

# Effects of seagrass *Thalassia testudinum* on sediment redox

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**ABSTRACT:** The redox conditions were compared in vegetated versus unvegetated sediments across a range of contrasting *Thalassia testudinum* (sometimes mixed with *Syringodium filiforme*) meadows at Puerto Morelos Mexico reef lagoon. Moreover, the role of seagrass photosynthetic activity in affecting the redox conditions was tested in one of the meadows by experimentally reducing seagrass photosynthesis through shading. The seagrass rhizosphere extended 26 to 40 cm into the sediment, and accounted for 23 to 504 g DW m<sup>-2</sup> of root material, mostly contributed by *T. testudinum*. *T. testudinum* placed 50% (i.e. centroidal depth) and 95% of its root biomass within 12.6 ± 0.58 and 54.4 ± 2.53 cm of the sediment surface, respectively; while *S. filiforme* placed 50 and 95% of its root biomass within 8.0 ± 0.87 and 34.7 ± 3.8 cm of the sediment surface, respectively. Vegetated sediments presented 50% of positive redox potential anomaly (i.e. redox potential in vegetated sediments – redox potential in adjacent bare sediments), remarkably similar (*t*-test, *p* > 0.5) to depths to the centroidal depth of the seagrass roots in the sediments. The shading experiment conducted *in situ* for 5 d demonstrated that the positive redox anomaly found at depth in vegetated sediments was derived from seagrass photosynthetic activity. The sediments around seagrass rhizosphere in the shaded plots were progressively reduced to reach an average decline of the redox conditions by about 45 mV by Day 5. The results presented show that seagrasses contribute to modify sediment redox conditions around their rhizosphere.

**KEY WORDS:** *Thalassia testudinum* · *Syringodium filiforme* · Rhizosphere · Redox conditions · Mexican Caribbean

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## INTRODUCTION

Seagrass beds, which rank among the most productive communities in the biosphere (Duarte & Chiscano 1999) maintain a number of ecosystem functions, such as carbon storage, food-web support, and oxygenation of the water column (e.g. Duarte & Cebrián 1996, Gattuso et al. 1998). Seagrasses live in the interface between the water column and the sediments, and extend metabolically active surfaces (leaves and roots) in both of these environments. Whereas the effects of seagrass metabolism on water-column properties have been extensively documented, the possible effects in

the sediments are still poorly investigated (Hemminga 1998). There is, however, solid evidence that seagrasses release oxygen through their roots (Pedersen et al. 1998, Connell et al. 1999, Terrados et al. 1999), which may affect the redox conditions of the sediment around the rhizosphere. This role of seagrass roots will, if confirmed, influence the metabolic pathways of the associated sediment bacteria, thereby influencing sediment biogeochemical processes.

Here, we examine the hypothesised effect of seagrass roots on sediment redox conditions across a range of seagrass meadows growing in the Mexican Caribbean. We first compare redox conditions in vegetated versus unvegetated sediments across a range of contrasting meadows within a reef lagoon, and then we test the role

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of seagrass photosynthetic activity in affecting the redox conditions by experimentally reducing seagrass photosynthesis *in situ* through shading.

## MATERIAL AND METHODS

We examined the effect of seagrass vegetation on sediment redox conditions in 7 seagrass meadows of a Mexican reef lagoon (Puerto Morelos, Quintana Roo, Yucatan) in October 1999. Of the 4 meadows examined which grow along the coastline, 2 are exposed to heavy wave action and 2 are situated in the coastal fringe somewhat deeper. Another 2 meadows are in the middle part of the lagoon, and 1 other meadow is close to the coral reef (Fig. 1). *Thalassia testudinum*, the most abundant Caribbean seagrass species, was present in all of the selected meadows, which differed in aboveground biomass and species composition (Table 1).

At each site, we harvested 5 replicated 20 by 20 cm<sup>2</sup> quadrats for aboveground plant biomass, and collected between 3 and 4 sediment cores to estimate root biomass and determine sediment redox conditions. In addition, we collected 2 to 3 cores from unvegetated sediments adjacent to the vegetated ones. The PVC cores had an internal diameter of 7.3 cm, were 50 cm long, and had 2 opposite vertical lines of 1.3 cm diameter holes, spaced every 4 cm and placed 2 cm out of phase on each line. The holes were sealed with waterproof adhesive tape prior to sampling. Sediment redox potential was measured immediately after sampling with a Crison redox electrode coupled to a portable pH meter (Crison model 507), calibrated with a redox standard solution at 25°C (Crison 468 mv). Sediment

redox potential values were obtained by carefully removing the waterproof adhesive tape covering each of the holes in the core wall, and inserting the electrode into the sediment. We repeated this procedure for each hole along the core, starting from the sediment-water interface down to the deepest sediment sampled. We alternately punched the sediment through the holes of each opposite and out-of-phase vertical line, obtaining redox measurements every 2 cm along sediment depth.

We chose to measure redox potential as an indicator of the general biogeochemical conditions in the sediment, while acknowledging the limitations of this approach (e.g. Stumm & Morgan 1996, Schüring et al. 2000). Platinum electrodes, as those used here, are not inert, forming Pt-oxides in oxic environments, which can be prevented by regularly cleaning and polishing them. Some redox couples ( $\text{NO}_3^- - \text{NO}_2^- - \text{NH}_4^+$ ;  $\text{CH}_4 - \text{CO}_2$ ) are not electro-active at the surface of the Pt electrode and, therefore, were missed. Yet, the nitrate concentrations in sediments and waters in the Caribbean areas investigated were very low (0.62 to 2.49  $\mu\text{M}$   $\text{NO}_3^- - \text{NO}_2^-$  in pore water; 0.07 to 1.99  $\mu\text{M}$   $\text{NO}_3^- - \text{NO}_2^-$  in water column, Pantoja-Reyes unpubl. data), indicating the error of Pt electrode estimates of sediment redox potential to be small. Similarly, an important  $\text{CH}_4 - \text{CO}_2$  component was unlikely, given the Eh values measured, to be present. Hence, the range of redox values and the oligotrophic conditions in the system investigated suggest that measurements by Pt electrodes provide an adequate approximation of redox potentials in this environment and that measurement bias is kept to a minimum. However, the redox potential measured with Pt electrodes reflects a mixture of several reactions, preventing a quantitative inference on the actual processes occurring.

