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To cite this article: Richard Devereux , Diane F. Yates , Jessica Aukamp , Robert L. Quarles ,
Stephen J. Jordan , Roman S. Stanley & Peter M. Eldridge (2011) Interactions of *Thalassia*
testudinum and sediment biogeochemistry in Santa Rosa Sound, NW Florida, Marine Biology
Research, 7:4, 317-331, DOI: [10.1080/17451000.2010.515227](https://doi.org/10.1080/17451000.2010.515227)

To link to this article: <http://dx.doi.org/10.1080/17451000.2010.515227>



Published online: 14 Apr 2011.



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ORIGINAL ARTICLE

Interactions of *Thalassia testudinum* and sediment biogeochemistry in Santa Rosa Sound, NW Florida

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Abstract

Thalassia testudinum belowground biomass weights, leaf weights, leaf growth rates, areal shoot densities (m^{-2}), and leaf C:N:P ratios were compared to a set of biogeochemical parameters to gain information on seagrass–sediment interactions that may influence seagrass growth. Data were compiled from three surveys conducted in Santa Rosa Sound, located in northwest Florida, at three different meadows in sequential years. Biomass measurements and leaf growth rates decreased between stations along transects from shallow to deeper water. Belowground biomass weights decreased and leaf C:P ratios increased with temperature reflecting a seasonal growth pattern. The *T. testudinum* parameters were highly correlated with each other. Sulfate reduction rates (at times exceeding $1000 \text{ nmol ml}^{-1} \text{ day}^{-1}$) were among the highest recorded for seagrass beds with temperature accounting for 79% of the variation. Even though sulfate reduction rates were high, total Fe:reduced S ratios indicated sufficient Fe to account for all reduced S as pyrite. Sediment Fe, C, N, and organic P concentrations increased with sediment depth, whereas inorganic P decreased with depth, suggesting burial of organic P and root uptake of inorganic P. Leaf C:N:P ratios indicated P-limited growth for two surveys. NH_4^+ was detected in water above the sediment surface during some surveys demonstrating *T. testudinum* meadows at times may serve as sources of inorganic N to the water column. Plant parameters correlated with concentrations of sediment organic C and N, Fe, S, and porewater NH_4^+ . These results highlight the importance of the organic matter and Fe contents of sediments to seagrass growth.

Key words: Biogeochemistry, seagrass, sediments, sulfate reduction

Introduction

Seagrasses have been termed ecological engineers because they can provide the biological and geophysical basis of a rich, productive estuarine ecosystem (Orth et al. 2006). These highly valued resources are increasingly at risk of being lost to the effects that human activities have on coastal waters, including those of the Gulf of Mexico (Orth et al. 2006; Handley et al. 2007). Seagrass growth and distribution depend largely on the availability of light, but can also be affected by wave energy, sediment composition and organic matter content, and inhibited by sulfide concentrations (Livingston et al. 1998; Koch 2001; Calleja et al. 2007).

The loss of seagrass from estuaries is most often attributed to water column nutrient enrichment. Nutrient enrichment promotes the growth of phytoplankton, epiphytic algae, and macroscopic algae which diminish the amount of light available for seagrass photosynthesis. Reduced light levels have compounding effects not only on seagrass physiology, but also on sediment biogeochemistry (Hemminga 1998; Holmer & Laursen 2002). Seagrass roots release oxygen that serves as an oxidant of potential phytotoxins in the sediments, such as sulfide. As light levels decrease, seagrass roots release less oxygen, which can allow porewater sulfide concentrations to reach levels toxic to seagrasses. In addition, phytoplankton and algal

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Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

biomass arising from nutrient enrichment can increase organic matter loading at the sediment surface and stimulate sulfate reduction with the potential for producing even more dissolved sulfide.

Thalassia testudinum is found throughout the Caribbean, Gulf of Mexico, and southeastern Florida coastal ecosystems, often as the dominant seagrass species (Hartog 1970). *T. testudinum* meadows in Florida Bay, at the tip of the Florida peninsula, suffered a wide-scale die-off in the 1990s and have received a great deal of attention with respect to effects of environmental stressors, including nutrients and sedimentary concentrations of Fe and dissolved sulfide (Koch et al. 2007). Florida Bay has carbonate-based sediments whereas other US Gulf of Mexico coastal sediments are terrigenous. This difference might mean that seagrasses in estuaries with terrigenous sediments are less susceptible to sulfide toxicity. Two field studies, one in south Texas and one in northern Florida, demonstrated decreased *T. testudinum* growth, and increased porewater sulfide concentrations or higher sulfate reduction rates (SRR), in shaded vs. non-shaded plots (Lee & Dunton 1997; Calleja et al. 2006). Even though the shade treatments would have slowed photosynthesis, the studies demonstrated the potential for a deleterious effect from sulfide accumulation.

Despite the importance of Fe in modulating dissolved sulfide concentrations, relatively few studies of seagrass bed sediment biogeochemistry have included measurements of Fe. Addition of Fe to carbonate sediments has been shown to increase seagrass growth and reduce SRR (Holmer et al. 2005). Ruiz-Halpern et al. (2007) also showed that additions of Fe oxides to carbonate sediments lowered dissolved sulfide levels and promoted *T. testudinum* growth even when SRR were stimulated by adding acetate to the sediments. Similarly, seagrass growth in carbonate sediments was positively correlated with rates of Fe deposition which were sufficient to limit porewater sulfide concentrations through formation of pyrite (Marbà et al. 2008). These studies suggest that Fe can buffer seagrasses against sulfide toxicity.

Sulfate reduction has been extensively studied in seagrass bed sediments and, in the course of those studies, concentrations of dissolved sulfide, acid volatile sulfide (AVS), chromium-reducible S (CRS), and total reduced S (TRS) have often been measured (Duarte et al. 2005; Holmer & Laursen 2002; Calleja et al. 2006). AVS is operationally defined as substances that release H_2S upon acidification with HCl and will include dissolved sulfide, metastable Fe sulfide minerals, and, potentially, sulfide from pyrite (Rickard & Morse 2005). CRS,

obtained by treatment of sediments with acidic chromium, originates in pyrite or elemental S (Fossing & Jørgensen 1989). TRS is CRS plus AVS. Fe measurements, when also available, can then be compared to CRS measurements to gain relative estimates of the pyrite and S pool sizes, and thus, the potential for dissolved sulfide in seagrass beds to partition into a solid, less-toxic phase.

We investigated the biogeochemistry of *T. testudinum* bedded sediments using a suite of parameters that included Fe, AVS, CRS, and SRR measurements to estimate S pool sizes. In addition, *T. testudinum* biomass weights, leaf growth rates, and C:N:P ratios were compared to a larger set of sediment geochemical measurements using a correlation analysis to identify potential relationships between seagrass and sediment parameters. The results provide additional information on biogeochemical cycles in seagrass beds, particularly Fe, P and S cycling and availability of P to the plants, and suggest seagrasses in terrigenous sediments can be susceptible to sulfide toxicity.

Materials and methods

Sampling locations and field surveys

The seagrass meadows studied were located in Santa Rosa Sound, part of the Pensacola Bay system in northwest Florida. The sites sampled were in, or near, East Sabine Bay, Tiger Point, Boone's Bayou, and Big Sabine Point (Figure 1). East Sabine Bay, Tiger Point and Boone's bayou are near residential developments whereas Big Sabine Point is within an area of natural preservation. The study was thus divided as follows: East Sabine Bay was surveyed in 2002 (ESB-02), Tiger Point and Boone's Bayou were surveyed in 2003 (TPBB-03), and Big Sabine Point was surveyed in 2004 to 2005 (BSP-0405).

