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Macronutrient status of tall and short forms of *Spartina alterniflora* in a South Carolina salt marsh

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ABSTRACT: Macronutrient concentration in shoot (all aboveground live biomass) and root (all belowground live biomass) tissues of tall (TS) and short *Spartina alterniflora* (SS) were measured monthly in North Inlet Estuary, Winyah Bay, South Carolina, USA. Seasonal changes in shoot N, P, and S concentrations occurred both in TS and SS, while root macronutrient concentrations remained constant throughout the seasons (seasonal root data not presented). Macronutrient concentrations between the 2 forms of *S. alterniflora* also differed. Concentrations of N (as NH_4^+) were greater in the shoots and roots of TS than in SS. Sulfur, however, was greater in SS shoots and roots than in TS. Interstitial waters at the SS site had lower Fe and redox potentials than the TS site. These conditions would result in higher sulfide levels which also decrease plant production. We suggest that decreased growth occurred when S was above the critical concentrations of 0.5 % in shoots and 1.0 % in roots. Our data support the hypothesis that differences in the nutritional status between TS and SS may account for the height and biomass differences between the 2 populations.

INTRODUCTION

Researchers recognize 2 or 3 growth forms of *Spartina alterniflora* Loisel. The tall form (about 1.5 m) is found along estuarine creeks and the short form (about 0.5 m) in high marsh, upland areas. An intermediate form may be found between these 2 sites. Evidence indicates that these height forms are ecophenes and that environmental differences are responsible for the *Spartina* marsh zonation (Shea et al. 1975, Anderson & Treshow 1980). Short-term research results indicate environmental factors that can influence *S. alterniflora* height and production include salinity (Miller & Egler 1950, Adams 1963, Phleger 1971, Chalmers 1979, Giurgevich & Dunn 1979, Anderson & Treshow 1980, Linthurst & Seneca 1981, Gosselink 1984); nitrogen (Broome et al. 1975, Eley et al. 1975, Chalmers 1979, Giurgevich & Dunn 1979, Anderson & Treshow 1980, Gallagher et al. 1980, DeLaune et al. 1981, Linthurst & Seneca 1981, Gosselink 1984, Hopkinson & Schubauer 1984, Smith 1984, Valiela 1984, Wolaver & Zieman 1984); and sulfur and/or redox potential (Howarth & Teal 1979, Linthurst 1979, Howes et al. 1981, Carlson & Forest 1982, King et al. 1982, DeLaune et al. 1983, Giblin & Howarth 1984). These and other short-term field studies show that factors which affect *S. alterniflora* growth are many and complex, making a comprehensive predictive model for *Spartina* saltmarsh production difficult and as yet undeveloped.

We tested the hypothesis that differences in the nutritional status of tall *Spartina alterniflora* (TS) and short *S. alterniflora* (SS) could account for the growth differences between the 2 populations. Biomass, height, and density of both forms were quantified by Dame & Kenny (1986) for the study site at North Inlet Estuary, Winyah Bay, South Carolina, USA. We took samples from that study for analysis of nutrient contents. Although previously cited studies have reported on selected macronutrients, this study reports the complete macronutrient status of the shoots for 46 mo and roots for 15 mo in both forms in a relatively pristine saltmarsh.

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METHODS

The North Inlet saltmarsh and estuary covers ca 32 km^2 near Georgetown, South Carolina, USA. *Spartina alterniflora* exists in this area in near-monoculture stands and can be found as the tall form on the creek banks and as the short form near the uplands. On average, the marsh is covered by water 30 % of the time (Kjerfve et al. 1982) and has a yearly-average salinity of 34.6 ppt. A more detailed description of our research area is given by Dame & Kenny (1986).

Tall *Spartina alterniflora* plants were collected from a site along the edges of Bread and Butter Creek (3 m from the creek edge). Short *S. alterniflora* plants were collected from a site ca 1 km inland from the TS site at the upper reaches of Bly Creek. Both sites were sufficiently large to ensure that less than 10 % of the total area would be cut during 5 yr of monthly sampling.

Biomass and macronutrient concentrations in shoots (leaf and stem) were determined monthly from June 1981 through March 1985. Shoot biomass, density and plant height measurements were determined from 0.25 m^2 plots. The TS measurements were replicated monthly using 10 plots and the SS measurements were replicated using 5 plots, which provided mean estimates with coefficients of variability of less than 20 %. Generally 3 of the replicate plots were randomly selected each month for nutrient analyses. Live and dead material was separated and chemical analyses of live material only are reported here.