Therefore, sediment redox potential in this study provided an indication of the gross geochemical conditions in the sedimentary environment, without providing insight into the actual processes taking place.

The plant samples and sediment cores were transported to the laboratory. We determined the species composition of the aboveground plant material, splitting them into 4 main groups: *Thalassia testudinum*, *Syringodium filiforme*, rhizophytic macroalgae, and non-rhizophytic macroalgae. The sorted samples were weighed after drying for 24 h at 60°C. Sediment cores were cut into 2 cm thick slices, and sieved to separate seagrass belowground material from sediment and debris. Alive rhi-

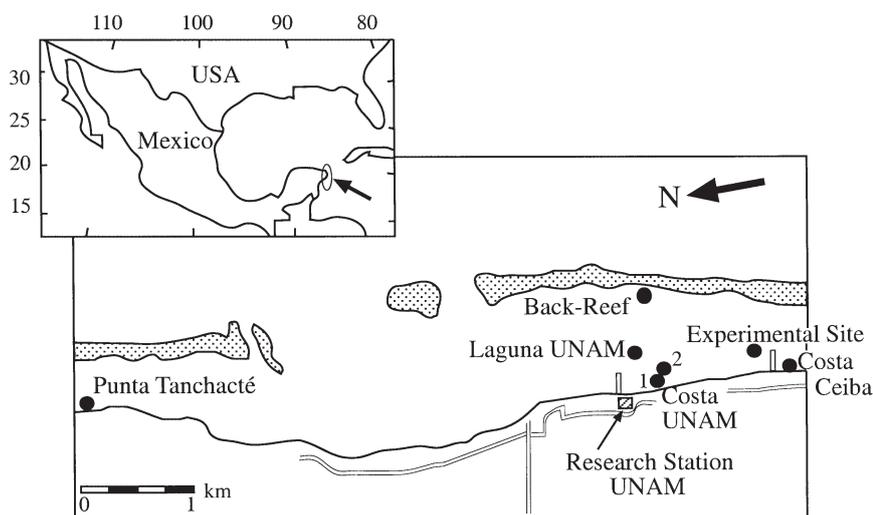


Fig. 1. Map of the reef lagoon of Puerto Morelos indicating sampling locations

Table 1. Average ( $\pm$  SE) seagrass and macroalgal biomass ( $\text{g DW m}^{-2}$ ) and organic content in the top 10 cm of sediment in the meadows studied. Plant biomass was estimated from 5 samples. The number of observations (n) of sediment organic content is given within parentheses

Site	Species	Aboveground	Rhizomes	Roots	Sediment organic content (%)
Costa UNAM1	<i>Thalassia testudinum</i>	25.7 $\pm$ 4.5	289.0 $\pm$ 27.5	162.0 $\pm$ 20.0	1.47 (5)
	<i>Syringodium filiforme</i>	0.6 $\pm$ 0.2	11.8 $\pm$ 4.2	18.3 $\pm$ 6.4	
	Non-rhizophytic algae	158.0 $\pm$ 101.0			
	Rhizophytic algae	20.5 $\pm$ 5.7			
Experimental site	<i>Thalassia testudinum</i>	30.6 $\pm$ 5.3	269.0 $\pm$ 75.0	274.9 $\pm$ 88.8	2.63 (1)
	<i>Syringodium filiforme</i>	2.1 $\pm$ 1.6	23.9 $\pm$ 18.5	35.9 $\pm$ 21.4	
	Non-rhizophytic algae	9.0 $\pm$ 6.0			
	Rhizophytic algae	24.5 $\pm$ 7.0	237.0 $\pm$ 70.0		
Arrecife	<i>Thalassia testudinum</i>	19.9 $\pm$ 2.2	22.0 $\pm$ 2.2	147.3 $\pm$ 24.8	2.38 (2)
	<i>Syringodium filiforme</i>	5.7 $\pm$ 2.6		23.4 $\pm$ 5.1	
	Non-rhizophytic algae	17.2 $\pm$ 19.3			
	Rhizophytic algae	15.4 $\pm$ 3.3			
Pta. Tanchacté	<i>Thalassia testudinum</i>	163.6 $\pm$ 6.5	372.0 $\pm$ 155.0	106.0 $\pm$ 40.0	2.98 (1)
	<i>Syringodium filiforme</i>	1.4 $\pm$ 1.5			
	Non-rhizophytic algae	0			
	Rhizophytic algae	0			
Costa UNAM 2	<i>Thalassia testudinum</i>	11.5 $\pm$ 6.9	125.0 $\pm$ 12.0	28.5 $\pm$ 7.8	4.59 (1)
	<i>Syringodium filiforme</i>	87.6 $\pm$ 22.4	195.0 $\pm$ 41.0	95.3 $\pm$ 20.6	
	Non-rhizophytic algae	104.6 $\pm$ 46.2			
	Rhizophytic algae	66.5 $\pm$ 29.9			
Laguna UNAM	<i>Thalassia testudinum</i>	29.8 $\pm$ 11.7	149.0 $\pm$ 44.2	159.0 $\pm$ 36.5	2.82 (2)
	<i>Syringodium filiforme</i>	11.4 $\pm$ 2.9	33.0 $\pm$ 12.1	32.8 $\pm$ 9.4	
	Non-rhizophytic algae	51.4 $\pm$ 26.7			
	Rhizophytic algae	15.9 $\pm$ 10.4			
Ceiba orilla	<i>Thalassia testudinum</i>	112.4 $\pm$ 6.6	765.0 $\pm$ 312.0	425.0 $\pm$ 85.0	1.79 (4)
	<i>Syringodium filiforme</i>	15.9 $\pm$ 8.4	29.9 $\pm$ 12.0	79.5 $\pm$ 33.4	
	<i>Halodule wrightii</i>	0.3			
	Non-rhizophytic algae	0			
	Rhizophytic algae	7.0 $\pm$ 4.7			

