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RELATIVE GROWTH OF *SPARTINA PATENS* (AIT.) MUHL. AND *SCIRPUS OLNEYI* GRAY OCCURRING IN A MIXED STAND AS AFFECTED BY SALINITY AND FLOODING DEPTH

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Abstract: Mixed stands of *Spartina patens* and *Scirpus olneyi* occur in brackish marshes along the Gulf Coast of Louisiana. *Scirpus olneyi* is considered to be an important wildlife food, and marshes are often managed to favor its dominance over *S. patens*. Two environmental factors that affect growth of the two species are salinity and water regime. The objectives of this study were to determine the effects of salinity and water depth, under controlled greenhouse conditions, on relative dominance of the two species, chemical properties of soil interstitial water, and nutrient concentrations in the plant tissue. Treatments imposed in a factorial design were salinities of 0, 5, 10, 15 and 20 ppt and water depths of −10, +10, and +30 cm relative to the soil surface. Results indicated that salinity treatments above 10 ppt reduced growth of both species, but *S. olneyi* was more drastically affected than *S. patens*. Increased flooding depth reduced growth of *S. patens* but had little effect on *S. olneyi*. Concentrations of inorganic ions (Na^+, K^+, Mg^{+2}, Ca^{+2}, Cl^{-1}) in plant tissue were greater in *S. olneyi* than *S. patens*, indicating that ion accumulation may be the principal salt tolerance mechanism of *S. olneyi*. Extrapolated to field conditions, these results indicate that increasing salinity favors productivity of *S. patens* relative to *S. olneyi*, while increased depth of flooding favors *S. olneyi*.

Key Words: brackish marsh, *Spartina patens*, *Scirpus olneyi*, salinity

INTRODUCTION

The grass *Spartina patens* (Ait.) Muhl. and the bulrush *Scirpus olneyi* Gray often occur in mixed stands in brackish marshes along the Gulf Coast of Louisiana. Muskrats (*Ondatra zibethicus* Linnaeus), which are important to the fur industry, are found in greatest abundance in marshes with dense stands of *S. olneyi*, a preferred food that makes up 80% of the muskrats' diet in these marshes (O'Neil 1949). *Scirpus olneyi* is also an important food for snow geese (*Chen caerulescens* Linnaeus) and nutria (*Myocaster coypus* Molina) (Hess et al. 1975), while *Spartina patens* is considered a less valuable wildlife food (St. Amant 1959). A thorough review of the literature on biology, ecology, and management of *Scirpus olneyi* was provided by Sipple (1978, 1979).

Declines in muskrat populations parallel the deterioration of marshlands once dominated by *S. olneyi* and *Scirpus robustus* Pursh (Palmisano and Newsom 1967). Factors thought to be responsible for the decline of *S. olneyi* are increased water-level fluctuation and salt-water intrusion associated with canals dredged for navigation, pipelines, and drainage (Ross and Chabreck 1972) and natural subsidence of the Mississippi River deltaic plain (Salinas et al. 1986). Due to a combination of factors, some marshes formerly occupied by *S. olneyi* are now dominated by *S. patens*, which is able to tolerate a wide range of environmental conditions (Chabreck and Narcisse 1981). Management practices are often used to favor dominance of *S. olneyi* over *S. patens* for the purpose of increasing muskrat production (Allan 1950). Several studies have shown that burning, salinity, and water regime are three principal factors that affect the relative dominance of *S.*

patens and *S. olneyi* in brackish marshes along the Gulf Coast.

Burning is a management practice that has long been used to increase growth of *S. olneyi* relative to *S. patens*. O'Neil (1949) described *S. olneyi* as a subclimax plant that can be eliminated by more dominant plants even under favorable soil and water conditions. Burning gives *S. olneyi* the advantage over slower growing competitors. Chabreck (1981) found that maximum production of *S. olneyi* was favored by burning early in the fall (October), but burning in February produced stands dominated by *S. patens*.

A number of studies utilizing field observations and controlled field and greenhouse experiments have investigated the effects of salinity and water regime on growth of *S. olneyi* and *S. patens*. Allan (1950) found that, along the Gulf Coast, *S. patens* is characterized by a wide range of salinity and water level. Salinity ranged from 7.5 to 35 ppt and water level from +10 to −10 cm. *Scirpus olneyi* was a co-dominant in areas where salinity ranged from 8 to 17.5 ppt and water level from +10 to −2.5 cm. Palmisano and Newsom (1967) found that *S. olneyi* was associated with slight depressions in marsh interiors where minimum water levels ranged from −8 to +5 cm. The maximum soil salinity recorded was 16 ppt and the minimum 10 ppt.

Ross and Chabreck (1972) investigated the effect of salinity and water depth on growth and survival of natural and planted stands of *S. olneyi* under field and greenhouse conditions. They concluded that management of marshes to favor *S. olneyi* production depends primarily on water level and secondarily on salinity. Best survival of transplants and growth occurred where the water level did not fall below an average minimum of 5 to 10 cm above the soil surface. Weirs and impoundments were suggested as means of maintaining water levels. Salinity was regarded as being less important in management because higher water levels moderate salinity effects and there is no practical means of regulating salinity over large areas. Greenhouse studies indicated that 10 ppt was the upper salinity limit for best growth of *S. olneyi*, and growth was greater at 5 and 10 cm water depths than with water levels at 0, 5, and 10 cm below the soil surface.