Root tissue samples were collected monthly from July 1983 to September 1984. Biomass and density measurements were determined from 0.25 m^2 plots. Statistical analysis indicated that 8 cores from the TS site and 12 cores from the SS site were necessary to obtain variability of 20 % or less. Cores containing root and rhizome material were taken from the plots harvested for root biomass. Each core was 10.2 cm in diameter and 40 cm deep. Core samples were washed to remove soil. Live and dead root tissues were separated. Generally 3 of the replicated plots were randomly selected each month for nutrient analyses.

Subsamples were ground to pass a 40-mesh (354 µm) screen and analyzed for the macronutrients nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S). N was determined by the Kjeldahl method and P by the ascorbic acid method (Council on Soil Testing and Plant Analysis 1980). The elements K, Ca, and Mg were determined by atomic absorption spectrophotometry (Council on Soil Testing and Plant Analysis 1980). Sulfur was determined by the turbidimetric (Butters & Chenery 1959) or the Leco combustion methods (Council on Soil Testing and Plant Analysis 1980). The turbidimetric and Leco methods of determining S have been found to be comparable (Jones & Isaac 1972).

Soil samples were collected 4 times in both the tall and short *Spartina alterniflora* sites (November 1981, February 1982, May 1982, and August 1982). Samples were collected at 2.5 cm interval depths from the surface to a depth of 27.5 cm. Means of selected chemical parameters were calculated by combining depths 0 to 7.5, 10 to 17.5, and 20 to 27.5 cm (Table 4). Redox potential (Eh) measurements were made with 5 mm platinum electrodes and a Corning model 130 meter (Corning Instrument Company, Corning, New York, USA). The electrodes were inserted into sealed chambers taken from appropriate depths and allowed to equilibrate for 3 h before a reading was recorded. Sulfide was determined using the method described by DeLaune et al. (1983). Samples were centrifuged to remove interstitial water and the supernatant was filtered through a 0.45 µm filter, acidified, and stored frozen until analyzed. Samples were analyzed for K, Ca, Mg, and Fe by atomic absorption spectrophotometry (AAS). Orthophosphate (Murphy & Riley 1962) and ammonia (O'Brien & Fiore 1962) were analyzed with the use of an Autoanalyzer II system (Technicon Instrument Company, Terrytown, New York, USA), while total dissolved phosphorus (TDP), and total dissolved nitrogen (TDN) were determined by a modified Kjeldhal digest procedure and a Technicon block digestor (Kammerer et al. 1967).

Data were analyzed by the general linear model procedure in the SAS computer program (SAS 1985). Mean separation was conducted using Duncan's New Multiple Range Test and Pearson's correlation coefficients were used to estimate goodness of fit within simple regression analysis.

RESULTS AND DISCUSSION

Spartina alterniflora tissues were selected randomly from the samples collected by Dame & Kenny (1986) in North Inlet and analyzed chemically for the mineral nutrient contents. The monthly aboveground biomass and height were significantly greater in TS than in SS throughout each year (Table 1; Fig. 1). Plant density, however, was greater in SS than in TS throughout each year. Belowground biomass at North Inlet estuary was higher in SS than in TS. Over a 15 mo period, 96.2 % of the biomass of SS was roots and rhizomes, compared to 83.9 % for TS.

Nitrogen

Shoot N concentrations of both TS and SS followed similar seasonal patterns (Fig. 2). Live shoot tissue N concentrations began to increase in December (2 mo after shoot lengths and biomass had peaked) and

Table 1. *Spartina alterniflora*. Yearly means of tall (TS) or short (SS) form shoot or root macronutrient concentrations, biomass, density, and plant heights. Values in a row followed by the same letter are not significantly different ($p < 0.05$, Duncan's Multiple Range Test). Shoot data represent means from 46 mo of data; $n \geqq 120$. Root data represent means from 15 mo of data; $n \geqq 34$. Growth parameter data from Dame & Kenny (pers. comm.)

Nutrient	Shoot		Root	
	TS	SS	TS	SS
N (%)	1.32a	1.20b	0.62a	0.56b
P (%)	0.19a	0.16a	0.14a	0.08a
K (%)	1.23a	1.29a	0.622	0.36b
Ca (%)	0.26a	0.22a	0.11a	0.12a
Mg (%)	0.35a	0.35a	0.32a	0.30a
S (%)	0.32b	0.81a	0.89b	1.21a
Biomass (g m^{-2})	439.1a	150.1b	2282.8b	3791.6a
Density (plants m^{-2})	113b	741a	–	–
Plant height (cm)	105.0a	29.3b	–	–

reached a maximum in February of 1.87 % in TS and 1.59 % in SS. From February, shoot N concentrations decreased to the lowest values of the year (about 0.98 % N in TS; 1.00 % N in SS) during the period July through November. This apparent decrease in N occurred primarily because of a dilution of tissue N as the aerial biomass of the TS and SS increased during this same period (Fig. 1). During the active spring growing period, stem N was utilized and diluted by increasing plant biomass, which resulted in the lower fall tissue concentrations of N (Fig. 2). The dilution effect was further evidenced by the negative correlation coefficients observed between N concentration and plant length or biomass (Table 2). In their model predicting yield of *Spartina alterniflora*, Woodhouse et al. (1974) obtained a positive correlation between yield and tissue N content in June, while at the end of September the correlation was negative. They reasoned that high concentrations of N in winter were indicative of high growth potential while at maturity (September) N concentrations were lowest in plants that had achieved the greatest growth and hence the greatest amount of N dilution.