zomes and roots were sorted by species, dried at 60°C for 24 h, and weighted. A sediment subsample of vegetated sediment was also dried at 60°C for 24 h, and burned at 400°C for 2 h. These measurements provided estimates of aboveground biomass, depth distribution of rhizosphere biomass, and sediment organic matter content.

We selected a middle lagoon meadow (3.3 m deep) to perform a shading experiment to test the link between seagrass photosynthetic activity and sediment redox conditions (Experimental Site, Fig. 1). We reduced the irradiance on three 2 m<sup>2</sup> seagrass plots by 73% of the ambient level, by placing 3 cages covered with a neutral (i.e. with a homogeneous light absorption spectrum along the PAR range) density net. Another three 2 m<sup>2</sup> plots with uncovered cages were used as controls. The light reduction in the shaded plots was determined *in situ*, 5 d after the start of the experiment, by measuring simultaneously scalar irradiance at 5 cm above the sediment in the middle of 1 shaded and 1 control plot, with two 4 $\pi$  sensors coupled to a Li-Cor data logger (LI-1400) over 4 h. Sediment redox condi-

tions and the photosynthetic activity of *Thalassia testudinum*, the dominant seagrass species, were measured at the beginning of the experiment, and 2, 5, and 10 d after the experiment was initiated. Between Days 5 and 10, a strong frontal system passed by, leading to disturbance derived from abrupt changes in water temperature (decrement of 3°C), and sediment resuspension, which reduced underwater light by 45%. Sampling of the plots was conducted at the time of peak irradiance (i.e. between 12:00 and 14:00 h). At each sampling, we collected 1 PVC sediment core from each plot and measured the vertical profile of sediment redox potential as described above.

We directly followed the response of the photosynthetic activity of *Thalassia testudinum* to shading by estimating Electron Transport Rate of photosystem II (ETR,  $\mu\text{mol e}^- \text{m}^{-2} \text{s}^{-1}$ ), which is the apparent relative rate of electron transport using a diving PAM fluorometer (Diving-PAM Walz, Germany). We did so measuring *in situ* the steady-state fluorescence ( $F_v/F_m'$ ) of the second youngest leaf of the shoot yield at 5 cm above the sediment, on 5 replicates per plot. We also deter-

mined leaf light availability at 5 cm above the sediment using a 2 mm diameter cosine corrected light sensor (Miniature Fiberoptics Diving-F1) connected to the Quantum sensor of the Diving-PAM housing. This sensor was previously calibrated against a LI-192SA cosine corrected light sensor attached to a data-logger (Li-Cor Inc., USA). Water temperature was recorded simultaneously using a water temperature sensor built in Diving-PAM device. *ETR* was estimated according to the equation proposed by Genty et al. (1989),

$$ETR = F_v/F_m' \times PAR \times Absorptance \times 0.5$$

where  $F_v/F_m'$  is the steady state fluorescence yield, *PAR* is the instantaneous photosynthetic active irradiance, *Absorptance* is the fraction of incident light absorbed by the leaf, and 0.5 is a constant derived from the fact that there are 2 coupled photosystems simultaneously absorbing light. Absorptance was determined for each sampling day by measuring spectrophotometrically leaf absorptance on 6 shaded and 6 control second leaves using a dual-beam spectrophotometer SLM-AMINCO (DW-2C, UV-VIS) equipped with 2 opal-glass units (Shibbata 1959).

Redox measurements were corrected to obtain Eh values relative to the standard hydrogen electrode (APHA 1992). We calculated the redox potential anomaly in each site as the difference between the average redox potential at similar depths into the sediment in vegetated and bare sediments. Similarly, the redox potential anomaly in the experimental plots was estimated as the difference between the average redox potential at similar depths into the sediment in control and shaded plots on Days 2, 5, and 10. We summarized the depth distribution of seagrass root biomass and redox potential anomaly using the model  $Y = 1 - \beta^d$  (Gale & Grigal 1987), where *Y* is the fractional cumulative (i.e. fraction between 0 and 1) root biomass and redox potential anomaly, respectively, from the sediment surface to depth *d* (cm), and  $\beta$  is the fitted extinction coefficient (Jackson et al. 1996). The equation was fitted using non-parametric regression (Wilkinson 1989). The centroidal depth of root biomass and redox potential anomaly is calculated using the model, as the sediment depth comprising 50 and 95% of the root biomass or positive redox potential anomaly.