The sampling design is not optimal for year-to-year or meadow-to-meadow comparisons because this study is part of an overall effort to determine what data are required to apply a model developed for one estuary (Eldridge et al. 2004), that links water column and sediment stressors (e.g. light availability and sediment sulfide levels) with seagrass growth, to another estuary. The data set was built largely for that purpose and to gain a representation of parameters in Santa Rosa Sound. The extensive field work and analyses required to parameterize the model meant that we could study only one meadow over several years or several meadows once a year. We chose the latter, to obtain a representative data set of plant and sediment parameters for Santa Rosa Sound, which is a large body of water. In addition, different meadows were sampled in order to mini-

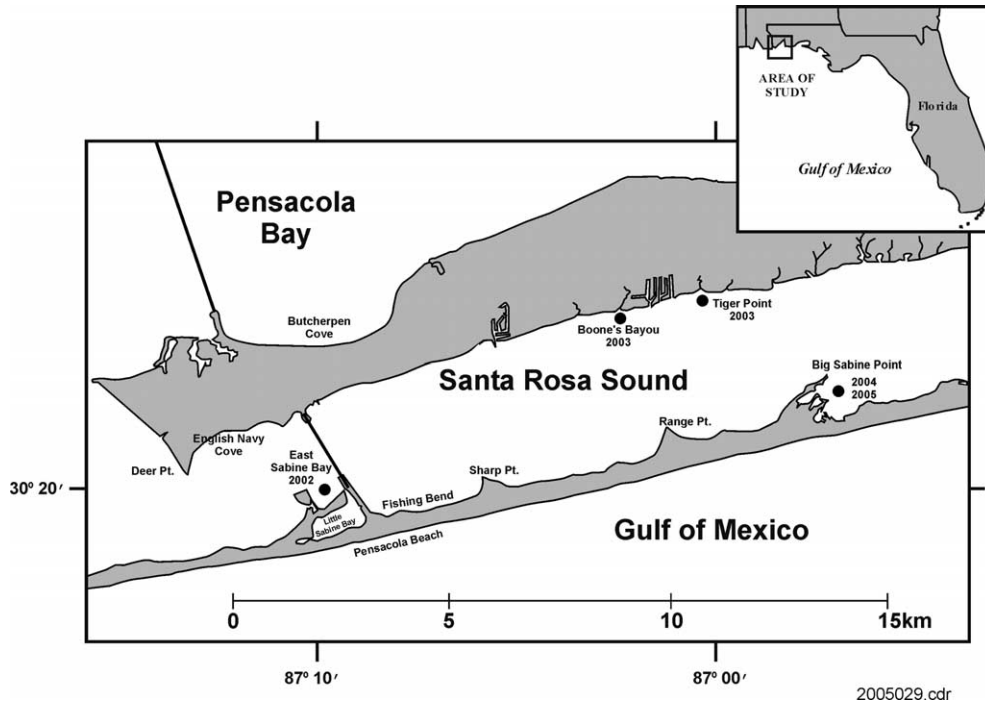


Figure 1. Sampling locations and the years that surveys were conducted in Santa Rosa Sound.

mize the amount of damage to seagrasses that core sampling would cause at any one meadow.

Three stations were sampled three or four times during the course of each survey. Stations for ESB-02 and BSP-0405 were designated as shore, middle and edge (Table I), referring to their relative location in the seagrass meadow along a transect perpendicular to the shoreline and into the sound. The edge stations were established towards the deep water side of the meadows in 1.5–2 m of water where the plants began to thin. The shallow and middle depth stations were in 1.0–1.5 m of water. For BSP-0405, the deep water edge of the meadow was at nearly the same depth as the mid station suggesting factors other than light attenuation may have influenced *Thalassia testudinum* distribution at this site. For TPBB-03 field work, *T. testudinum* at Tiger Point extended into the sound with very little topographical slope and limited space for a third station. Shore and middle stations were thus established at Tiger Point. The Boone's Bayou location, having less *T. testudinum* than observed at Tiger Point, was used as the third station and is referred to as the 'bayou' station rather than the 'edge' station.

Synoptic *T. testudinum* biomass measurements and sediment biogeochemical measurements were obtained at each sampling trip with two exceptions. For BSP-0405, sediment biogeochemical measurements were not taken in October and *T. testudinum* biomass was not measured in December.

Water temperatures and salinities were obtained at the time of sampling with a Hydrolab water quality sensor. LiCor 2 π planar light sensors, one on board the boat and one at the seagrass canopy, were used to determine the percent of light transmitted to the seagrasses at the time of sampling.

Thalassia testudinum biomass and growth measurements

Triplicate 15.2-cm diameter, 30-cm deep cores were collected by SCUBA divers at each station. Care was taken to assure leaves originating from shoots within the perimeter of the corer were included with the core. The core was released into a 1-mm sieve and measurements of depths beneath the sediment–water interface where the rhizomes occurred and the roots penetrated were recorded. The *T. testudinum* cores were first gently washed with seawater to remove sediments and the biomass samples were then rinsed with fresh water to remove remaining sediment, salt, epiphytes, and other non-plant material, and then separated into leaf, root, and rhizome subsamples. Each subsample was dried at 60°C for at least 48 h prior to being weighed. The numbers of shoots in each core were recorded. Plant parameters were compared between surveys or stations using one-way ANOVAs and Tukey post-hoc tests.

Dried seagrass leaves were ground to a fine powder for determination of C, N and P content.

Table I. Water temperature ($^{\circ}\text{C}$), salinity (PSU), and light penetration (% surface irradiance) at the leaf canopy in seagrass beds sampled in 2002 to 2005.

Survey/ station	April			June			July			September			November			December			February		
	Temp	Salinity	Light	Temp	Salinity	Light	Temp	Salinity	Light	Temp	Salinity	Light	Temp	Salinity	Light	Temp	Salinity	Light	Temp	Salinity	Light
ESB-02																					
Shallow				28	32	38	29	28	23	29	30	38	21	25	4						
Mid				28	32	20	30	27	26	29	30	19	21	26	10						
Deep				29	32	16	30	27	15	29	30	14	21	25	19						
TPBB-03																					
Shallow				29	21	55	28	13	34	29	18	23	24	24	31						
Mid				29	21	36	30	12	9	29	19	19	24	24	29						
Bayou				29	21	26	30	12	3	29	18	10	24	25	32						
BSP-0405																					
Shallow	25	25	50				29	19	55							18	20	50	15	25	35
Mid	24	26	46				29	19	39							18	20	39	15	25	45
Deep	24	26	62				30	19	34							18	20	40	16	25	49

Leaf C and N contents were determined on an Elementar Vario EL elemental analyzer. P concentrations were determined colorimetrically as described by Fourqurean et al. (1992). The measurements were then converted to moles g dry weight⁻¹.

Thalassia testudinum leaf growth rates were determined by the hole punch technique (Zieman 1974). Leaves were pierced with a hypodermic needle just above the meristem and harvested 7–10 days later. The new growth, the section of leaves between the hole made by the needle and the tip of the meristem, was excised from the leaves, dried at 60°C for 48 h, and weighed. Growth rates were calculated by dividing the number of days between when the leaves were marked and harvested into the new growth dry weights.

Porewater and solid phase biogeochemical measurements

Sediment porewater and solid phase analyses were performed on cores collected in triplicate from each station. The cores were taken by divers with 7.5 cm diameter, clear plastic tubes and included *Thalassia testudinum* shoots and belowground biomass. The cores were sliced inside a N₂-filled glove bag into 2.0 cm sections to a depth of 16 cm. The sandy composition of the sediments prevented them from compacting sufficiently during centrifugation to expel porewater. Porewater was therefore obtained by centrifuging the sediments in specially constructed filter tubes. The filter tubes were made by piercing holes through the bottoms of 50-ml polypropylene centrifuge tubes and then placing a glass fiber filter in the bottom of the tubes to cover the holes. The tubes were filled with sediment and placed inside 250-ml polypropylene centrifuge bottles which were then tightly closed using caps with rubber o-ring seals. The bottles were taken from the glove bag and centrifuged at 5000 g for 10 min. The bottles were then opened inside an anaerobic chamber (Coy Laboratories), filled with 95% N₂:5% H₂, and the porewater was collected from the bottom of the centrifuge bottles with syringes. The porewater samples were passed through 0.22-μm filters and distributed into vials for chemical analyses. In addition, samples of water overlying the sediments were collected in 30-ml plastic syringes by drawing in water while the tip of the syringe was kept within 1 cm above the sediment–water interface. These samples were filtered and analyzed as with the porewater samples.