Chabreck and Narcisse (1981) found that number and length of culms were greater when *S. olneyi* was grown at water depths of 15 and 30 cm than when grown at 45 cm or less than 15 cm. Transplant experiments with *S. olneyi* in impoundments indicated that salinity of 10 ppt and water depths of 0 to 10 cm produced good growth (Hess et al. 1975).

Although salinity and water depth are well recognized as influencing the growth of both *S. olneyi* and *S. patens*, information is lacking concerning how these factors affect dominance of the two species when growing together. Therefore, this study was conducted to determine the effects of salinity and water depth under controlled greenhouse conditions on (1) relative growth of the two species in a mixed stand, (2) chemical properties of the soil and interstitial water, and (3) mineral nutrient concentrations in the plant tissue.

METHODS

Greenhouse Experiment

The effects of salinity and water depth on growth of a mixed stand of *S. patens* and *S. olneyi* were determined in a 3 × 5 factorial greenhouse experiment with 3 flooding depths and 5 salinity levels. The experimental units were cores of marsh sod and vegetation taken on February 10, 1988 from the Pointe Au Chien Wildlife Refuge in southeastern Louisiana. Each core was 15 cm in diameter and 18 cm in depth and contained stems of *S. patens* and *S. olneyi*. Seventy cores with above-ground shoots were placed in plastic pots and transported to a greenhouse at Louisiana State University. At the time the cores were taken from the marsh, samples of interstitial water were taken (40 cm depth) from 12 points along a transect across the area. Redox potential was determined at each sampling point at depths of 1 cm and 10 cm using platinum electrodes and a calomel electrode as a reference (+244 mv was added to the meter reading and reported as Eh). Five composite soil samples were also taken from the area.

The above-ground shoots were clipped at the soil surface, and equal numbers of pots were randomly placed into five plastic tanks and submerged to maintain a water level 2.5 cm below the soil surface. Salinities of water in the tanks were 0, 5, 10, 15, and 15 ppt (g L^{-1} Instant Ocean in tap water). The solutions were changed weekly in order to adjust the interstitial water of the cores to the salinities of the water in the tanks. The highest salinity treatment was raised gradually from 15 to 20 ppt, as the water was changed, in order to minimize salt shock. During the third and fourth weeks, water was maintained at 2.5 cm above the soil surface to enhance equilibration of interstitial water with the treatment solutions.

At the end of the four-week salinity acclimation phase (immediately before depth-of-flooding treatments were imposed), the number of stems and stem lengths of each species were recorded for each pot. The two pots with the poorest regrowth of vegetation were eliminated from each tank. Interstitial water samples were also taken from each pot at a depth of 10 cm, and redox potential was measured by inserting brightened platinum electrodes to a depth of 10 cm.

The three flooding depth treatments were created by placing the pots at three different elevations within

Table 1. Properties of soil water and water from the bayou at the Pointe Au Chien marsh in February 1988 (±1 standard error; n = 12 for soil water and n = 3 for bayou water)

	Marsh	Bayou
pH	6.61 ± 0.02	7.17 ± 0.04
Salinity (ppt)	12.4 ± 0.3	3.0 ± 0.0
Eh at 1 cm (mv)	343 ± 13	–
Eh at 10 cm (mv)	−116 ± 22	–
Sulfides (mmoles L^{-1})	2.45 ± 0.12	–
Ammonium (μmoles N L^{-1})	676 ± 67	52 ± 9
Mineral elements (mmoles L^{-1})		
P	0.051 ± 0.002	0.0087 ± 0.0014
K	2.40 ± 0.11	0.49 ± 0.01
Ca	4.63 ± 0.12	1.02 ± 0.04
Mg	17.70 ± 0.48	2.21 ± 0.05
Na	152.16 ± 3.91	23.04 ± 0.97

each tank with four replications (pots) at each depth. Flooding depths were 10 cm below (−10), 10 cm above (+10), and 30 cm above (+30) the soil surface. Support for the pots was provided by similar pots containing gravel and stacked to the appropriate height. The pots were randomly placed within the tanks.

Salinity in the tanks was monitored every two to three days and water was added as needed to replace that lost by evapotranspiration. The plants grew an additional five weeks after depth treatments were imposed and were harvested on April 18. At the time of harvest, interstitial water was collected, Eh was measured, plants were clipped at the soil surface, separated by species, dried in a forced air oven, weighed, and ground in a Wiley mill to pass a #60 mesh sieve for chemical analyses as described below.

Analytical Methods

Interstitial water was sampled in the field and from pots in the greenhouse by inserting rigid plastic tubing to the desired depth and drawing a sample with a syringe with flexible tubing attached (McKee et al. 1988). An aliquot of the water was added to an antioxidant buffer for determination of sulfide concentrations (McKee et al. 1988). The remainder of the water was stored refrigerated in 250 mL plastic bottles until analyzed. The analyses performed were conductivity and salinity, pH, NH_4 (EPA method 353.2, U.S. Environmental Protection Agency, 1979), and P, K, Ca, Mg, and Na (inductively coupled plasma argon emission spectrometry).

Plant growth was measured by counting numbers of stems of each species, measuring stem length, and determining above-ground dry weight. Stem length was determined by measuring the height of individual stems (including leaves) and totaling each species in each pot.

Plant tissue was analyzed by the Department of Soil Science Analytical Service Laboratory at North Carolina State University. Carbon and nitrogen were determined with a CHN analyzer, and P, K, Ca, Mg, S, Na, and Cl by inductively coupled plasma argon emission spectrometry. Only the −10 and +10 cm treatments were included in the analyses of plant tissue because of poor growth of the plants in the +30 cm depth treatment.