Stem N concentrations in both *Spartina alterniflora* forms from North Inlet were in the range of values reported by other investigators (Table 3) and were above the critical concentrations of 0.7 % (below which would limit growth) experimentally derived by Smart & Barko (1980). Based on Smart & Barko's results, N in North Inlet did not appear to be limiting.

Researchers have reported increased SS growth with N fertilization. Gallagher (1975) observed a rapid growth response when N (as ammonium nitrate) was applied to SS plots, but no response in TS plots. The author inferred from this that SS plants were N deficient. Others also have demonstrated increased growth following N fertilization (Sullivan & Daiber 1974, Valiela & Teal 1974, Broome et al. 1975, Valiela et al. 1975, 1976, Mendelssohn 1979b). However, Morris (1980) showed that N uptake in SS should not be limited by NO_3 availability since the affinity constant for NO_3 (K_s) is lower than ambient NO_3 concentrations. The enhanced plant growth noted after N fertilization by the above researchers may be a secondary response after an unknown limiting factor was amended. Nitrogen fertilization may have overcome the effect of sulfide toxicity or high salinity, which may have been limiting growth. For example, Shea et al. (1975) were able to alleviate both temperature and salinity stress in *Spartina alterniflora* by applying additional N. Stevenson (1982) reported that N additions to an anaerobic marsh soil may generate a variety of responses including changes in microbial activity, microbial populations, redox potential, acidity, and specific ion concentrations.

Monthly root N concentrations did not fluctuate significantly throughout the year (root concentrations not presented). However, the 15 mo average root N concentration of TS was significantly greater ($p < 0.05$, $n = 41$) than SS (Table 1).

Phosphorus

The pattern of monthly fluctuations of shoot P concentrations closely paralleled those of shoot N concentrations (Fig. 2). The Pearson's correlation coefficients between shoot P and N for TS and SS were 0.93 and 0.76 (both $p < 0.001$, $n = 128$), respectively. Gallagher et al. (1980) reported P concentrations were greater in SS than TS during the growing season. In winter, however, they found that P concentrations of TS were equal to or above those in SS. In North Inlet we found no statistically significant ($p > 0.05$) differences between TS and SS in either shoot or root P concentrations over the study periods