Porewater dissolved inorganic C (DIC) and NH₄⁺ concentrations were determined by flow injection analyses (Hall & Aller 1992). Porewater pH was measured with a mini electrode (Corning). Sulfate

concentrations were measured using a BaCl_2 assay (Tabatabai 1974). Sediments obtained after the removal of pore water were used for solid phase analyses. Total Fe concentrations were measured in hydrofluoric acid digests (Stucki 1981) by inductively coupled plasma-mass spectrometry. Sediment particulate C (PC) and particulate N (PN) concentrations were determined by Dumas combustion analysis. Sediment inorganic P (IP) and organic P (OP) concentrations were determined colorimetrically as described by Aspila et al. (1976).

Whole sediments from parallel cores were used to determine sediment densities and porosities (by drying known volumes of sediment). Concentrations of chlorophyll *a* (chl*a*) in sediments were measured on one core from each station and sampling time by fluorometry of extracts obtained with 0.5 g wet sediment in 10.0 ml methanol (Welschmeyer 1994).

Sulfate reduction rates and reduced sulfur

SRR were determined in triplicate on intact 2 cm diameter \times 16 cm deep cores taken adjacent to *Thalassia testudinum* shoots. The cores were equilibrated for 2 h in the dark at the temperature of the overlying water, then injected through pre-drilled holes with 1.5 mCi of carrier-free $^{35}\text{SO}_4^{2-}$ at 1.0 cm intervals, and incubated for an additional 4–5 h. The cores were extruded and sliced at 2.0 cm intervals into tubes containing 10 ml of 20% zinc acetate which were immediately mixed to disperse the sediment. The samples were held at -20°C until analyzed. Reduced S in the sediment samples was obtained using a two-step distillation procedure carried out under N_2 to separate AVS and CRS fractions (Fossing & Jørgensen 1989). The sulfide liberated during each step was trapped in 20% zinc acetate. SRR were calculated per ml porewater using ^{35}S counts obtained from the zinc acetate traps and the specific activity of the porewater sulfate as described by Fossing & Jørgensen (1989). Concentrations of AVS and CRS obtained in traps were measured by the Cline (1969) assay.

Results

Salinity, water temperature and percent light penetration to the seagrass canopy are provided in Table I. Temperatures during the study ranged from 15 to 30°C and salinity ranged from 12 to 32. Low salinity during TPBB-03 was associated with heavy rainfall which totaled 84 cm from June to September (Northwest Florida Water Management District, <http://www.nwfwmd.state.fl.us/rmd/rain/miscrain.htm>).

Thalassia testudinum biomass measurements and growth rates

Thalassia testudinum belowground biomass (combined root and rhizome weights), mass of leaves, numbers of shoots, and leaf production rates in Santa Rosa Sound were determined from the ESB-02 (Figure 2), TPBB-03 (Figure 3) and BSP-0405 (Figure 4). The mean weights of below ground biomass and the mean numbers of shoots for all samples differed significantly ($P < 0.001$) between surveys. Mean leaf mass and mean leaf production rates did not differ between surveys. Biomass weights and shoot numbers tended to be lower at the edge and bayou stations than at the two shallower stations.

The ESB-02 edge station, averaged over the three sampling times, had lower mean belowground biomass weights (84 g dry weight m^{-2} , $SE = 13.0$) than the shore (304 g dry weight m^{-2} , $SE = 46.2$) or middle stations (418 g dry weight m^{-2} , $SE = 49.3$) (Figure 2). *T. testudinum* measurements within ESB-02 stations varied with sampling time on some occasions. Most noticeably, the middle station had greater amounts of belowground (600 g dry weight m^{-2} , $SE = 37.5$) and leaf (321 g dry weight m^{-2} , $SE = 46.2$) biomass, and more shoots, in June than during the following sampling times. ESB-02 shoot-specific leaf growth rates were highest in June (4.2 mg dry weight shoot $^{-1}$ d $^{-1}$, $SE = 0.26$, for all shoots measured) and did not differ by station. At each station, the leaf production rates obtained in September were lower than June rates.

Results from TPBB-03 were similar to those of ESB-02 (Figure 3). The bayou station had less leaf and belowground *T. testudinum* biomass than the shore and middle stations. Leaf biomass at the middle station declined between June and November, but the belowground biomass was the same in November as it was in June. Mean shoot numbers varied at the middle and bayou stations where they were higher in September than when the stations were first sampled in June. TPBB-03 shoot-specific leaf growth rates, as with ESB-02, were highest in June (2.8 mg dry weight shoot $^{-1}$ d $^{-1}$, $SE = 0.27$) and did not differ significantly with station or from the ESB-02 June rates.

ESB-0405 included April and February sampling times to measure *T. testudinum* parameters outside of the most active growth period. Edge station belowground biomass weights, leaf weights, and shoot numbers were all markedly higher in October and July than they were in April and February (Figure 4). Belowground biomass weights at the shore station were lower in April than in the following October and February, and there were no differences in

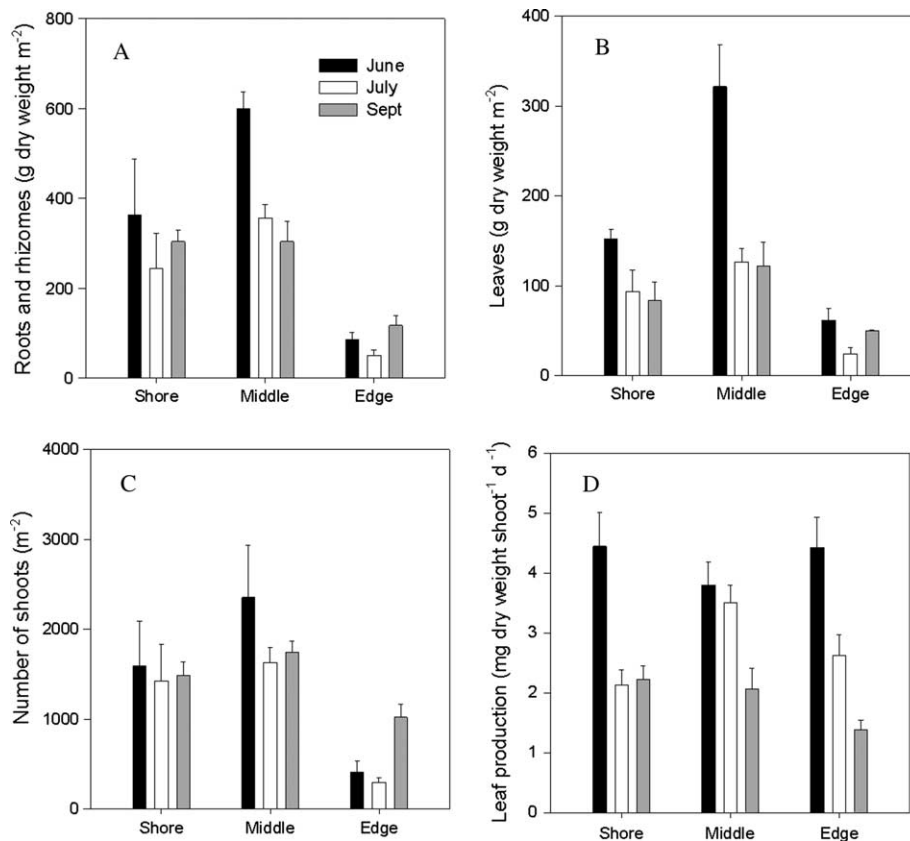


Figure 2. *Thalassia testudinum* measurements obtained from the ESB-02 survey at three stations over three sampling trips. Results are the means of root plus rhizome weights (A), leaf weights (B) and numbers of shoots (C) obtained with triplicate cores. Mean leaf production rates (D) were obtained from 10 shoots. Error bars represent the standard errors of the means.

belowground biomass weights between sampling times at the middle station. Shore and middle station leaf biomass weights increased between April and July. Leaf growth rates measured for BSP-0405 were similar in April and July, and were very low to negligible in December. The large increases in BSP-0405 leaf weights between April and July suggest growth rates were substantially higher between those sampling times.