## RESULTS

The meadows surveyed ranged widely in macrophyte biomass (Table 1), with 2 of the meadows dominated by *Thalassia testudinum* and the rest of them comprising a mixed seagrass (*T. testudinum* and *Syringodium filiforme*) and algal community (Table 1). The communities were all growing over carbonate

sediments (mostly coral rubble and *Halimeda*-derived carbonate, Duarte et al. 1995) with relatively low organic content (2.1% DW, Table 1). The seagrass rhizosphere extended 26 to 40 cm into the sediment (Fig. 2), and jointly contributed 23 to 504 g DW m<sup>-2</sup> of root material, representing 14 to 46% of the total seagrass biomass, mostly contributed by *T. testudinum* (Table 1). 50 and 95% of the root biomass was comprised within the sediment layer 10 to 15 and >40 cm deep, respectively (Table 2), but this depth differed significantly (*t*-test, *p* < 0.01) between seagrass spe-

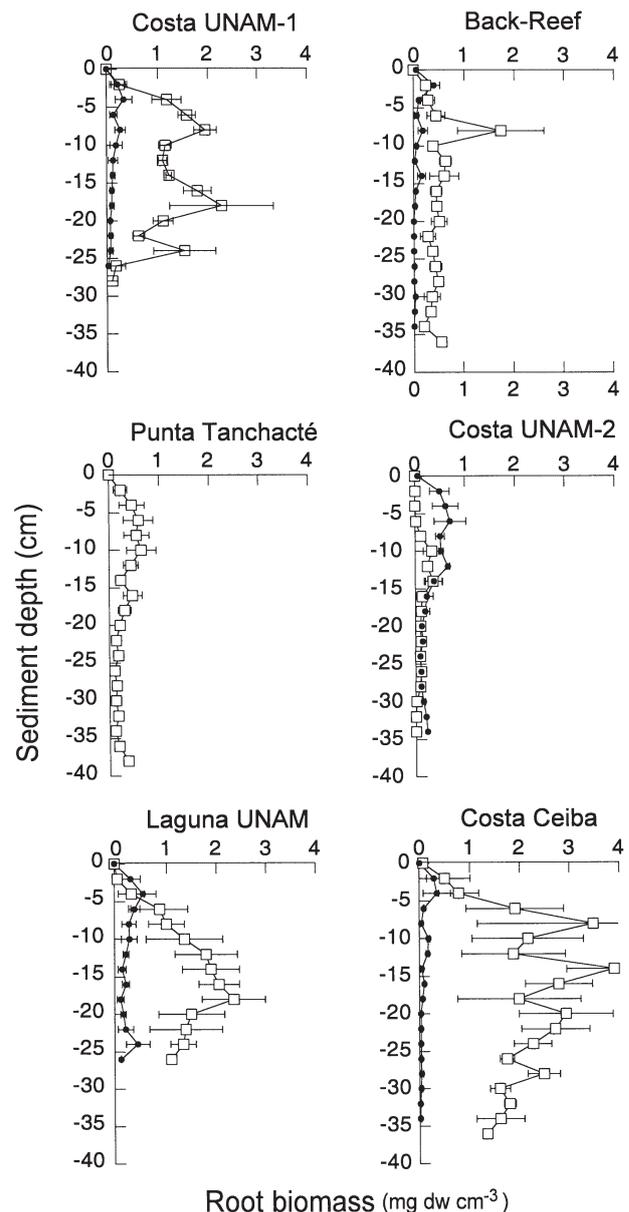


Fig. 2. Depth profile of mean  $\pm$  SE root biomass ( $n = 4$ ) of *Thalassia testudinum* ( $\square$ ) and *Syringodium filiforme* ( $\bullet$ ) within seagrass rhizosphere at 6 meadows at the Puerto Morelos reef lagoon

Table 2. The sediment depth comprising 50 and 95% of the root biomass of *Thalassia testudinum* and *Syringodium filiforme*, community root biomass, and positive redox potential anomaly in the meadows studied; the mean ( $\pm$  SE) value for all meadows is given

Centroidal depth site	<i>Thalassia testudinum</i> (cm)		<i>Syringodium filiforme</i> (cm)		Seagrass rhizosphere (cm)		Positive redox potential anomaly (cm)	
	50%	90%	50%	90%	50%	90%	50%	90%
Costa UNAM 1	10.1	43.7	6.8	29.7	9.7	42.1	10.6	45.9
Experimental site	13.9	60.2	11.8	50.9	13.5	58.4		
Arrecife	12.8	55.4	5.0	21.6	11.7	50.7	14.2	61.5
Punta Tanchacté	11.3	48.9			11.3	48.9	10.4	44.8
Costa UNAM 2	12.1	52.4	8.58	37.1	9.3	40.2		
Laguna UNAM	13.1	56.5	9.2	39.6	12.3	53.2	6.5	28.3
Ceiba orilla	14.7	63.4	6.8	29.5	14.3	61.8		
Mean	12.6	54.4	8.0	34.8	11.7	50.8	10.4	45.1
SE	0.6	2.5	0.9	3.8	0.7	3.0	1.1	4.8

cies, with *T. testudinum* placing 50 and 95% of its root biomass within  $12.6 \pm 0.58$  and  $54.4 \pm 2.53$  cm of the sediment surface, respectively, while *S. filiforme* placed 50 and 95% of its root biomass within  $8.0 \pm 0.87$  and  $34.7 \pm 3.8$  cm of the sediment surface, respectively.