Five soil samples (upper 10 cm) were taken from the marsh where the cores for the greenhouse experiments were obtained. The samples were air-dried, passed through a 2 mm sieve, and analyzed by the North Carolina Department of Agriculture Soil Testing Laboratory using the Mehlich 3 extractant. Total N and C were determined with a CHN analyzer.

Statistical Methods

Analysis of variance and regression analyses were performed on the data using the SAS statistical analysis package (SAS 1982). Significant effects were determined using the F-test at the 0.05 and 0.01 levels of probability and least significant difference (LSD).

RESULTS AND DISCUSSION

Field Observations

Results of analyses of water samples taken from the Pointe Au Chien marsh and *in situ* Eh measurements are presented in Table 1. Redox potential at the soil surface indicated moderately reduced conditions, a level at which oxygen would usually be undetectable (Patrick and Delaune 1977). The redox measurements at 10 cm below the soil surface indicated reduced conditions at which nitrogen, manganese, iron, and sulfur may be

Table 2. The effects of salinity treatments on properties of soil water and plant growth after 4 weeks (before flooding treatments were initiated) (n = 12 for each salinity treatment).

Variable	Salinity treatment (ppt) (df = 4)							
	0	5	10	15	20	F	P > F	LSD (.05)
Salinity (ppt)	4.0	6.9	11.0	14.3	17.6	471.81	0.0001	0.7
pH	6.2	5.9	6.2	6.2	6.2	8.20	0.0020	0.1
Eh at 10 cm depth (mV)	−87	−79	−107	−104	−103	0.53	0.7157	NS
Sulfide (mmoles L^{-1})	0.0043	0.0023	0.0035	0.0170	0.0259	1.19	0.3635	NS
Ammonium (μmoles N L^{-1})	13	26	13	16	14	6.80	0.0042	7.3
P (mmoles L^{-1})	0.012	0.017	0.023	0.025	0.027	20.81	0.0001	0.004
K (mmoles L^{-1})	1.04	1.57	3.24	3.65	4.08	69.11	0.0001	0.43
Ca (mmoles L^{-1})	0.87	1.84	3.60	4.50	5.41	231.50	0.0001	0.33
Mg (mmoles L^{-1})	3.2	9.8	15.0	20.4	23.1	180.64	0.0001	2.0
Na (mmoles L^{-1})	52	89	139	184	212	104.76	0.0001	24
Number of stems (per pot)								
S. olneyi	15	18	15	14	13	1.35	0.3079	NS
S. patens	24	29	20	19	23	2.92	0.0673	NS
Stem length (cm per pot)								
S. olneyi	468	529	354	314	263	4.38	0.0205	146
S. patens	558	675	493	443	518	3.19	0.0529	NS

present in the reduced form. Salinity of the interstitial water (12.4 ppt) was within the salinity range expected for this marsh type. Salinity of the bayou water, which is more directly dependent on season and rainfall, was much lower (3 ppt).

The mean organic carbon content of five soil samples taken from the marsh was 22% (approximately 44% organic matter) by weight (73.2 kg m^{-3} C on a volume basis). The organic C content and depth of the organic horizon qualifies the soil to be classified as organic (Histosol). Total N content was 1.26% by weight or 4.2 kg m^{-3}. Bulk density was 0.33 g cm^{-3}, pH in water was 4.3, and extractable P was 24.7 g m^{-3}.

Greenhouse Experiment

Four weeks after the experiment was initiated, which was at the end of the salinity acclimation phase and immediately before depth treatments were imposed, interstitial water was sampled and stem length and numbers per pot were determined (Table 2). Salinity of the interstitial water had reached levels close to that of the treatments imposed except for the O ppt treatment. Salinity treatments alone had not affected Eh or sulfide levels. Phosphorus concentration increased slightly as the salinity treatments increased, and concentrations of the cations K, Ca, Mg, and Na increased greatly. The pH was lower and ammonium concentration higher in the 5 ppt treatment.

Number of stems per pot was not affected by salinity treatment for either *S. olneyi* or *S. patens*. Stem length of *S. olneyi* was reduced by salinity treatments of 10 ppt and above, but *S. patens* stem length was not affected (Table 2).

At the end of the experiment, which was five weeks after the water-level treatments were imposed, interstitial water was again sampled in each pot and growth measurements were taken. Chemical properties of the soil water were significantly affected by the salinity and depth treatments (Table 3). The difference in salinity and associated cation concentrations due to depth of flooding was a result of evaporation from the surface of the −10 cm pots. This resulted in higher salinity and cation values in the −10 cm depth treatment for salinity treatments 5, 10, 15, and 20 ppt (Figure 1a–e). There were no significant differences in salinity due to depth at the 0 ppt treatment.

A combination of increased salinity and flooded conditions was necessary to increase sulfide concentrations (Figure 1g). At the O salinity treatment, there was no increase in sulfide due to flooding, and at the −10 cm depth treatment, there was no increase in sulfide with increasing salinity. Saturated soils were necessary for reduction of sulfate to sulfide, and the higher salinity treatments provided the source of sulfate. Values for pH increased as salinity increased (Figure 1h).