Leaf nutrient contents

Average leaf C:N:P ratios determined for each survey are provided in Table II. C:P and N:P ratios determined during BSP-0405 were substantially lower than found for the preceding two surveys. Considering C:N:P ratios of seagrasses tend toward 550:30:1 (Atkinson & Smith 1983), TPBB-03 *T. testudinum* demonstrated P-limitation in June and July at the shore and mid stations whereas *T. testudinum* for BSP-0405 was P replete.

Sediment characteristics

Sediments at all stations consisted of 97–99% quartz sand with the remainder silt and clay. Sediment

porosities ranged from 0.31 to 0.56, mean = 0.42. Sediment averaged 0.28 mmol C g⁻¹ over the core fractions (95% CI = 0.19, n = 859, min = 0.01, max = 1.07) and 0.02 mmol N g⁻¹ (95% CI = 0.001, n = 861, min < 0.001, max = 0.095). Sediment chl_a concentrations were highest in the top sediment fraction indicating an active benthic microalgal community (Figure 5A).

Sulfate reduction rates

SRR were determined on 108, 16-cm long cores at 2.0 cm intervals, representing triplicate measurements at three stations and four sampling times in each of three surveys. SRR were highest in the uppermost sediment fractions and decreased with depth (Figure 5B). High SRR in top sediments were likely supported by high concentrations of labile organic matter as suggested by chl_a profiles (Figure 5A). For ease of discussion of differences in SRR between stations and sampling times, SRR at each station and sampling trip were averaged for the 0–2 cm sediment interval (where chl_a concentrations were maximal), and the remaining 2–16 cm interval (Figure 6). The average rates obtained for the 2–12 cm sediment intervals, which would account

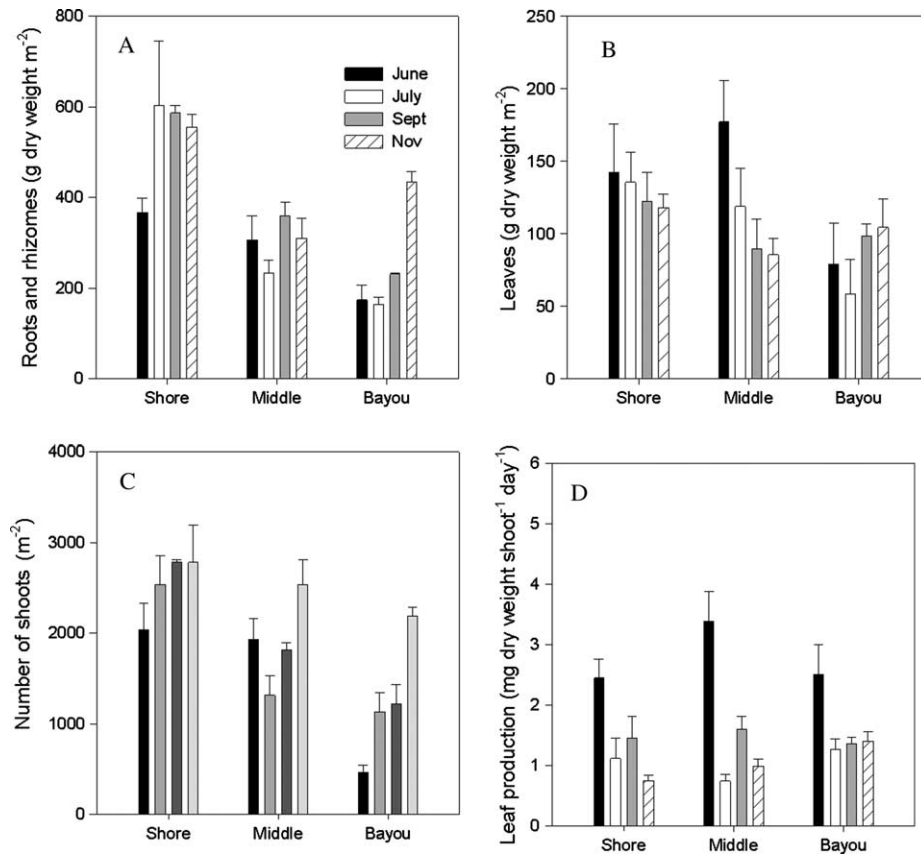


Figure 3. *Thalassia testudinum* measurements obtained from TPBB-03 at three stations and four sampling trips. Results are the means of root plus rhizome weights (A), leaf weights (B) and numbers of shoots (C) obtained with triplicate cores. Mean leaf production rates (D) were obtained from 10 shoots. Error bars represent the standard errors of the means.

for the root zone, and the 12–16 cm intervals, which lie beneath the root zone, did not differ. The highest SRR ($780 \text{ nmol ml}^{-1} \text{ d}^{-1}$, $SE = 360$) occurred in 0–2 cm sediment fractions at the ESB-02 middle station. SRR were highest in the top sediment fractions for 13 out of 36 determinations over the three surveys, and lower than the average beneath the 0–2 cm layer only three times (TPBB-03 middle station in June and September, and TPBB-03 bayou station in July). On an integrated basis, the amount of sulfate reduced in the 0–2 cm intervals, even at the highest SRR, was less than in the 2–16 cm interval.

SRR varied with station and sampling time. The differences between sampling times were particularly apparent in the 0–2 cm fractions. Rates in the 0–2 cm fractions were usually higher in the summer months and September than in November, December, February and April (Figure 6). For ESB-02, however, 0–2 cm sediment SRR at the shore station were higher in November than September, even though November was 4–5 °C colder than September. The most notable difference in SRR between stations was observed with TPBB-03. TPBB-03 SRR in 0–2 cm fractions for

June, July and September were higher at the shore station than they were at the middle and bayou stations. Additionally, BSP-0405 July SRR were lower at the edge station than observed at the other two stations.

