects on photosynthetic processes. Similar responses have been reported for other species (LONGSTRETH and NOBEL, 1979; WALKER *et al.*, 1982). PEARCY and USTIN (1984) found reductions in assimilation rates in *Spartina* and *Scirpus* species as a result of diffusional limitations and metabolic effects when soil salinity increased.

Both populations continued growth under the salinity treatments for 10 weeks. However, reductions in growth and biomass production in response to the elevated salinities were evident. The Lake Tambour population grew faster than the Leeville population under our experimental salinity regimes in different growth parameters measured (Table 2). Such differences may be of great importance since it may provide great competitive advantages for the Lake Tambour population. Traits such as height, leaf area and culm regeneration are closely associated with competitive characteristics, which are traits influencing success of genetic materials in different environments (SILANDER, 1985). These traits show the integrated genetic and environmental effects on plant and plant physiological components (NOBLE and ROGERS, 1992). Salinity responses observed were in agreement with field observations showing the relative position of the two populations in the natural range of *S. alterniflora* on the U.S. Gulf coast. The Lake Tambour population is associated with an area where sediment salinity is great-

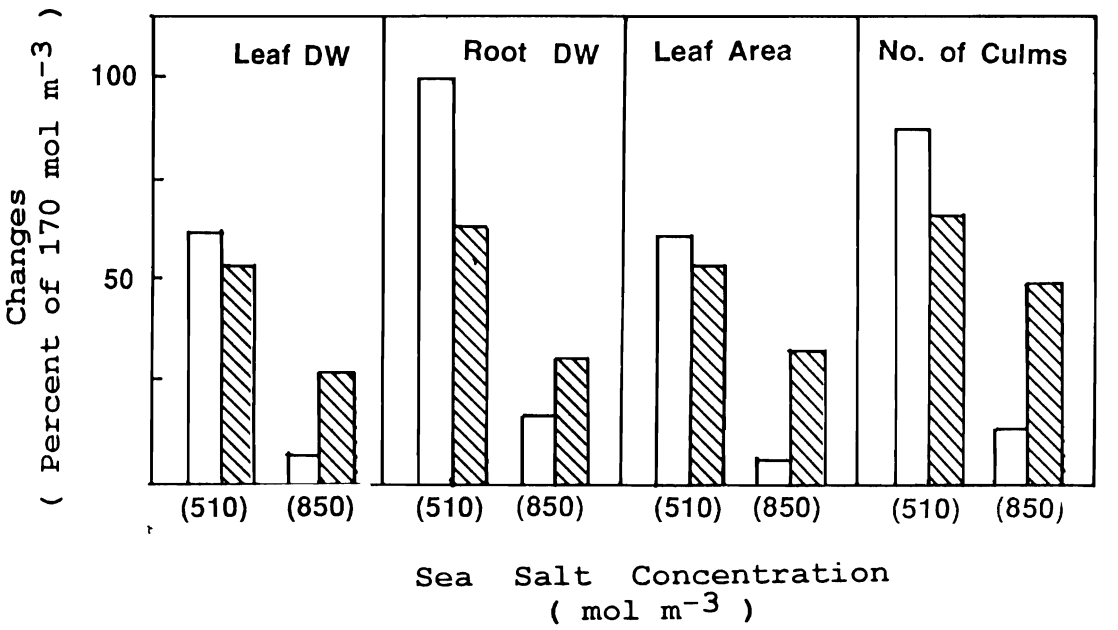

Figure 1. Percent changes in foliage dry weight, root dry weight, leaf area and numbers of culms in two populations of *Spartina alterniflora*, Leeville population (open bars) and Lake Tambour population (hatched bars) under various salinity treatments. Percentages represent changes compared to 170 mol m^{-3} treatment for respective population-treatment combinations showing relative responses to elevated salinities on a comparative basis.

er and redox potential is lower than the site where the Leeville population is found (DeLaune and Pezeshki, unpublished data). Overall, there was evidence of differences in growth patterns of the study populations in response to the combined salinity/flooding treatments.

Soil anaerobiosis and salinity are major environmental factors which influence plant distribution and growth in coastal marshes (DeLaune *et al.*, 1983). For instance, *S. alterniflora*'s growth is known to be adversely affected by excess salinity (Gosselink *et al.*, 1977). The apparent differentiation between the two populations of *S. alterniflora* is further evidenced by examination of differences in growth traits under different treatments which revealed significant differences between the two populations. The primary environmental factor to which such differentiation may be attributed is the sediment water salinity which creates a substantial selection pressure for plants. Population differentiation, as a means by which plants can cope with environmental heterogeneity (Heslop-Harrison, 1964; Ehrlich and Raven, 1969), has been a topic of considerable interest to plant ecophysiologists and geneticists. Through the evolutionary process, under a selection pressure of a distinct habitat, a homogeneous species may gradually evolve into diverse specialized populations. Such differentiation has been reported for many species (Gray and Scott, 1980; Jefferies *et al.*, 1981; Boorman, 1967; Huiskes *et al.*, 1985, and Eleuterius, 1989). The existence of height forms in *S. alterniflora* in saltmarshes of U.S. Atlantic and Gulf Coast (Mooring *et al.*, 1971; Shea *et al.*, 1975; Nestler, 1977, and DeLaune *et al.*, 1983), population differentiation in *S. patens* (Silander, 1985; Pezeshki and DeLaune, 1991) and *S. foliosa* (Cain and Harvey, 1983) have provided substantial data in favor of this hypothesis. In the present study, it is difficult to distinguish between evolutionary divergence of isolated populations and site-specific differential survival of offspring from a common gene pool. Such determination requires isozyme analysis which was beyond the scope of this study.

CONCLUDING REMARKS

The success of marsh restoration projects is governed by many factors. Selecting physiologically adapted plants for wetland creation or res-

toration requires matching of plant species with wetland edaphic conditions. Along the U.S. Gulf Coast, salt and brackish marshes, *S. alterniflora* and *S. patens,* are the dominant species which have been used extensively in marsh planting efforts in different coastal areas (WOODHOUSE *et al.*, 1974, 1976). Our results indicate population differentiation in *S. alterniflora* and suggest the need for evaluation of additional populations of this species under laboratory/greenhouse conditions as well as field *in situ* transplanting. Such efforts will allow further evaluation and comparison of performance of the selected populations under field conditions. The information is important from a practical point of view because of the potential for selection of stress-tolerant populations capable of tolerating extreme salinities. Identification of genetically distinct populations which are tolerant to elevated salinities is useful in developing strategies for stabilization and revegetation of deteriorating marshes. In revegetating programs on various wetland sites which may differ in soil physicochemical characteristics, selection of one genetic strain alone would not be sufficient. To develop stocks tolerant to hypersalinity, germplasm must be collected from additional populations of *S. alterniflora* from the natural occurrence of this species covering a wide range of salinity. Our present data suggest the need for mass selection from additional populations of *S. alterniflora* which occur in the U.S. Gulf Coast to represent adequate genetic pools in the selection process.

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