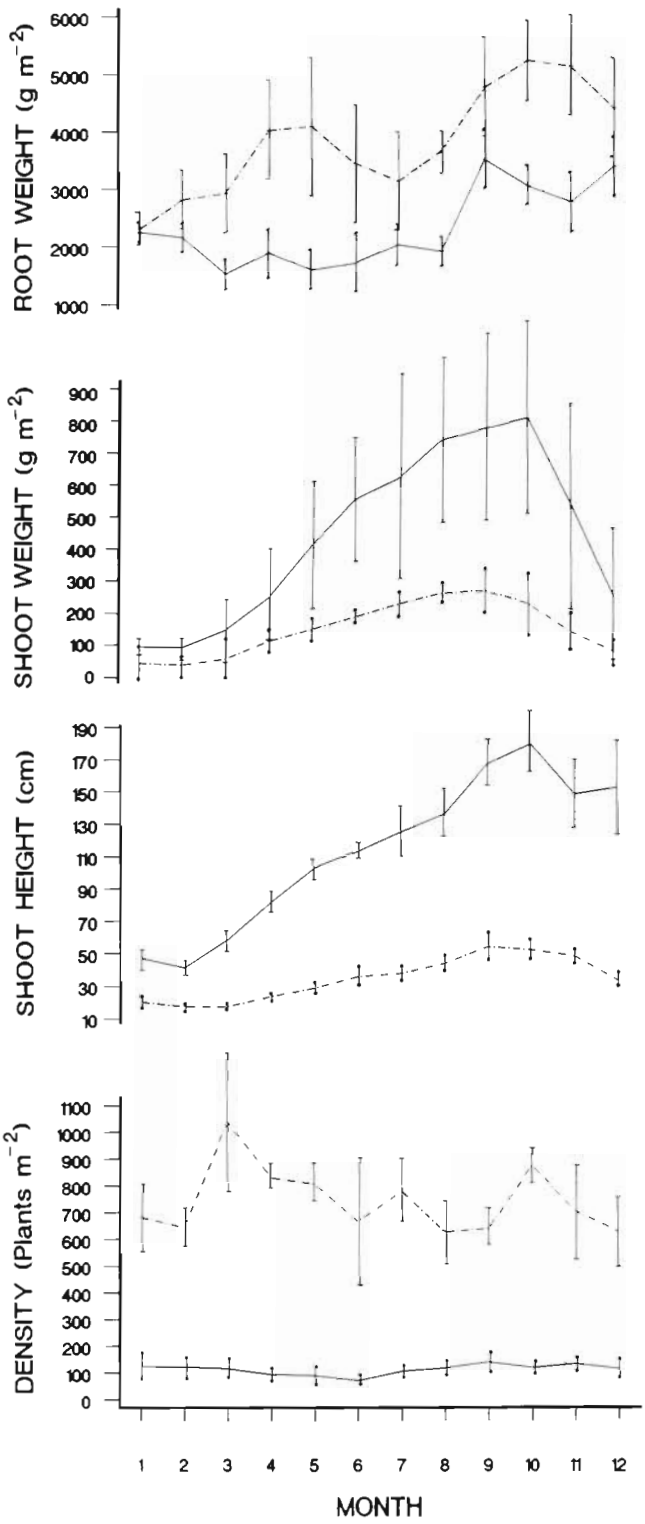

Fig. 1. *Spartina alterniflora*. Monthly means and standard deviations of root weight, shoot weight, shoot height, and plant density for tall (solid line) and short (broken line) forms. Data supplied by R. Dame (pers. comm.). Root weight means with standard deviations calculated from 8 samples TS and 12 samples SS each month

(Table 1). Therefore, P was probably not a limiting factor in our study. Whitney et al. (1981) reported that P is seldom limiting in salt marshes and Patrick & DeLaune (1976) found that P additions did not affect plant growth. Furthermore, through a greenhouse study conducted by Smart & Barko (1980), the critical concentration of P was calculated to be 0.44 mg P kg^{-1}. All the shoot and root P concentrations from North Inlet were well above this critical concentration and within the range reported by other investigators (Table 3).

Potassium, calcium and magnesium

There were no significant differences between TS and SS shoot concentrations of K, Ca and Mg (Table 1). The similarity of their seasonal dynamics in shoots of TS and SS is shown in Fig. 2. Unlike the dramatic seasonal changes observed for N and P, the concentrations of K, Ca, and Mg did not change significantly over time. Shoot length and biomass of SS were positively correlated to Ca and Mg concentrations (Table 2). This suggests that Ca and Mg may be limiting to SS, however such correlations do not prove a cause and effect relationship.

Root concentrations of Ca and Mg were generally similar in the TS and SS except that K was significantly greater in TS than in SS ($p < 0.05$, $n = 41$) (Table 1).

Sulfur

Monthly and yearly means of shoot S concentrations were significantly ($p < 0.05$) greater in SS than in TS (Table 1; Fig. 2). Short *Spartina alterniflora* shoot S concentrations averaged 0.81 % and TS averaged 0.32 % ($p < 0.001$, $n = 152$) (Table 1). Root S concentrations averaged 1.21 % in SS and 0.89 % in TS ($p < 0.001$, $n = 36$) (Table 1). The ratio of root S concentration to shoot S concentration in SS was 1.5:1. The significantly lower ratio (2.8:1) found in TS indicates that a greater proportion of S was being transported to the shoots in SS than was being transported to shoots in TS (Table 1; Fig. 2). Other researchers have found that S concentrations in aerial portions of *S. alterniflora* were negatively correlated with growth (Broome et al. 1975, Linthurst 1979).

Further examination of the data suggested that there were critical concentrations of S above which only SS occurred (Fig. 3). For shoot biomass, shoot height, and plant density, the critical shoot S concentration was estimated to be about 0.50 % (Fig. 3). For root weight, the critical root S concentration was 1.0 % S.