Porewater and solid phase profiles

Profiles of porewater DIC and NH_4^+ concentrations provide evidence of the importance of the top sediment fractions for C and N mineralization in Santa Rosa Sound seagrass beds (Figure 7). Mean DIC concentrations increased from 1.6 mM in the overlying water to 2.6 mM in the top 4 cm of sediment porewater and declined sharply with increasing depth. Mean porewater pH decreased from near 8.0 in the overlying water to 7.6 in the top 2.0 cm fractions and thereafter remained near constant with depth. NH_4^+ concentrations showed a peak between 2 and 8 cm beneath the sediment surface (Figure 7). Mean NH_4^+ concentrations in 0–2 cm fractions over all surveys were $24 \text{ } \mu\text{M}$, compared with $76 \text{ } \mu\text{M}$ in the 2–4 cm fractions. This indicates high rates of NH_4^+ production in the 2–4 cm fractions, and suggests NH_4^+ oxidation

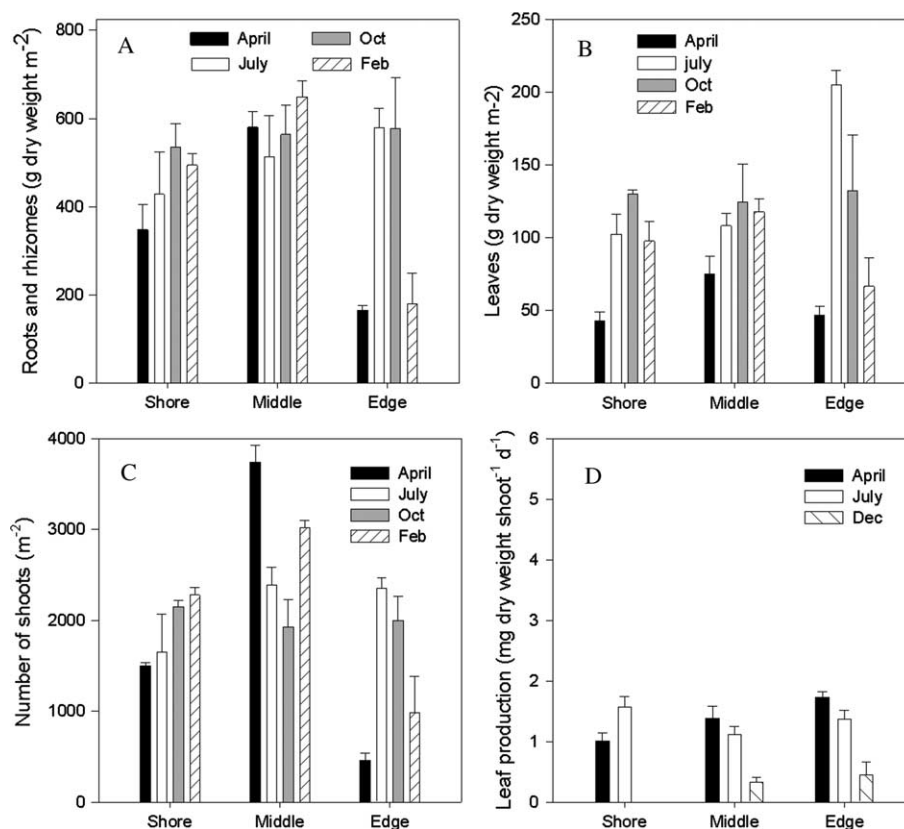


Figure 4. *Thalassia testudinum* measurements obtained from BSP-0405 at three stations and four sampling trips. Results are the means of root plus rhizome weights (A), leaf weights (B) and numbers of shoots (C) obtained with triplicate cores. Mean leaf production rates (D) were obtained from 10 shoots and were not measured in Oct. Error bars represent the standard errors of the means.

in the 0–2 cm fractions as it diffuses upwards from below. It is also likely that NH_4^+ production occurred in the 0–2 cm fractions because SRR

were highest in those fractions and DIC concentrations, indicative of microbial respiration in the breakdown of organic matter, did not differ in

Table II. Molar ratios of *Thalassia testudinum* leaf material collected at each station for three surveys in Santa Rosa Sound by month and station.

		ESB-02		TPBB-03		BSP-0405	
		C:P	N:P	C:P	N:P	C:P	N:P
April	Shore					241.8	13.0
	Middle					206.5	11.6
	Edge					211.8	12.3
June	Shore	628.4	34.9	743.7	33.2		
	Middle	653.0	34.3	1215.7	54.5		
	Edge/Bayou	517.7	25.7	788.8	37.7		
July	Shore	750.2	39.1	764.2	39.6	279.6	13.5
	Middle	610.1	30.7	726.1	36.5	275.5	11.7
	Edge/Bayou	521.0	26.1	469.6	28.9	317.4	12.8
September	Shore	603.3	32.3	531.0	24.7		
	Middle	576.3	31.2	573.6	28.2		
	Edge/Bayou	419.0	24.8	475.8	26.4		
October	Shore						
	Middle						
	Edge						
February	Shore					299.5	12.7
	Middle					241.3	9.6
	Edge					267.6	13.4

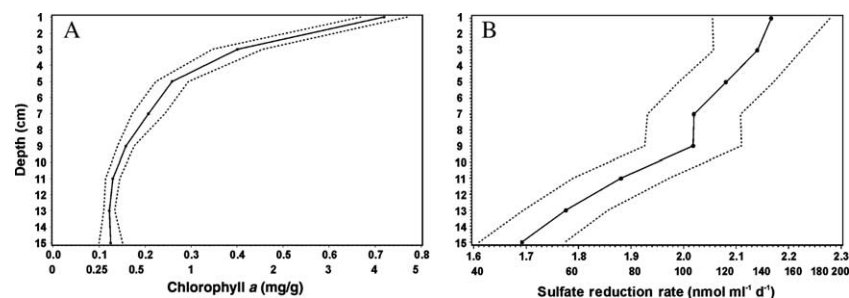


Figure 5. Sediment chlorophyll *a* concentrations (A) and sulfate reduction rates (B) of data compiled from all stations, sampling times, and surveys. Filled circles are means (log10) of 36 cores for chl*a* and 108 cores for SRR. Dashed lines are 95% confidence limits. The upper horizontal scale is in log10 units of the concentration after adding 1 to remove zeros. The lower horizontal scale is in arithmetic units, back-transformed from the log scale.

fractions between 0 and 4 cm. Additional support for high rates of NH_4^+ production in the 0–2 cm fractions comes from detection of NH_4^+ in water overlying the sediment surface for ESB-02 and TPBB-03 (Table II). Concentrations of NH_4^+ above the sediments were particularly high in November samples of both surveys (29.5–37.4 μM) and in June ESB-02 samples (18.6–31.9 μM). NH_4^+ was not detected in the overlying water with the BSP-0405 survey.

Mean concentrations of PC and PN increased with depth into the sediments; peak concentrations occurred in fractions between 6 and 12 cm deep (Figure 8). Similarly, concentrations of CRS, Fe, IP, and OP increased with depth and also attained peak concentrations in the sediment fractions beneath

6 cm (Figure 9). AVS represented a small portion of the TRS and AVS concentrations decreased with depth into the sediments.

Pyrite (FeS_2) is considered an important sink for dissolved sulfide in seagrass bed sediments (Marbà et al. 2008). Sediment pyrite Fe concentrations can be estimated as $\text{CRS}/2$ (Aller et al. 2004). The slope of the regression line obtained by plotting CRS against total Fe was 0.8705 indicating Fe was available in excess of that which would be present in CRS as pyrite (Figure 10).

Comparisons of sediment and plant parameters

Corresponding shapes of concentration profiles among sediment parameters demonstrate correlations in regard to changes in concentrations with

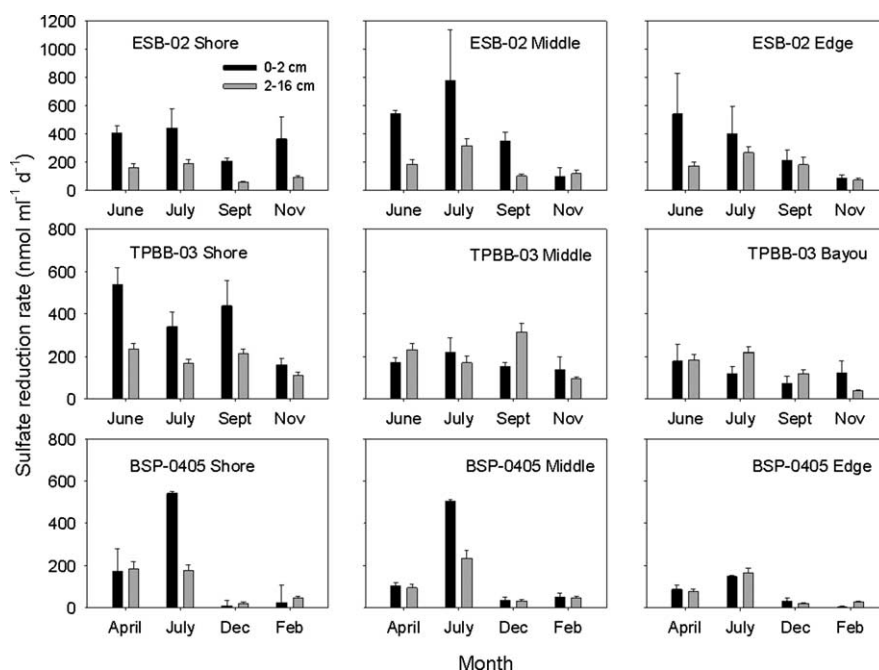


Figure 6. Average sulfate reduction rates determined for the three surveys. Rates were measured at 2.0 cm intervals on triplicate cores at each station and sampling time. The rates are presented as averages of the 0–2 cm sediment intervals and the 2–16 cm intervals. Error bars represent the standard errors of the means.