Negative redox potentials were encountered between 4 and 18 cm below the sediment surface (Fig. 3). There were important differences in the redox potential between vegetated and bare sediments, with surface sediments often having more positive redox potentials in bare sand than under plant canopies (Fig. 3). However, this tendency was reverted with increasing depth, such that the vegetated sediments maintained redox potentials above those of the adjacent bare sediments from depths greater than 10 to 16 cm (Fig. 3). The sediment layer with higher redox potentials in vegetated compared to adjacent bare sediments (i.e. positive anomaly) had a centroidal depth (i.e. the depth comprising 50% of the anomaly) ranging from 6 to 14 cm (Table 2), which was remarkably similar ( $t$ -test,  $p > 0.5$ ) to the centroidal depth of the seagrass roots in the sediments (Table 2). The centroidal depth of the positive redox anomaly in vegetated sediments was much closer to that of the root biomass of *Thalassia testudinum*, which comprised most (79% on average) of the root biomass, compared to that of *Syringodium filiforme* (Table 2). The rhizosphere of the examined meadows presented maximum values of the positive anomaly ranging from 39 to 211 mV. The vertical coupling between sediment redox conditions and rhizosphere biomass suggests that seagrass roots modify the redox conditions of the colonised sediments.

Whether the positive redox anomaly found at depth in vegetated sediments derives from seagrass photosynthetic activity, was tested by shading vegetated plots to experimentally reduce seagrass photosynthetic activity. We found significant differences in the photo-

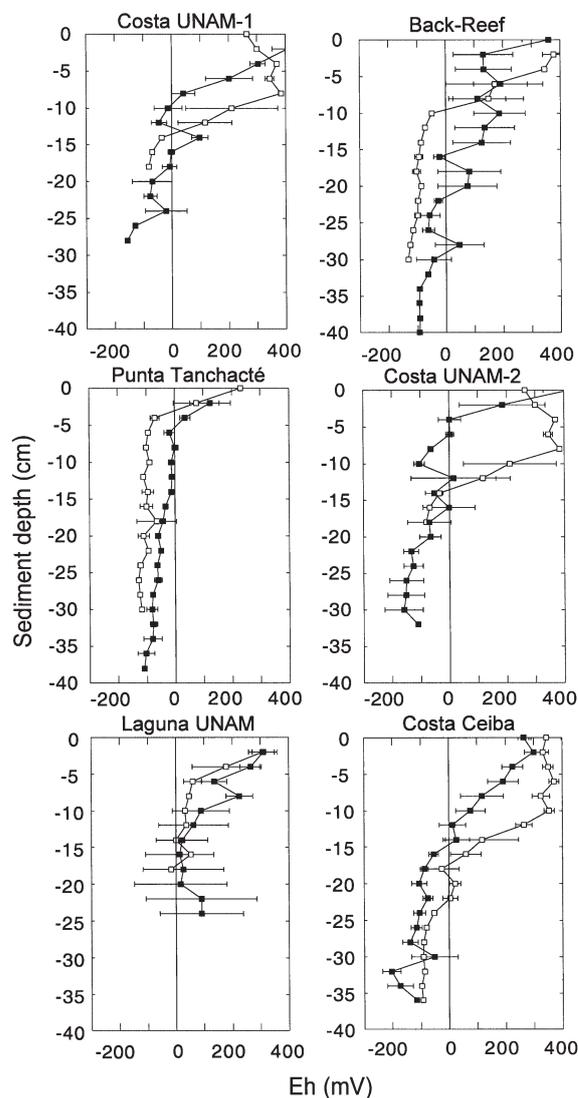


Fig. 3. Depth profiles of mean  $\pm$  SE redox potential in vegetated ( $\blacksquare$ ,  $n = 4$ ) and adjacent bare ( $\square$ ,  $n = 3$ ) sediments at 6 sites from Puerto Morelos reef lagoon

synthetic rates, estimated as electron transport rates ( $ETR$ ), between control and shaded leaves ( $t$ -test  $p < 0.01$ ), and between initial (Day 2) and final (Day 10)

values for both treatments ( $t$ -test  $p < 0.01$ , Fig. 4c). The differences in  $ETR$  of control and shaded *Thalassia testudinum* leaves closely matched those in the incident PAR (Fig. 4a,c), with the  $ETR$  of shaded *T. testudinum* leaves being about 4-fold lower on average than those of control plants, similar to the reduction in PAR imposed by shading (4.5-fold on average). The steady-state fluorescence yield ( $F_v/F_m'$ ) increased significantly (9% greater on average) in the shaded plants ( $t$ -test,  $p < 0.01$ ), 2 d after the onset of shading. These differences were observed along the experiment (Days 5 and 10) although a significant reduction (4 to 6% lower on average) was associated to a progressive decrease in  $F_v/F_m'$  for both treatments. The reduction observed in  $F_v/F_m'$  along the experiment was probably due to the stress caused by the passage of the frontal storm. To describe the effect of the experimentally induced reduction in light availability together with the effect of the frontal storm on leaf photosynthetic performance of *T. testudinum*, we used a descriptor of excitation pressure on PSII sensu Maxwell et al. (1995), estimated as  $1 - [(F_v/F_m')/F_v/F_m]$ , where  $F_v/F_m$  is the maximum yield showed by dark-adapted leaves at the beginning of the experiment, and  $F_v/F_m'$  is the *in situ* steady-state yield measured at the peak of irradiance. According to the former definition, PSII excitation pressure varies between 0 (no pressure) and 1 (maximum pressure). The values estimated reflected lower PSII excitation pressure for the shaded leaves and a significant increase for both treatments at the end of the experiment (Fig. 4b). The maximum photochemical yield ( $F_v/F_m$ ) of dark-adapted leaves showed a similar 9% decrease for both control and shaded treatments ( $F_v/F_m = 0.73 \pm 0.007$ ) at the end of the experiment (Day 10), confirming that *T. testudinum* photosynthetic performance was affected by the frontal storm. However, the values of the excitation pressure on PSII were all  $< 0.2$  (Fig. 4b), indicating low PSII pressure along the experiment on both treatments. In addition, light (PAR-average) absorption by the leaves (*Absorptance*) increased by 11% with increasing shading along the course of the experiment (initial =  $69.27 \pm 1.4\%$ , 10 d after shading:  $76.2 \pm 1.2\%$ , Fig. 4b), indicating a fast photoacclimation response of *T. testudinum* leaves