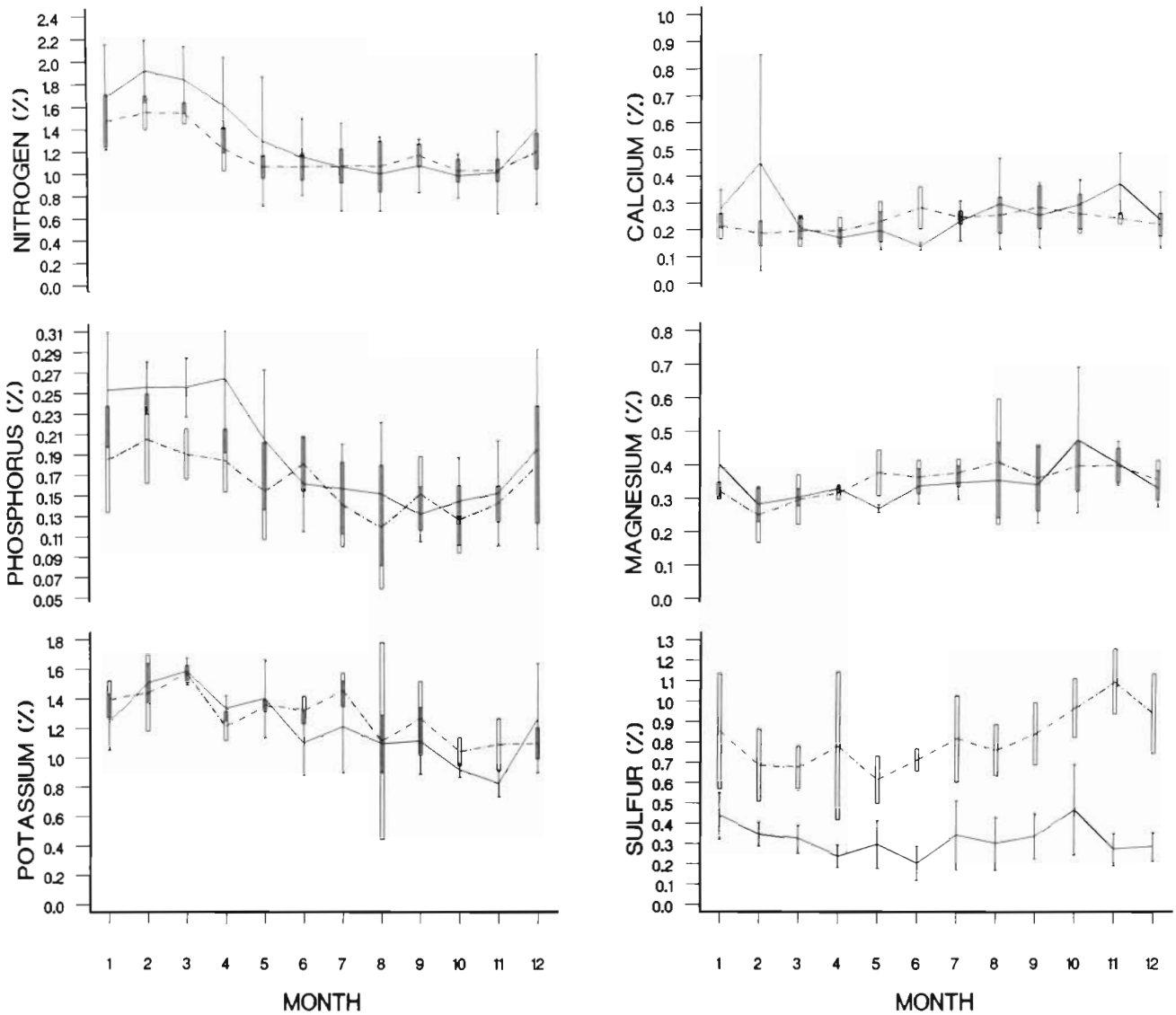

Fig. 2. *Spartina alterniflora*. Monthly means and standard deviations of shoot tissue concentrations (% dry wt) of N, P, K, Ca, Mg, and S for tall (solid line) and short (broken line) forms

Table 2. *Spartina alterniflora*. Pearson's correlation coefficients (r) between shoot and root macronutrient concentrations and shoot and root growth parameters. TS: tall form; SS: short form

	Shoot						Root	
	TS			SS			TS	SS
	Length (cm)	Biomass (g m^{-2})	Density (plants m^{-2})	Length (cm)	Biomass (g m^{-2})	Density (plants m^{-2})	Biomass (g m^{-2})	Biomass (g m^{-2})
N (%)	−0.89•••	−0.93•••	NS	−0.76••	NS	NS	0.57•	NS
P (%)	−0.91•••	−0.94•••	NS	−0.82•••	−0.85•••	NS	NS	NS
K (%)	−0.76••	−0.74••	NS	−0.66••	NS	NS	NS	NS
Ca (%)	NS	NS	0.65•	0.82•••	0.86•••	NS	−0.57•	NS
Mg (%)	NS	NS	NS	0.82•••	0.78••	NS	−0.57•	NS
S (%)	NS	NS	NS	0.58•	NS	NS	NS	NS

• $p<0.05$; •• $p<0.01$; ••• $p<0.001$; NS: not significant; $n = 12$

Table 3. *Spartina alterniflora*. Reported macronutrient concentrations (%) for shoot tissues. TS: tall form; SS: short form