Due to drainage and aeration, the redox potential, when measured at both 1 cm and 10 cm below the soil surface, was greater in the −10 cm flooding treatment than in the +10 and +30 cm treatments, which were not significantly different (Figure 1i and j). Ammonium concentration was much higher in the +30 cm treat-

Table 3. Analysis of variance table for interstitial water properties at the end of the greenhouse experiment (n = 60).

	Salinity (df = 4)		Depth (df = 2)		Salinity × Depth (df = 8)	
	F	P > F	F	P > F	F	P > F
Salinity	404.99	0.0001	15.69	0.0001	2.30	0.0370
pH	6.70	0.0003	1.87	0.1664	1.47	0.1966
sulfide	10.04	0.0001	17.36	0.0001	3.11	0.0071
Eh (1 cm)	0.62	0.6519	87.89	0.0001	1.55	0.1680
Eh (10 cm)	2.88	0.0333	5.73	0.0061	1.74	0.1146
Ammonium	2.08	0.0993	8.63	0.0007	1.89	0.0867
P	58.54	0.0001	19.78	0.0001	0.67	0.7142
K	160.93	0.0001	6.09	0.0046	1.84	0.0940
Ca	392.88	0.0001	14.42	0.0001	2.51	0.0244
Mg	578.80	0.0001	24.95	0.0001	3.84	0.0017
Na	80.65	0.0001	7.16	0.0020	1.96	0.0743

ment, probably because poor plant growth at that depth resulted in less ammonium uptake (Figure 1k). Phosphorus concentrations increased as salinity and depth increased (Figure 1f).

Growth measurements determined at the end of the experiment were number of stems, stem length, dry weight, and the change in stem numbers and stem length from the time flooding treatments were im-

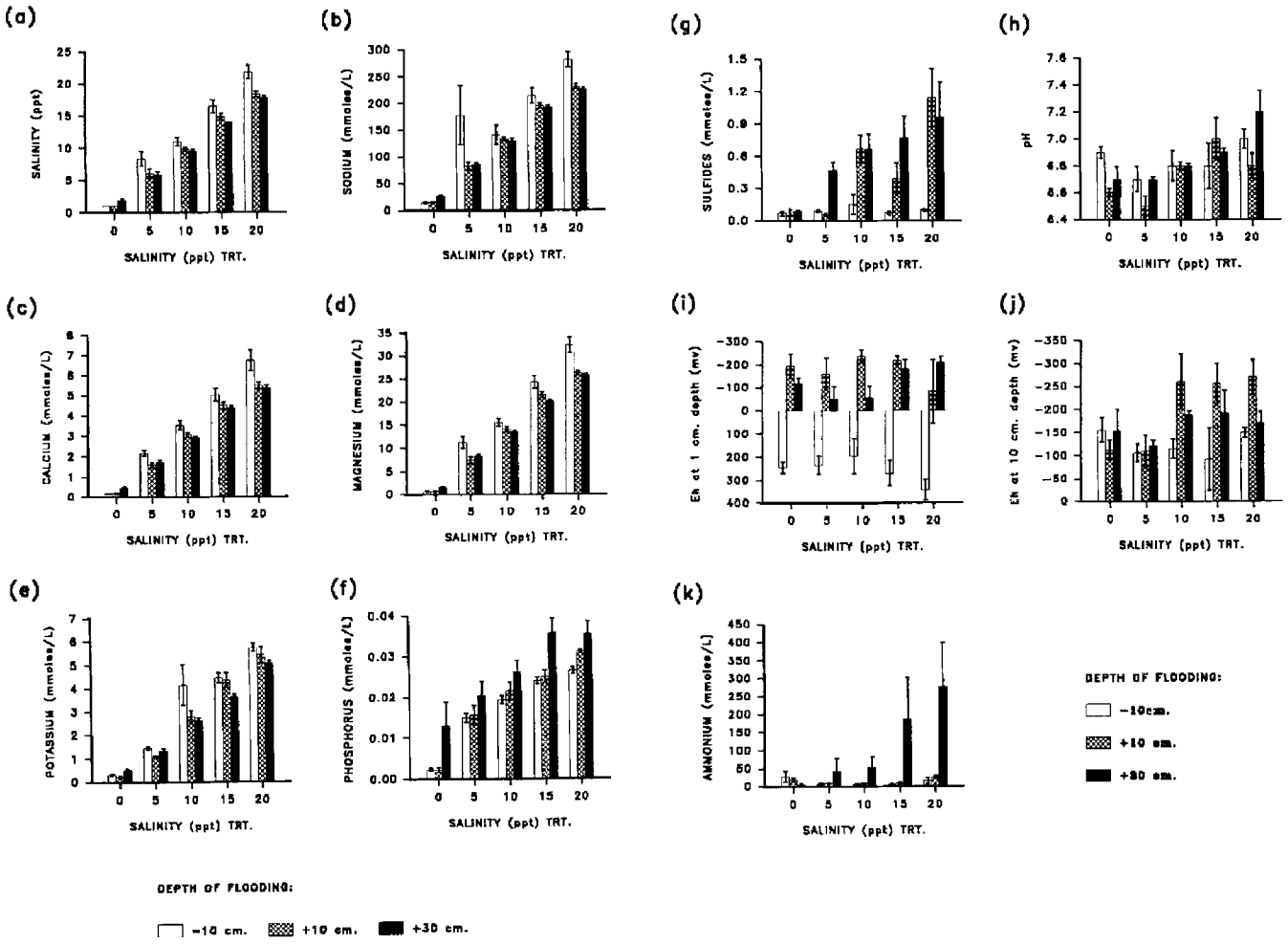

Figure 1. Effects of salinity and depth treatments on chemistry of interstitial water at the end of the experiment (± 1 standard error).