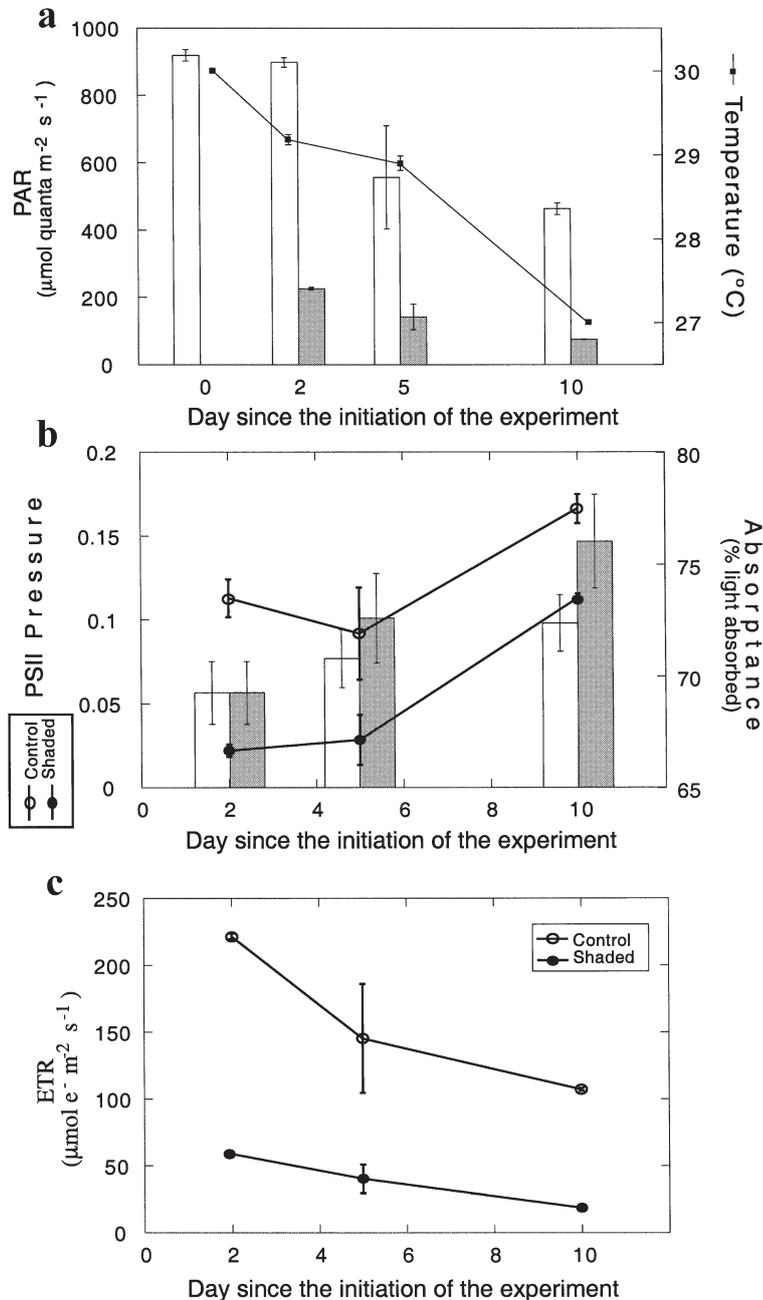


Fig. 4. (a) Mean  $\pm$  SE of PAR irradiance along the course of the experiment for control (open bars) and 73% shading treatment (filled bars), and mean  $\pm$  SE water temperature ( $^{\circ}\text{C}$ ) during sampling (middle panel); (b) mean  $\pm$  SE of PSII pressure defined as  $[1 - (\text{steady-state yield})/(\text{maximum yield of dark adapted leaves})]$ , and leaf absorptance (percentage of light absorbed by the leaf).  $\circ$ : PSII pressure of control treatment leaves, and  $\bullet$ : PSII pressure of shaded leaves; open bars represent absorptance values of control leaves, and filled bars represent absorptance values of shaded leaves. (c) Mean  $\pm$  SE of Electron Transport Rate ( $ETR$ ) throughout the experiment.  $\circ$ : control treatment and  $\bullet$ : shading treatment

over the short term of the experiment. Because the changes in  $F_v/F_m'$  and *Absorbance* were moderate (about 6 to 10%) compared to the shading imposed (4.5-fold), the *ETR* variation was dominated by shading.

The passage of the frontal system caused stronger reductions in the photosynthetic rates than those induced by the experimental setup, due to the additional reduction in light availability and the effect of water temperature on plant photosynthetic performance. As a consequence, differences in sediment redox conditions between control and shaded plots were only significant for the first 5 d (Figs 5 & 6). The time series of redox conditions clearly showed a shift in the redox conditions of the shaded plots with time, involving a progressive reduction of the sediments (Fig. 5) to reach an average decline of the redox conditions by about 45 mV by Day 5 (Fig. 6). A significant reduction of the sediments was already evident 2 d after shading was imposed at the depth where the positive redox anomaly associated to the presence of the plant was greatest (6 to 25 cm, Wilcoxon sign ranked test,  $p < 0.01$ , Fig. 6). The anomaly extended throughout the entire sediment layer occupied by the plants (0 to 40 cm, Wilcoxon sign ranked test,  $p < 0.00055$ ) 5 d following the onset of shading (Fig. 6). The maximum negative anomaly at that time was found at the sediment surface and the deeper (>35 cm) layers.