Source	N		P		K		Ca		Mg		S	
	TS	SS	TS	SS	TS	SS	TS	SS	TS	SS	TS	SS
This study	1.32	1.20	0.19	0.16	1.23	1.29	0.26	0.22	0.35	0.35	0.32	0.81
Linthurst & Seneca (1981)	1.07	1.20	0.20	0.18	1.28	1.16	0.30	0.26	0.35	0.40	0.35	0.46
Broome et al. (1986)	0.7		0.09		0.78		0.25		0.46		0.50	
Gallagher et al. (1980)	1.0	0.80	0.17	0.17	1.0	1.0	0.15	0.15	0.33	0.33	–	–
Carlson & Forrest (1982)	–	–	–	–	–	–	–	–	–	–	0.13	
Mendelssohn (1979b)	1.69	1.53	–	–	–	–	–	–	–	–	–	–
Linthurst (1979)[a]	0.78–0.88		0.11–0.12		1.02–1.43		0.15–0.30		0.24–0.30		0.21–0.49	
Broome et al. (1975)[a]	0.76–1.10		0.09		0.80–1.00		0.20–0.30		0.40–0.46		0.68–0.84	
Gallagher (1975)[a]	0.7–0.9		0.14		–	–	–	–	–	–	–	–
Patrick & DeLaune (1976)[a]	0.7–0.9		0.08–0.15		–	–	–	–	–	–	–	–
Chalmers (1979)	1.40		–	–	–	–	–	–	–	–	–	–
Valiela (1984)	1.40		–	–	–	–	–	–	–	–	–	–
Hopkinson & Schubauer (1984)	1.05		–	–	–	–	–	–	–	–	–	–
Burkholder (1956)	–	–	1.07		–	–	0.90		–	–	–	–
Smart & Barko (1980)[b]	0.66–0.80		0.04–0.05		–	–	–	–	–	–	–	–

[a] Reported range of nutrient concentrations, height form not specified
[b] Critical concentrations for adequate nutrition