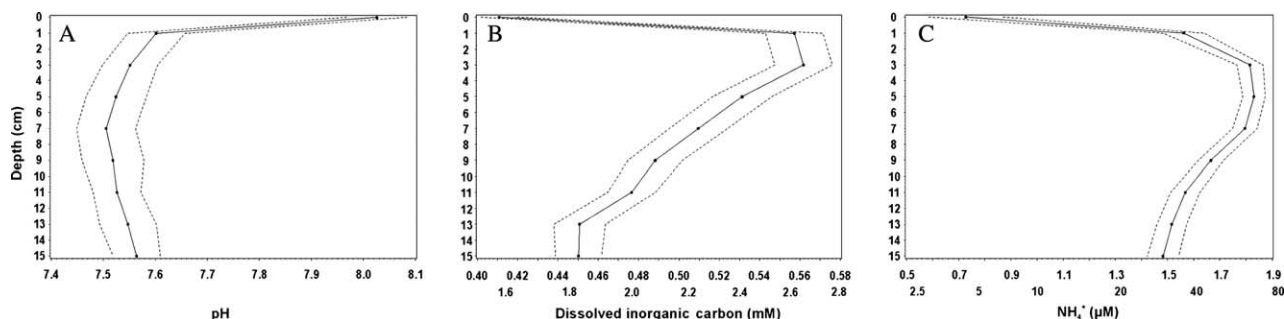


Figure 7. Sediment porewater and overlying water pH (A), dissolved inorganic carbon (B), and NH_4^+ (C) concentrations compiled from all stations, sampling times, and surveys. Measurements of water overlying the sediment are plotted at 0 cm depth. Filled circles are means (log10) of porewater concentrations from 108 cores and overlying water samples ($n=96$ for pH and DIC; 82 for NH_4^+). Dashed lines are 95% confidence limits. The upper horizontal scale is in log10 units of the concentration after adding 1 to remove zeros. The lower horizontal scale is in arithmetic units, back-transformed from the log scale.

depth. However, it is of additional interest to determine if the apparent correlations hold in comparisons that include station and sampling time, and between sediment and plant variables. In order to make those comparisons, Pearson correlation coefficients were determined between average concentrations of the sediment biogeochemical parameters in cores collected per sampling time and station, and average plant variables obtained per time and station. The results are presented in Table IV. Porewater DIC concentrations were strongly correlated with total sediment Fe concentrations ($r=0.387$; $P=0.02$). DIC concentrations were also correlated with CRS ($r=0.330$) and porewater NH_4^+ ($r=0.334$) concentrations ($P=$

0.05 for both) and pH ($r=0.459$; $P=0.007$). Porewater NH_4^+ concentrations were also correlated with sediment IP concentrations ($r=0.457$; $P=0.005$). Correlations existed among most of the solid-phase sediment biogeochemical parameters, except between total Fe and IP or AVS and PC or PN. SRR was significantly correlated with temperature ($r=0.787$; $P<0.001$) with temperature explaining almost 80% of the variation in SRR. SRR and temperature correlated with leaf C:P ratios ($r=0.406$; $P=0.04$ and $r=0.498$; $P=0.008$, respectively), whereas SRR and temperature were not correlated with any of the other sediment or plant parameters.

As expected, plant biomass weights and shoot numbers correlated with each other. In comparison

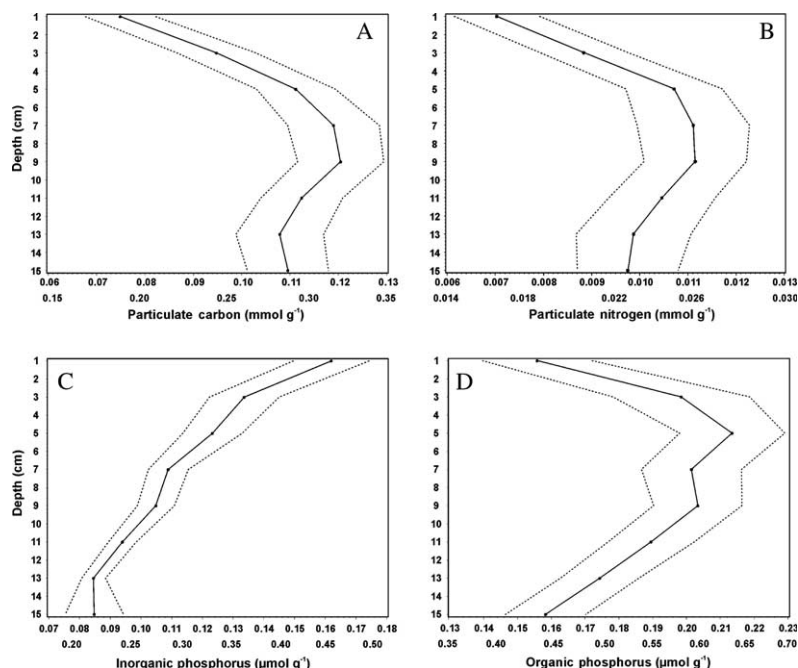


Figure 8. Sediment particulate carbon (A), particulate nitrogen (B), inorganic phosphorus (C), and organic phosphorus concentrations (D). Filled circles are means (log10) of 108 cores. Dashed lines are 95% confidence limits. The upper horizontal scale is in log10 units of the concentration after adding 1 to remove zeros. The lower horizontal scale is in arithmetic units, back-transformed from the log scale.

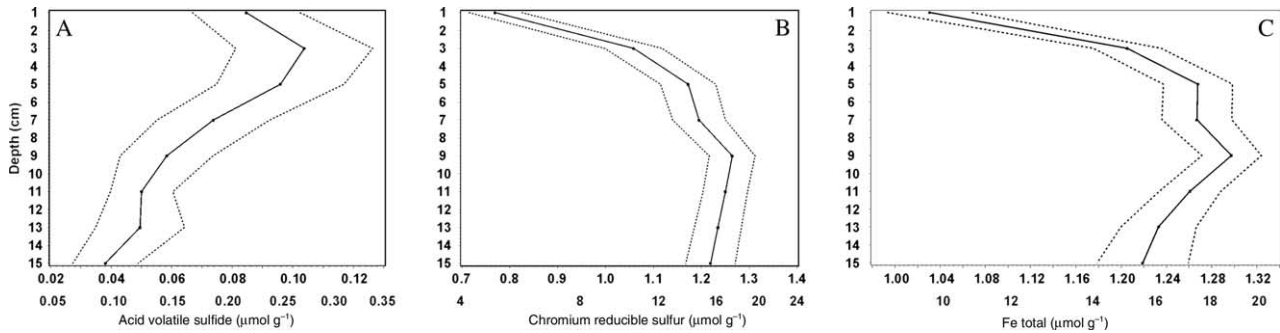


Figure 9. Sediment acid volatile sulfide (A), chromium reducible sulfur (B), and total Fe (C) concentrations. Filled circles are means (log10) of 108 cores. Dashed lines are 95% confidence limits. The upper horizontal scale is in log10 units of the concentration after adding 1 to remove zeros. The lower horizontal scale is in arithmetic units, back-transformed from the log scale.

to sediment parameters, belowground biomass weights, shoot numbers, and leaf growth rates were positively correlated with sediment PC and PN concentrations (Table IV). Additionally, leaf growth rates correlated with porewater NH_4^+ concentrations ($r = 0.434$; $P = 0.03$). Belowground biomass weights and numbers of shoots were correlated with total Fe concentrations whereas weights of belowground biomass and leaf biomass were correlated with CRS concentrations. Leaf C:P ratios, as mentioned above, were positively correlated with temperature and SRR.