## DISCUSSION

The results presented show that seagrasses contribute to modify sediment redox conditions around their rhizosphere. This effect includes an increase in sediment redox potential around the rhizosphere, which most probably results from oxygen released by the roots (Pedersen et al. 1998, Connell et al. 1999, Terrados et al. 1999). This is supported by: (1) the observation of a similar distribution between the root biomass and the redox anomaly in the vegetated sediments; and (2) the direct evidence that a 3-fold reduction in the photosynthetic activity of the plants, due to shading, results in a reduction of the sediments. Oxygen release comprise a significant fraction of the photosynthetic oxygen evolved (10% in *Cymodocea rotundata* Pedersen et al. 1998), as well as an apparent gradient-driven passive oxygen flow from the water to the sediment through the seagrass tissues (Pedersen et al. 1998).

Shading alone altered the photosynthetic activity of *Thalassia testudinum*, but the effect was not always proportional to the reduction of light intensity. In the first place, because the irradiance in the meadows was above the saturation irradiance ( $I_k = 300 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ , Enríquez et al. 2000). Secondly, because the plants are capable of rapid photoacclimation (e.g. the average leaf elongation rate for the second youngest

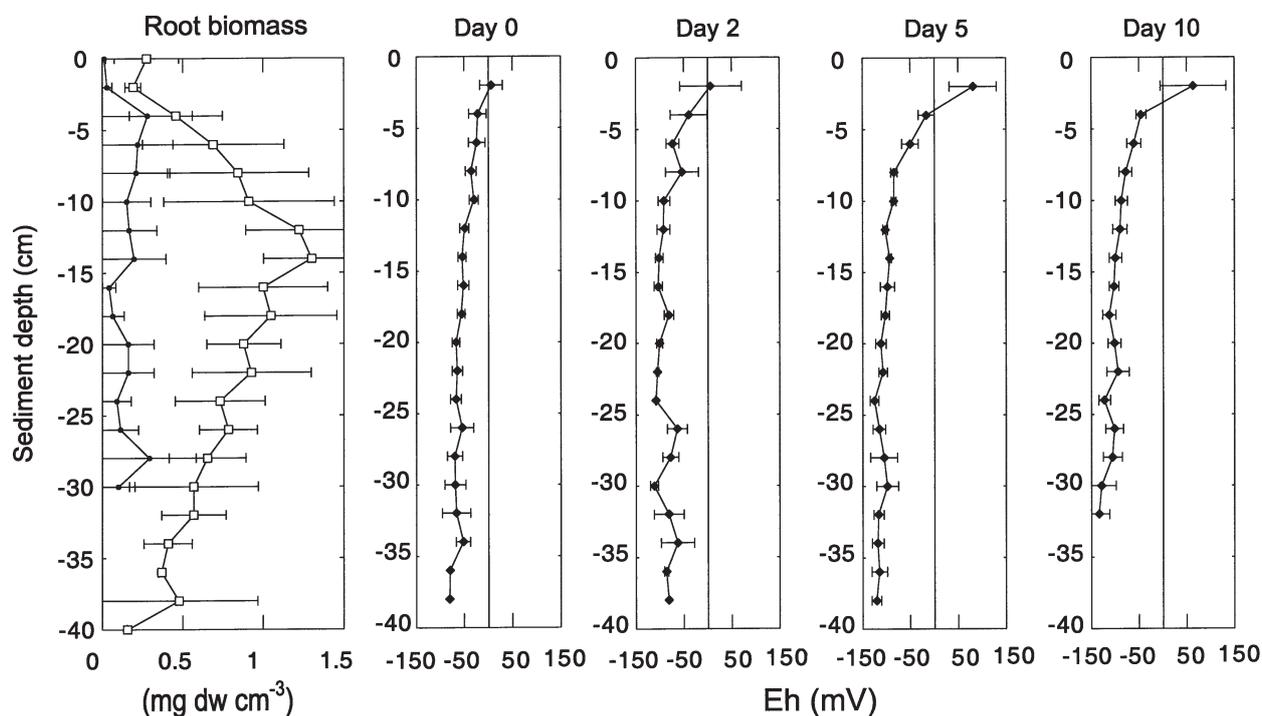


Fig. 5. Depth distribution of mean  $\pm$  SE root biomass of *Thalassia testudinum* ( $\square$ ,  $n = 4$ ) and *Syringodium filiforme* ( $\bullet$ ,  $n = 4$ ), and mean  $\pm$  SE redox potential at Days 0, 2, 5, and 10 ( $n = 3$ ) after the initiation of the experiment within seagrass rhizosphere at the experimental site