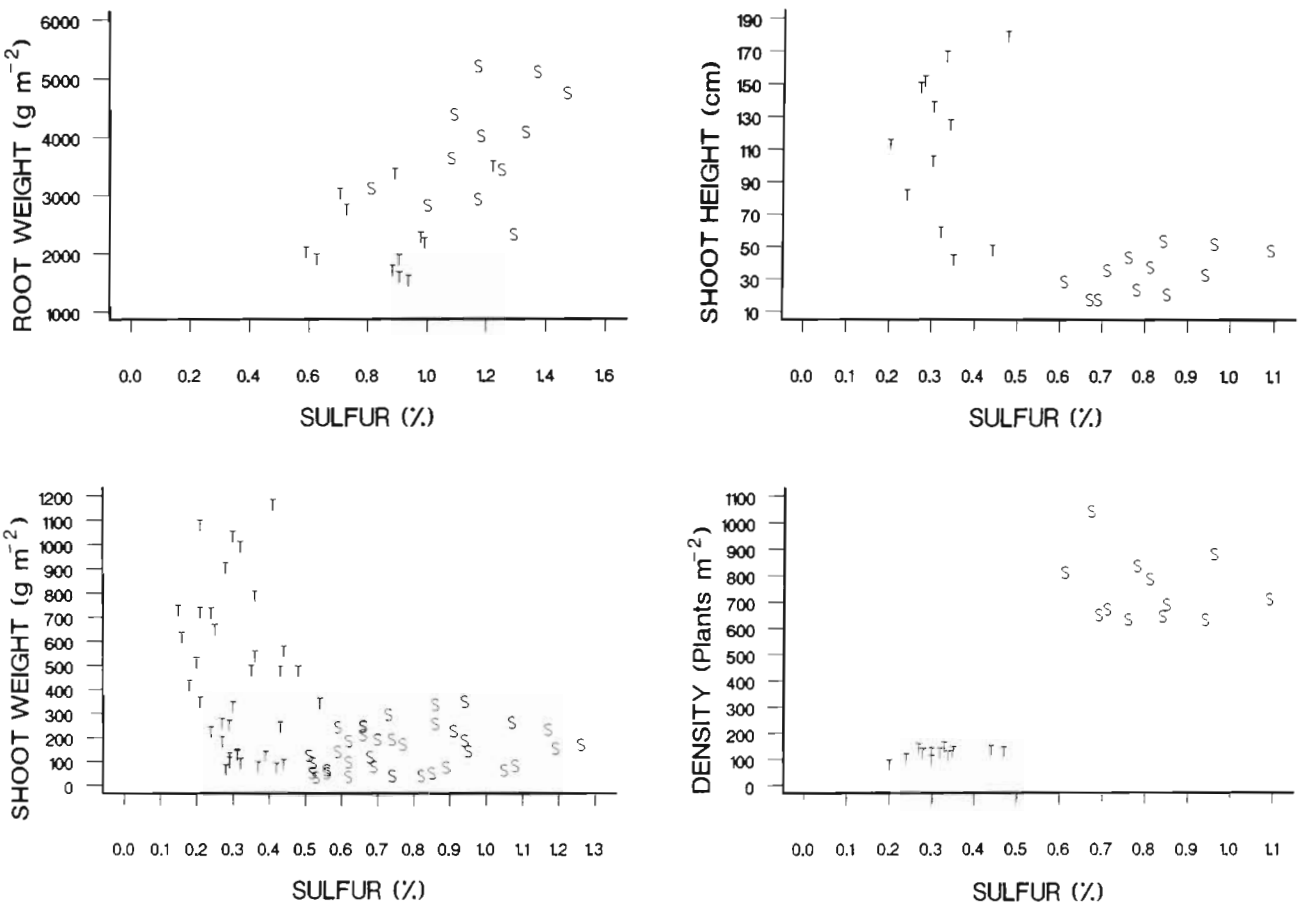

Fig. 3. *Spartina alterniflora*. Tissue S concentrations (% dry wt.) and root weight, shoot weight, shoot height, and plant density for tall (T) and short (S) forms

Substrate nutrient concentrations

The literature suggests that high soil sulfide levels may (1) directly affect production by *Spartina alterniflora* as a result of increased mortality (Linthurst 1979, DeLaune et al. 1983), (2) inhibit the transport system involved in N uptake (Mendelssohn 1979a, Morris 1980, Howes et al. 1981, DeLaune et al. 1983), and (3) lower oxygen availability, thereby changing patterns of catabolism (Mendelssohn et al. 1981). Several researchers have suggested that depressed oxygen transport, which is conducive to denitrification, and sulfide toxicity may be the cause of stunted growth of *S. alterniflora* (Howes et al. 1981, Mendelssohn et al. 1981, King et al. 1982). Howarth & Teal (1979) reported that sulfide concentrations as low as 0.20 m*M* killed *S. alterniflora* plants grown hydroponically.

King et al. (1982) proposed that the gradients in the edaphic factors that regulate *Spartina alterniflora* production are controlled not only by interstitial sulfide concentration but also by the dynamic relationship among tidal water movement, iron concentration and bacterial sulfate reduction. Natural water movement in soil is much greater in TS than in SS marshes, as documented by several studies that reveal significant vertical and lateral movement in the TS areas and virtually no movement in the SS areas (Nestler 1977). In soils where water movement and aeration were increased, plant growth was stimulated; where movement was restricted, plant growth was inhibited (Linthurst 1979). In North Inlet, there was a significant ($p < 0.05$, $n = 16$) difference in the average annual sediment redox potential (Eh) between the tall and short *S. alterniflora* sites at the 20 to 27.5 cm depth (Table 4). This result was not surprising since water flow was minimal at the SS site. In a similar comparison of TS and SS sites in Louisiana, USA, DeLaune et al. (1983) found higher Eh levels only in the surface 10 cm site of the TS, while the lower depths at both sites had similar Eh values.

Sulfide concentrations varied markedly in Sapelo Island marshes (Georgia, USA) and were inversely correlated with soil water flow and plant production (Nestler 1977, Gallagher et al. 1980, Howes et al. 1981). DeLaune et al. (1983) reported that free sulfide concentrations greater than 10 mg S kg^{-1} dry soil adversely affected *Spartina alterniflora* and that root production was significantly reduced when the free sulfide concentration rose above 50 mg S kg^{-1} dry soil. In North Inlet, the reduced substrate conditions co-existed with very high levels of free sulfide (average for all depths = 66 ± 28.8 mg SO_3 kg^{-1} dry soil; Table 4). King et al. (1982) reported a similar inverse relation between Eh and sulfide concentrations in interstitial water. *S. alterniflora* growing in these conditions had decreased plant heights and increased root biomass. The average sulfide level in TS soils (average for all depths = 13.3 ± 1.2 mg SO_3 kg^{-1}) was significantly ($p < 0.05$, $n = 16$) less than in the SS soils. In Louisiana, DeLaune et al. (1983) also noted a significant difference of free S^{-2}, but not acid-soluble S^{-2}, at the 20 to 27.5 cm depth between tall and short sites. They concluded that S was among the primary environmental factors responsible for the height difference in the 2 forms of *S. alterniflora* and that sulfide indirectly inhibited nitrogen uptake.