Table 4. Growth measurements of *Scirpus olneyi* and *Spartina patens* (main effect means for five salinity treatments). Means in each column followed by the same letter are not significantly different at $P < 0.05$ using the F test.

Salinity (ppt)	Dry Weight (g/pot)	No. of Stems (per pot)	Stem Length (cm/pot)	Change in No. of Stems[1] (per pot)	Change in Stem Length[1] (cm/pot)
			Scirpus olneyi (n = 12)		
0	5.4 AB	28 AB	1445 AB	13 A	978 AB
5	6.5 A	35 A	1640 A	17 A	1112 A
10	3.8 B	27 AB	1080 B	13 A	726 B
15	2.1 C	21 BC	661 C	7 B	346 C
20	1.3 C	16 C	444 C	3 B	181 C
F	13.83	4.92	12.07	10.34	16.05
P > F	0.0001	0.0022	0.0001	0.0001	0.0384
LSD (0.05)	1.7	10	415	5	284
			Spartina patens (n = 12)		
0	2.7 A	23 A	805 A	0 A	247 A
5	2.8 A	23 A	785 A	−6 B	111 B
10	2.4 A	19 A	599 AB	−1 A	106 B
15	1.9 A	16 A	485 B	−2 AB	42 B
20	1.8 A	18 A	510 B	−5 B	−8 B
F	2.21	1.21	3.54	3.04	4.56
P > F	0.0826	0.3191	0.0135	0.0266	0.0035
LSD (0.05)	NS	NS	228	4	128

[1] Change during the five-week period when depth treatments were imposed.

posed. There were significant differences between the response of the two plant species to the salinity and depth treatments. Analyses of variance of the growth measurements by species revealed no significant salinity × depth interactions, indicating that the treatment effects were independent; therefore, main effect means were used to interpret results (Tables 4 and 5).

Growth of both species decreased as salinity increased, but the effects were more pronounced for *S. olneyi* than *S. patens*. There was little difference in growth of *S. olneyi* between the 0, 5, and 10 ppt treatments but a general decline above 10 ppt (Table 4). Ross and Chabrek (1972) also reported that 10 ppt was the upper limit for best growth of *S. olneyi*.

Table 5. Growth measurements of *Scirpus olneyi* and *Spartina patens* (main effect means for three water depths). Means in each column followed by the same letter are not significantly different at $P < 0.05$ using the F-test.

Flooding Depth[1] (cm)	Dry Weigth (g/pot)	No. of Stems (per pot)	Stem Length (cm/pot)	Change in No. of Stems[2] (per pot)	Change in Stem Length[2] (cm/pot)
			Scirpus olneyi (n = 20)		
+30	3.2 B	21 A	982 A	6 B	575 B
+10	4.7 A	28 A	1220 A	14 A	835 A
−10	3.5 AB	27 A	959 A	12 A	595 B
F	3.14	1.91	1.64	9.85	3.51
P > F	0.0529	0.1593	0.2054	0.003	0.0384
LSD (0.05)	1.3	NS	NS	4	220
			Spartina patens (n = 20)		
+30	0.9 B	12 C	383 C	−10 C	−142 C
+10	2.8 A	19 B	640 B	−3 B	126 B
−10	3.2 A	29 A	888 A	4 A	314 A
F	24.79	17.24	16.54	35.31	43.24
P > F	0.0001	0.0001	0.0001	0.0001	0.0001
LSD (0.05)	0.7	6	177	4	99

[1] Depth of water above (+) or below (−) the soil surface.
[2] Change during the five-week period when depth treatments were imposed.

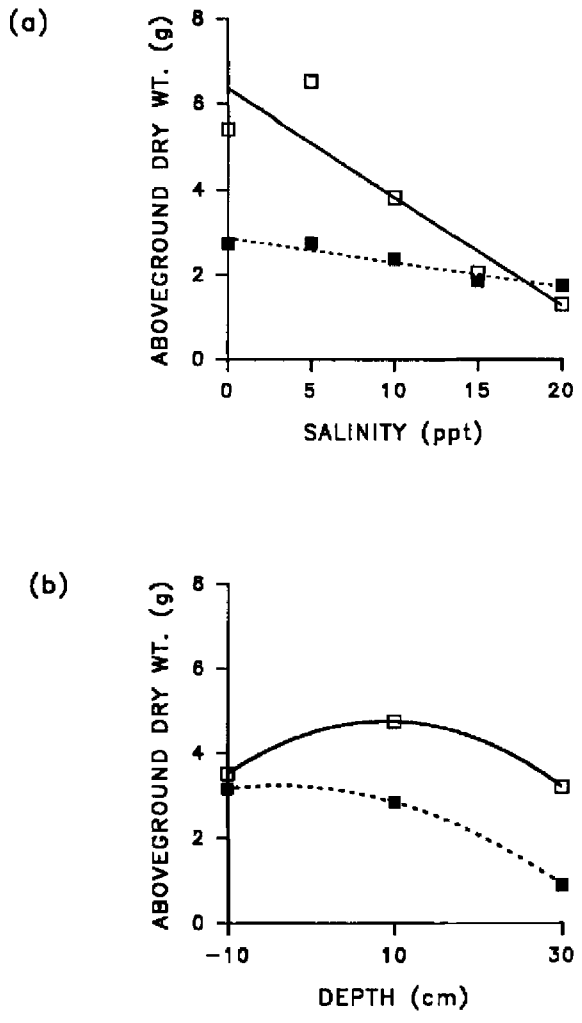

Figure 2. The effects of salinity (a) and flooding depth (b) on dry weight of *Scirpus olneyi* and *Spartina patens*. *Spartina patens* dry weight (grams per pot) = 3.78 − 0.0571 salinity − 0.0157 depth − 0.00204 depth^2 (R^2 = 0.52). *Scirpus olneyi* dry weight (grams per pot) = 7.00 − 0.253 sal. + 0.0608 depth − 0.00343 depth^2 (R^2 = 0.45).