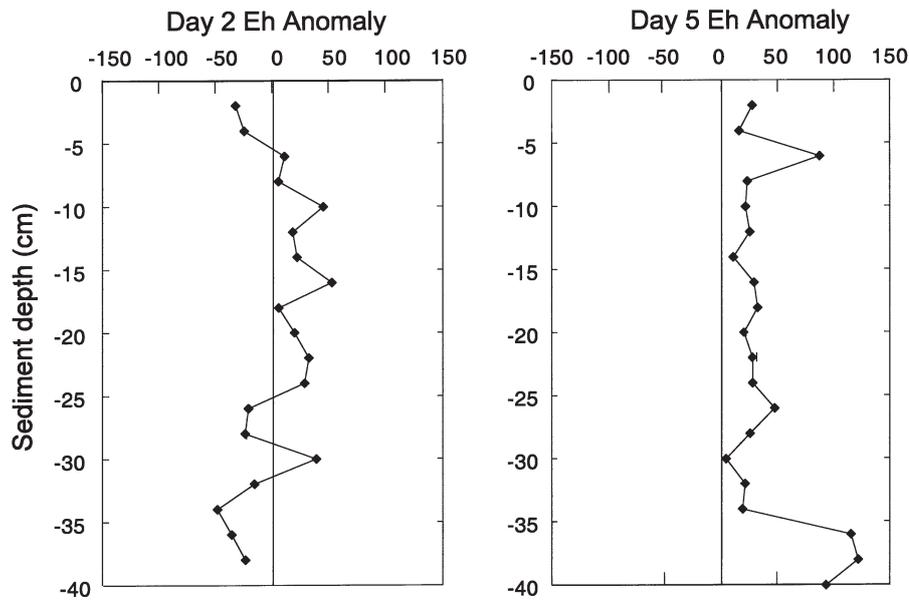


Fig. 6. Depth distribution of mean redox potential anomaly at Days 2 and 5 after the initiation of the experiment in the experimental site

leaf in the area, is close to  $0.4 \text{ cm d}^{-1}$ , van Tussenbroek 1995). The leaves were indeed able to photoacclimate to the experimental shading as reflected in the significant increment in the light they absorbed. The differences observed in photosynthetic activity between treatments may also result from differences in the diel variation of the steady-state fluorescence yield. PAM measurements were recorded at the peak of irradiance, which generally coincide with the natural diel reduction in  $F_v/F_m$  that has been extensively documented for algae, corals and seagrasses (i.e. Hanelt 1992, Hanelt et al. 1993, Franklin et al. 1996, Ralph et al. 1998, Enríquez unpubl. data). Control leaves showed significantly lower  $F_v/F_m$  values than shaded leaves, but the differences were not sufficiently large (PSII pressure  $<0.2$ ) to lead to photoinhibition, as we did not observe any significant reduction in *ETR*. The observed reduction in the photosynthetic activity between control and shaded plots was, therefore, mainly derived from differences in PAR irradiance resulting from the shading imposed. This difference resulted, on average, in a 4-fold reduction in the photosynthetic activity of the *T. testudinum* leaves assayed in the shaded plots, which should lead to a reduced oxygen flow to the roots, accounting for the enhanced reducing sediment conditions in the shaded plots.

In addition to the effects of the seagrass rhizosphere on raising sediment redox, the upper layer (up to 0 to 10 cm in depth) of vegetated sediments tended to have more negative redox potential than bare sediments. This effect may be derived from: (1) a greater respiration in the upper sediment driven by the likely in-

creased organic inputs under the seagrass canopy (Pedersen et al. 1997); (2) a reduced activity of benthic microalgae in the surface sediments shaded by the seagrass canopy; or (3) greater instability of surface sediments from unvegetated areas (e.g. Terrados & Duarte 1999). Resuspension of surface sediments should enhance the exchange of pore waters with the overlying oxygenated waters. Hence, sediment instability would lead to increased redox potential.

The time series of redox measurements following experimental shading clearly indicates these effects to be cumulative, and to propagate from the sediment layers containing the bulk of the rhizosphere (10 to 25 cm) to the deeper layers (down to 40 cm below the surface) within a few days. Indeed,

examination of the redox conditions in vegetated versus bare sediments shows that the redox anomaly has a similar depth distribution as that of the root biomass, with the centroidal depth of the anomaly being similar to that of the root biomass.

Root biomass was large in the meadows reaching up to  $504 \text{ g DW m}^{-2}$ , and comprised a large fraction (14 to 46%) of the total seagrass biomass, consistent with the nutrient limitation demonstrated for these meadows (Duarte et al. 1998). Seagrass roots form an extensive network within the sediments ( $0.89 \text{ m}^2$  of roots  $\text{m}^{-2}$  for *Thalassia testudinum* in the Puerto Morelos reef lagoon, Duarte et al. 1998), and can therefore efficiently extend their effects throughout the sediment layer. Seagrass activity during the present study was able to attenuate sediment reduction by increasing sediment redox potential by about 69 mV on average in the root layer. The increase of redox potential promoted by *T. testudinum* should modify the geochemistry of the sediments, as hypothesised by Hemminga (1998). In particular, the processes affected include: (1) stimulation of microbial activity associated to the rhizosphere (e.g. increase of sulphate reduction and nitrogen fixation, Welsh et al. 1997, Blaabjerg et al. 1998, McGlathery et al. 1998, Hansen et al. 2000); (2) prevention of the accumulation of toxic metabolites (e.g. sulphide, Terrados et al. 1999) in the rhizosphere; and (3) changes in nutrient (P and N) availability within in the rhizosphere (Reddy et al. 1989, Stumm & Morgan 1996). However, the results presented here cannot, because of limitation of the Pt-electrode measurements used, provide direct insight into the effect of

seagrass activity on sediment processes. Hence, future examination should combine measurements of seagrass activity with direct measurements of biogeochemical processes.

The examination of the effects of seagrasses on sediment conditions and the processes governing them is still in its infancy, particularly when compared to the knowledge already available on the metabolic interactions between seagrass leaves and the water column. However, seagrass-sediment interactions are important components of the functions of seagrasses in the ecosystem, and our results suggest, together with previous studies of root-sediment interactions (Kenworthy et al. 1982, Isaksen & Finster 1996, Holmer & Nielsen 1997, McGlathery et al. 1998), that seagrass play an important engineering (sensu Jones et al. 1997) role in controlling sediment biogeochemical conditions, thereby affecting the life of sediment infauna and key processes for the cycling of carbon and nutrients in these ecosystems.

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