In our study, ammonia as well as total dissolved nitrogen concentrations were statistically ($p < 0.05$, $n = 16$) similar at both study sites, suggesting that N availability was not limiting SS growth. Although N is often proposed as limiting the growth of *Spartina alterniflora* based on increased productivity following fertilization, the addition of N to the plant may mask other nutrient problems such as sulfide toxicity (King et al. 1982). The

Table 4. Means of selected chemical properties of interstitial water extracted from 0 to 7.5, 10 to 17.5, and 20 to 27.5 cm depth. Soil samples collected in November 1981, February 1982, May 1982, and August 1982. TS: tall form; SS: short form of *Spartina alterniflora*. TDN: total dissolved nitrogen; TDP: total dissolved phosphorus; Eh: redox potential. Means within a row and for the same soil depth are not significantly different if followed by the same letter ($p < 0.05$, Duncan's Multiple Range Test, $n = 16$)

Property		0–7.5 cm		10–17.5 cm		20–27.5 cm	
		TS	SS	TS	SS	TS	SS
NH_4-N	(mg kg^{-1})	95a	65a	113a	80b	86a	84a
PO_4	(mg kg^{-1})	6b	11a	16a	10b	13a	13a
SO_3	(mg kg^{-1})	14b	34a	14b	90a	12b	74a
K	(mg kg^{-1})	306a	296a	305a	285b	311a	299a
Ca	(mg kg^{-1})	334a	283a	316a	255a	311a	270a
Mg	(mg kg^{-1})	975a	926a	919a	853a	887a	957a
Fe	(mg kg^{-1})	0.13a	0.10a	0.40a	0.01b	0.58a	0.01b
TDN	(mg kg^{-1})	321a	251a	272a	306a	280a	220a
TDP	(mg kg^{-1})	19a	17a	26a	16b	24a	17a
Eh	(mV)	162a	−31b	120a	−140b	116a	−156b

high sulfide conditions also may have induced shifts from oxidative to fermentative metabolism in the root tissue because of lowered soil redox potentials (Howes et al. 1981, Mendelssohn et al. 1981). Such a shift would result in decreased energy for nutrient uptake and growth. This may have occurred in the SS sites of North Inlet as indicated by the inverse relationships between shoot S and shoot N ($r = -0.39$, $p < 0.01$, $n = 124$), P ($r = -0.50$, $p < 0.001$, $n = 124$), and K ($r = -0.24$, $p < 0.01$, $n = 124$). The results of other researchers (King et al. 1982, DeLaune et al. 1983) support these findings.

The third interstitial water parameter, along with Eh and sulfide, that differed between the 2 study sites was Fe concentration (Table 4). Pools of Fe were greater at the TS site than at the SS site. King et al. (1982) explained that concentrations of sulfide at Sapelo Island were the result of differential precipitation of iron sulfide at the various sites. Perhaps the potential for precipitation of sulfide was much less in SS than in TS sites because of the smaller pools of dissolved interstitial Fe in the SS soils.

Ratios of nitrogen to other macronutrients

The ratios of N:K, N:Ca, and N:Mg were similar between TS and SS stems and TS and SS roots (Table 1). However, the ratio of N:P in TS roots (4.4:1) was lower than that in SS roots (7.0:1) ($p < 0.05$, $n = 126$). Since N concentrations in TS roots were significantly greater than in SS roots (Table 1), this means there was a greater proportion of P in TS roots than in SS roots. This greater proportion of P to N in TS roots may have influenced the TS and SS growth forms.

The N:S ratio was another apparent nutrient disproportionality between TS and SS (4.1:1 and 1.5:1, respectively). Although the N concentrations were significantly greater in TS stems than SS stems (Table 1), we concluded that there was likely a critical proportionality of N:S which, in the case of SS, was probably exceeded by significantly greater S concentrations in SS stems than in TS stems (Table 1).

CONCLUSIONS

Our results support the hypothesis that the macronutrient status may account for the height and biomass differences between the tall and short forms of *Spartina alterniflora*. Ammonia as well as total dissolved nitrogen concentrations were similar in the soils of both TS and SS sites suggesting that N availability was not limiting SS growth. However, N concentrations were greater in shoots and roots of TS than in SS. This is one indication that the N status of SS was deficient relative to that of the tall form. Soil sulfide also may have played a role in the height and biomass differences between the 2 forms. Both shoot and root S concentrations were greater in SS than in TS. We speculate that the high concentrations of S in SS may have prevented the uptake or assimilation of N. Lower Fe levels were noted in the SS than TS interstitial waters. Lower redox potentials (Eh) and Fe availability resulted in higher sulfide levels which may have decreased plant production.

Seasonal patterns of macronutrient concentrations in both TS and SS followed similar trends. Shoot tissue N, P, and S changed over time while K, Ca, and Mg generally did not change throughout the year.

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