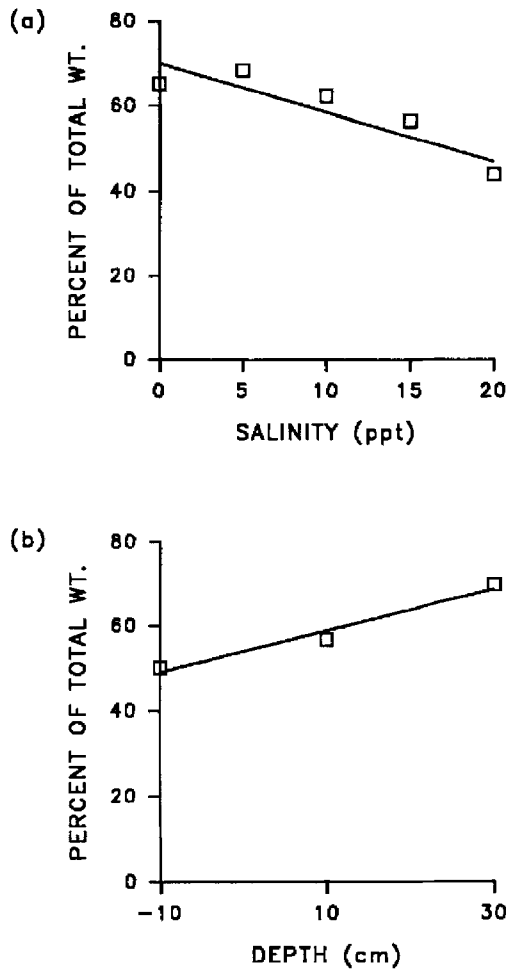

Figure 3. The effect of salinity (a) and depth (b) on the percentage of the total weight that is made up of *S. olneyi*. *Scirpus olneyi* (% of total weight) = 65.2 − 1.11 sal. + 0.488 depth (R^2 = 0.25).

There were no significant differences in dry weight and number of stems of *S. patens* due to salinity, although there was a gradual decrease as salinity increased. However, growth of *S. patens* as measured by stem length and change in stem length was significantly reduced as salinity increased (Table 4). Similar results were reported by Mendelsohn and McKee (1992), who found a decrease in rate of leaf elongation of *S. patens* grown in salinities greater than 12 ppt.

Increased flooding depth had a greater negative effect on growth of *S. patens* than *S. olneyi* (Table 5). Optimum growth of *S. olneyi* occurred at +10 cm, while the −10 and +30 cm depths produced nearly equal growth. There was no difference in dry weight of *S. patens* at the −10 and +10 cm depths, but the other four growth measurements indicated that growth was significantly better at −10 cm, the treatment with the best drainage. *Spartina patens* barely survived at the +30 cm depth. These results are consistent with other research results that reported good growth of *S. olneyi* at water depths of 15 and 30-cm (Chabreck and Narcisse 1981) and a limited tolerance of *S. patens* to excessive waterlogging (Naidoo et al. 1992).

Regression analyses of the growth measurements also indicated significant differences in response of the two species to the salinity and flooding depth treatments. Since the growth measurements were highly correlated, only the graphs of dry weight are presented. Aboveground dry weight of each species decreased linearly as salinity increased; however, the slope for *S. olneyi* was much steeper, indicating a more drastic effect of increasing salinity (Figure 2a). Increased flooding depth

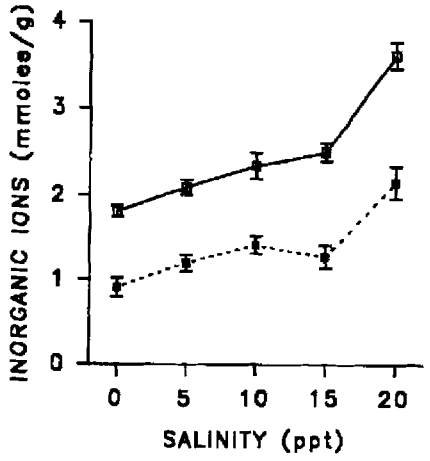

Figure 4. The effect of salinity on total inorganic ion concentration ($Na^+ + K^+ + Mg^{2+} + Ca^{2+} + Cl^-$) in the plant tissue (± 1 standard error).