Discussion

Seagrasses have profound effects on sediment biogeochemistry which can feedback to affect seagrass growth (Devereux 2005; Duarte et al. 2005). The effects of sediment biogeochemistry can be detrimental, for example in the accumulation of toxic levels of sulfide, or beneficial, as in providing essential nutrients. The main purpose of this study was to investigate potential relationships between seagrasses and sediment biogeochemistry in terrigenous sediments, particularly with respect to Fe, S and P cycling. Santa Rosa Sound was good study area for this purpose because it has numerous seagrass beds that experienced changes in temperature, salinity, and water clarity which can influence seagrass growth (Murrell et al. 2007). *Thalassia testudinum* is near its northern range of distribution in Santa Rosa Sound and undergoes a seasonal cycle of leaf standing crop decreasing with the onset of winter and increasing in the summer (Macauley et al. 1988). In the present study, *T. testudinum* shoot numbers varied between sites, and leaf and belowground biomass varied with time (Figures 1–3). This allowed comparison of differences in sediment biogeochemistry with differences in seagrass parameters.

Plant–sediment interactions

Plant biomass measurements and growth rates correlated with each other as would be expected. Differences in plant measurements between stations were most apparent between the deep stations and the shallower stations. *Thalassia testudinum* requires around 18% of incident light for growth and survival (Lee et al. 2007). Light levels measured at the ESB-02 edge and TPBB-03 bayou stations were 16–19% and 3–32% of incident light, respectively. ESB-02 edge station *T. testudinum* plant parameter values were consistently lower than those of the shallower stations, consistent with effects of reduced light availability (Lee et al. 2007). The seasonal cycling of leaf biomass abundance previously observed with Santa Rosa Sound *T. testudinum* (Macauley et al. 1988; Smith et al. 2004) was most apparent for ESP-0405 when samples were collected in April, July, and

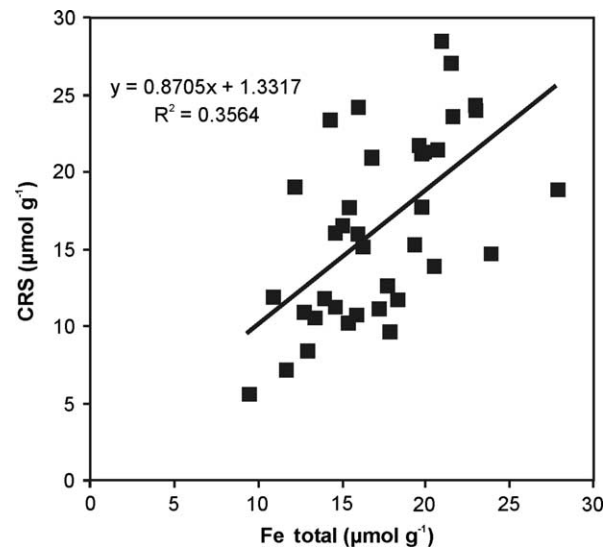


Figure 10. Comparison of total Fe and chromium reducible sulfur concentrations in sediments. Values plotted are the mean concentrations for triplicate cores collected at each station and sampling time ($n = 36$).

Table III. Concentrations of NH_4^+ (μM) in water samples collected within 1 cm above the sediment water interface (n.d., not detected). Values are means (SE) of triplicate samples.

Survey station	June	July	$\mu\text{M NH}_4^+$ September	November
ESB-02 Shore	31.9 (4.9)	5.5 (1.0)	6.7 (1.3)	29.5 (3.3)
ESB-02 Middle	18.6 (11.2)	n.d.	8.9 (1.1)	25.9 (3.3)
ESB-02 Edge	30.4 (10.4)	n.d.	13.0 (1.7)	30.4 (4.2)
TPBB-03 Shore	7.6 (7.6)	5.9 (2.3)	n.d.	29.2 (4.2)
TPBB-03 Middle	n.d.	6.8 (1.6)	n.d.	32.5 (2.3)
TPBB-03 Bayou	n.d.	6.4 (2.6)	n.d.	37.4 (1.4)

February. In addition, an earlier observation that Santa Rosa Sound *T. testudinum* belowground biomass weights were higher in winter than summer (Smith et al. 2004) was consistent with the ESP-0405 measurements and in the negative correlation of belowground biomass with temperature. Seagrass roots and rhizomes can store carbohydrates as an energy reserve for periods and utilize them when photosynthesis rates are low, such as in winter (Touchette & Burkholder 2000). Storage of carbohydrates in belowground biomass appears to be an important mechanism for *T. testudinum* in Santa Rosa Sound.

Seagrasses raise the organic content of sediments through their own production and by that of other organisms, particularly the benthic and epiphytic algae that coexist with them (Duarte et al. 2005). This is reflected in the correlations ($P < 0.02$ to < 0.001) of belowground biomass weights, shoot numbers, and leaf growth rates with sediment PC concentrations and PN concentrations. The only plant parameter correlated with NH_4^+ concentration was leaf growth rate. This correlation might be related to *T. testudinum* N requirements whereby growth is stimulated by availability of NH_4^+ .

Ammonium concentrations were highest in the root zone and the detection of nitrate in the Santa Rosa sound *T. testudinum* sediments, as previously reported by Smith et al. (2004), suggests rapid rhizosphere N cycling. Inhibition of nitrification by sulfide (Joye & Hollibaugh 1995), coupled with the intense microbial activity observed in the top sediment layers, could have contributed to the flux of ammonium into the overlying water (Table III). The *T. testudinum* beds may thus be a source or a sink for inorganic N that could vary with season and meadow. *Zostera marina* apparently can tolerate high levels of ammonium in the sediment but is more sensitive to ammonium ($\sim 25 \mu\text{M}$) in the water column (van Katwijk et al. 1997). The potential toxicity of ammonium to *T. testudinum* requires further investigation.

Sulfate reduction

Sulfate reduction is the dominant terminal electron acceptor in seagrass bed sediments (Devereux 2005; Duarte et al. 2005). Seagrass bed SRR vary with time of year, amount of light reaching the leaf canopy, plant biomass, numbers of shoots per area, sediment composition and percent organic matter. SRR are ultimately dependent on the decomposition of organic matter that provides suitable electron donors, such as the small organic acids, generated by fermentative microbial communities (Westrich & Berner 1988). Consequently, environmental factors and plant variables that promote the input and decomposition of organic matter in seagrass bed sediments will enhance sulfate reduction.

Sulfate reduction in seagrass beds has often, but not always, been positively correlated with belowground biomass and negatively correlated with shoot density (Holmer et al. 2003; Duarte et al. 2005). Smith et al. (2004) had previously found that SRR in Santa Rosa Sound *T. testudinum* beds were positively correlated with above ground biomass and negatively correlated with below ground biomass. That result was obtained from two measurements, one summer and one winter, so the SRR and biomass measurements were greatly different. SRR did not correlate with plant biomass weights or shoots m^{-2} in this study because we did not always observe significant differences in the *T. testudinum* parameters between stations or monthly sampling times.

Similar to Smith et al. (2004), we found the highest SRR in the top sediment fractions (Figure 5). High SRR in upper seagrass bed sediments result from the decomposition of deposited organic matter and inputs of labile organic matter from benthic algae (Boschker et al. 2000; Holmer et al. 2003; Papadimitriou et al. 2005). Seagrass roots release organic C compounds that support sulfate reduction (Blaabjerg & Finster 1998; Blaabjerg et al. 1998; Holmer et al. 2003; Jones et al. 2003; Kaldy et al. 2006). The top 2 cm of sediments in this study contained few roots so it is likely that detritus, rather than *T. testudinum* root exudates, fueled sulfate reduction in the top sediment layer. SRR, including

Table IV. Pearson correlation coefficients (upper) and p values (lower) for sediment biogeochemical and *Thalassia testudinum* parameters. Comparisons were between means of sediment chemical concentrations; mean sediment pore water pH values; DIC and NH_4^+ concentrations; water temperature at time of sampling; and mean *T. testudinum* values per station and sampling time ($n = 24-36$). *T. testudinum* parameters: L CN, leaf C:N ratio; L CP, leaf C:P ratio; L GR, leaf growth rate; SSM, shoots per square meter; BGM, belowground biomass weight; L, leaf biomass weight.

	pH	Temp	SRR	Fe	AVS	CRS	OP	IP	PC	PN	DIC	NH ₄	L CP	L GR	SSM	BGM	L
pH	-																
Temp	-	-	0.787		-0.529						0.459		0.498			-0.393	
SRR	<0.001		-										0.406				
Fe				-													
AVS	0.002					0.597	0.637	0.655	0.717	0.539	0.387				0.410	0.360	
CRS				<0.001	0.02	0.400	0.568	0.340	0.540	0.334	0.330					0.358	0.368
OP				<0.001	<0.001	<0.001	-	0.676	0.569	0.400							
IP				<0.001	<0.001	0.04	<0.001	-			0.457						
PC				<0.001	<0.001	<0.001	<0.001		<0.001	0.867				0.499	0.598	0.520	
PN				<0.001	<0.001	0.05	0.02		<0.001	-		0.334		0.474	0.518	0.403	
DIC				0.02		0.05		0.005			0.05	-		0.434			
NH ₄																	
L CP		0.008	0.04										-		0.519	0.560	0.778
L GR				0.02					0.01	0.02	0.03		0.01		-	0.816	0.395
SSM				0.04					<0.001	0.002			0.004		0.07	-	0.582
BGM		0.02				0.04			0.002	0.02			<0.001		0.02	<0.001	-
L						0.03											

those measured by Smith et al. (2004), reached over 1000 nmol m⁻¹ day⁻¹ in Santa Rosa Sound *T. testudinum* beds and are among the highest reported for seagrass beds.

SRR were determined on cores incubated in the dark so effects of benthic algal photosynthesis on sulfate reduction in the seagrass bed sediments are not known. Oxygen produced from benthic algal photosynthesis is expected to inhibit sulfate reduction, although high SRR are known to occur under oxic conditions in photosynthetically active microbial mats (Fründ & Cohen 1992). SRR in the seagrass beds may have been inhibited during the day by oxygen fluxing from the algae which also would provide a potent oxidant of NH_4^+ . NH_4^+ can also be oxidized with NO_2^- under anaerobic conditions via the ANAMMOX reaction which may be prevalent in estuarine sediments and account for 1–11% of N_2 production (Nicholls & Trimmer 2009). Another alternative is a potential for anaerobic NH_4^+ oxidation coupled to sulfate reduction as recently proposed to occur in deep sea sediments (Schrum et al. 2009). If sulfate-reducing bacteria are able to oxidize NH_4^+ , then NH_4^+ diffusing upwards into the zone of high SRR could be oxidized through sulfate reduction.

Sulfur, iron, and phosphorus

High SRR can lead to the accumulation porewater sulfide. However, sulfide can be efficiently oxidized in seagrass beds because oxygen is released through the roots during photosynthesis (Holmer et al. 2003). Porewater sulfate concentrations measured in this study, for the most part, remained constant with sediment depth (not shown) indicating rapid turnover of sulfide. Previously, Smith et al. (2004) found that sulfate was enriched in Santa Rosa Sound *Thalassia testudinum* seagrass bed sediments whereas it was lowered in unvegetated sediments in July, and that February sulfate concentrations remained constant with depth in both vegetated and non-vegetated sediments. Likewise, Holmer et al. (2003) noted that sulfate was not depleted in sandy carbonate sediments supporting *Posidonia oceanica*. These studies suggest that seagrass bed sediment sulfide produced from sulfate reduction can be efficiently oxidized to sulfate.

An additional sink for sulfide in sediments is reaction with Fe to form AVS and CRS. The AVS pool was a very small fraction of TRS, indicating sulfide is rapidly oxidized to sulfate, as mentioned above, or incorporated into pyrite especially with depth into the sediment. Fe and CRS concentrations were strongly correlated ($P < 0.001$) and there was sufficient Fe in the sediments to account for all CRS in the form of

FeS₂ (Figure 9). It is possible that some of the CRS would be in the form of S⁰ as an end product of sulfide oxidized with oxygen released through the roots. However, we did not assay for S⁰ directly and do not have information on relative amounts of reduced and oxidized Fe in the sediments. The concentrations of Fe and CRS in Santa Rosa Sound sediments did not differ substantially from those measured in Florida Bay (Chambers et al. 2001). Therefore, seagrasses in Santa Rosa Sound, and other Gulf of Mexico estuaries having terrigenous sediments, could be exposed to similar levels of dissolved sedimentary sulfide as those in Florida Bay.

Leaf C:P ratios were correlated with temperature ($P=0.008$) and SRR ($P=0.04$) and likely reflect C being taken up more efficiently than P during growth and leading to P limitation. The recycling of P and binding of P to oxidized forms of Fe when SRR are high may affect availability of P to the plants. Leaf C:P ratios did not correlate with sediment P concentration. Instead of a simple relationship with sediment P, availability of P appears to depend on complex interactions of P, Fe and S (Holmer et al. 2005). OP had peak concentrations in sediments between 3 and 10 cm. The correlations of OP, PC, and PN concentrations, and the similarities in the shapes of the depth profiles, indicate burial of P with organic matter perhaps through accumulation of belowground biomass. IP concentration profiles showed decreased concentrations with depth and may reflect IP uptake by *T. testudinum* roots, incorporation into leaf biomass, and then deposition and mineralization of OP on the sediment surface where OP and IP concentrations are nearly equivalent. Such P cycling and conservation of P may explain a lack of correlation between P concentrations and plant growth rates or biomass weights despite the apparent P limitation.

The basis of seagrasses as ecological engineers (Orth et al. 2006) begins with their own growth and the transformation of sediments through enrichment with organic matter that supports their growth (Duarte et al. 2005). This concept is illustrated by our study where the growth and biomass of *T. testudinum* in Santa Rosa Sound were related to concentrations of sediment organic matter and the biogeochemical cycles driven by organic matter decomposition.

Acknowledgements

We thank the GED field and dive teams for their assistance with sample collections; Jed Campbell, Will Davis, Peggy Harris, Becky Hemmer, Deborah Santavy, and Sherry Vickery; Brad Blackwell, and George Smith for additional technical support; and Paul Soderlind for preparation of figures. The information in this document has been funded

wholly or in part by the US Environmental Protection Agency. It has been subjected to review by the National Health and Environmental Effects Research Laboratory and approved for publication. Approval does not signify that the contents reflect the views of the Agency, nor does mention of trade names or commercial products constitute endorsement or recommendation for use. This is contribution no. 1344 from USEPA NHEERL Gulf Ecology Division.

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Editorial responsibility: Kjersti Sjøtun