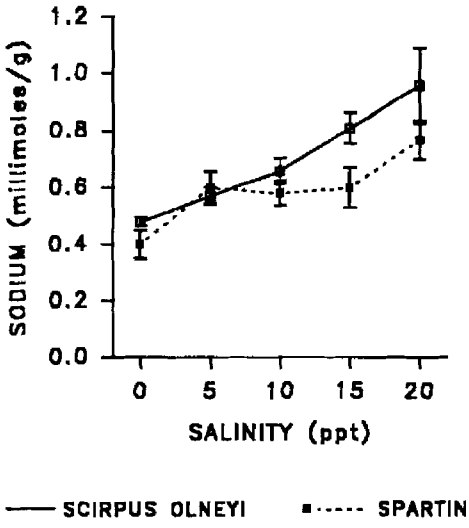

Figure 5. The effect of salinity on Na^+ concentration in the plant tissue of *S. olneyi* and *S. patens* (± 1 standard error).

had a greater negative effect on aboveground dry weight of *S. patens* than *S. olneyi* (Figure 2b). Optimum growth of *S. olneyi* was at the +10 cm flooding depth, while optimum growth of *S. patens* occurred at −10 cm.

The percentage of the total dry weight of aboveground plant material made up of *S. olneyi* is shown in figures 3a and 3b. As the salinity increased, the percentage of *S. olneyi* decreased, and as the flooding depth increased, the percentage of *S. olneyi* increased.

Mineral Ion Concentrations in the Plant Tissue

Concentrations of inorganic ions ($Na^+ + K^+ + Mg^{2+} + Ca^{2+} + Cl^-$) per gram of dry weight increased with salinity and were greater in *S. olneyi* than in *S. patens* (Figure 4). The higher concentration of ions in *S. olneyi* may be related to the more succulent nature of the plant and possibly differences in physiological mechanisms for coping with salinity stress. Ion accumulation could be the dominant salt-tolerance mechanism for *S. olneyi*. Osmotic adjustment by halophytes may occur as a result of ion uptake, synthesis of organic solutes, or both (Naidoo and Rughunanan 1990). Inorganic ions accounted for 6 to 11 percent of the dry weight of *S. olneyi* and 2 to 5 percent of the dry weight of *S. patens*. The increase in inorganic ions as a percentage of dry weight was greatest for both species between the 15 and 20 ppt treatments.

Sodium concentrations in the two species were similar at 0, 5, and 10 ppt but were greater in *S. olneyi* at 15 and 20 ppt (Figure 5 and Table 6). Concentrations of Na in *S. patens* were equal at the 5, 10, and 15 ppt treatments but increased at 20 ppt (Table 7). This is an indication that *S. patens* was able to regulate Na concentrations in the 5–15 ppt range by exclusion and/or excretion. Salt glands are present on the leaves of *S. patens* (Ungar 1991), and salt crystals were visible on the leaves throughout the study. Sodium accounted for 60 to 65 percent of the total cations in *S. patens* even at the lower salinity treatments (Figure 6), perhaps indicating that Na is the principal ion involved in osmoregulation for the species. Sodium accounted for 40% of the total inorganic ions in *S. olneyi* at the 0, 5, and 10 ppt treatments and increased at 15 and 20 ppt.

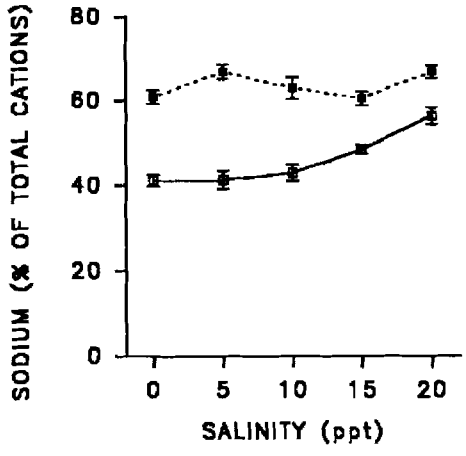

Figure 6. The effect of salinity on the percentage of total cations in the plant tissue that is made up of Na^+ (molar basis) (± 1 standard error).

Table 6. Mineral nutrient concentration in plant tissue of *S. olneyi* (mmoles g^{-1}). Main effect means for salinity and depth of flooding. Means in each column followed by the same letter are not significantly different at $P < 0.05$ using the F test.

	C	N	P	K	Ca	Mg	S	Na	Cl
Salinity (ppt) (n = 8)									
0	32.4 A	0.80 C	0.040 A	0.530 A	0.062 B	0.103 C	0.199 C	0.480 C	0.628 D
5	32.3 A	0.86 BC	0.043 A	0.593 A	0.069 B	0.150 BC	0.267 BC	0.566 C	0.724 CD
10	31.5 AB	0.90 AB	0.049 A	0.585 A	0.090 A	0.210 A	0.350 A	0.657 BC	0.809 C
15	29.7 BC	0.98 A	0.043 A	0.586 A	0.072 B	0.193 AB	0.341 AB	0.808 AB	0.918 B
20	28.1 C	0.93 AB	0.038 A	0.487 A	0.069 B	0.209 A	0.320 AB	0.959 A	1.291 A
Depth (cm) (n = 20)									
−10	30.3 A	0.93 A	0.040 A	0.598 A	0.082 A	0.204 A	0.320 A	0.721 A	0.890 A
+10	31.2 A	0.86 B	0.045 A	0.515 A	0.064 B	0.143 B	0.270 B	0.663 A	0.731 B

Summary of analysis of variance

Source	df		C	N	P	K	Ca	Mg	S	Na	Cl
Sal	4	F	7.53	5.43	1.49	0.96	4.05	7.85	5.63	7.18	29.74
		P > F	0.0003	0.0021	0.2305	0.4462	0.0099	0.0002	0.0018	0.0004	0.0001
Depth	1	F	2.07	7.88	2.61	3.88	14.86	17.59	4.84	0.99	19.14
		P > F	0.1601	0.0087	0.1173	0.0586	0.0006	0.00020	0.0360	0.3291	0.0002
Sal × Depth	4	F	0.33	3.02	0.40	0.75	1.22	0.93	1.36	0.47	2.72
		P > F	0.8581	0.0332	0.8049	0.5679	0.3329	0.4602	0.2734	0.7566	0.0546

Potassium concentrations were about three times greater in *S. olneyi* than *S. patens* (Tables 6 and 7), possibly indicating that K has a greater role in maintaining osmotic potential in *S. olneyi*. Concentrations of K were greater than Na in *S. olneyi* at the 0 and 5 ppt salinity level, while Na concentrations were higher than K in *S. patens*. There was a significant increase in Na concentrations in *S. olneyi* and *S. patens* as salinity treatment increased but no change in K (Tables 6 and 7). Possibly, *S. olneyi* was able to selectively take up and accumulate K at lower salinity levels but not above 5 ppt because of interference by Na. The higher K concentrations in *S. olneyi* resulted in higher K-to-Na ratios as compared to *S. patens*.

Table 7. Mineral nutrient concentration in plant tissue of *S. patens* (mmoles g^{-1}). Main effect means for salinity and depth of flooding. Means in each column followed by the same letter are not significantly different at $P < 0.05$ using the F test.

	C	N	P	K	Ca	Mg	S	Na	Cl
Salinity (ppt) (n = 8)									
0	35.0 A	0.728 A	0.032 A	0.157 A	0.045 B	0.044 C	0.048 C	0.396 C	0.250 C
5	34.8 A	0.673 A	0.036 A	0.173 A	0.045 B	0.068 B	0.068 C	0.600 B	0.398 B
10	34.4 AB	0.731 A	0.039 A	0.172 A	0.065 A	0.104 A	0.130 B	0.576 B	0.417 B
15	33.3 BC	0.710 A	0.038 A	0.195 A	0.067 A	0.121 A	0.156 AB	0.598 B	0.481 B
20	32.1 C	0.704 A	0.029 A	0.180 A	0.079 A	0.111 A	0.171 A	0.774 A	0.840 A
Depth (cm) (n = 20)									
−10	33.3 B	0.705 A	0.036 A	0.191 A	0.066 A	0.115 A	0.106 A	0.676 A	0.561 A
+10	34.5 A	0.713 A	0.033 A	0.158 B	0.053 B	0.060 B	0.102 A	0.499 B	0.370 B

Summary of analysis of variance

Source	df		C	N	P	K	Ca	Mg	S	Na	Cl
Sal	4	F	6.865	0.39	2.65	0.87	6.80	17.68	27.62	8.21	27.61
		P > F	0.0005	0.8121	0.0552	0.4950	0.0006	0.0001	0.0001	0.0002	0.0001
Depth	1	F	8.28	0.06	1.23	6.96	6.44	64.52	2.06	17.54	40.20
		P > F	0.0073	0.8152	0.2767	0.0137	0.0173	0.0001	0.1629	0.0003	0.0001
Sal × Depth	4	F	0.69	1.01	1.72	0.84	4.95	2.40	5.71	1.00	1.50
		P > F	0.6017	0.4154	0.1740	0.5130	0.0040	0.0752	0.0018	0.4259	0.2433

SUMMARY AND CONCLUSIONS

Increasing salinity above 10 ppt resulted in reduced growth of both *S. olneyi* and *S. patens,* but *S. olneyi* was more drastically affected. Apparently *S. patens* is able to tolerate higher Na concentrations in the soil water by exclusion and/or excretion. Conversely, increased flooding depth reduced growth of *S. patens* more than *S. olneyi.* Growth of *S. patens* was best with the water level 10 cm below the surface slightly reduced with the water level at 10 cm above the surface and very poor at the 30-cm depth. There was very little difference in growth of *S. olneyi* among the three flooding depths.

Ion accumulation is apparently the principal salt tolerance mechanism of *S. olneyi. Spartina patens* seems to regulate Na concentrations in the 5 to 15 ppt range by exclusion and excretion.

Extrapolated to field conditions, implications are that relative growth of the two species in mixed stands is altered by changes in salinity and flooding depth. Increasing salinity reduces growth of both species but favors greater productivity of *S. patens* relative to *S. olneyi.* Hydrologic changes that result in increased depth of flooding without increasing salinity favor *S. olneyi.*

These results have important management implications. Marsh management procedures that affect hydroperiod and salinity are likely to change the relative dominance of these species in Louisiana brackish marshes. If management results in greater water depths, *S. olneyi* should dominate. If, however, higher salinities result from the marsh management practice, *S. patens* will likely gain dominance. Structural marsh management (Cahoon and Groat 1990), a popular management tool that uses weirs, adjustable water-control structures, and levees to directly manipulate water levels and flows, is designed to stabilize water levels and to retard salt-water intrusion. If successful, these conditions of low salinity and more stable water levels should favor the dominance of *S. olneyi.* However, if this management does not perform as expected, species composition could be altered. Extreme conditions of high salinity and water level may occur during hurricane events when salt water is pushed into management areas but may not quickly recede due to levees and constricted outfall. The combined salinity and water-level stress may exceed the tolerance limit of these two species, resulting in a drastic change in species composition and productivity (Meeder 1987).

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