

## Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment

J. W. Fourqurean<sup>1,\*</sup>, J. C. Zieman<sup>1</sup> and G. V. N. Powell<sup>2,\*\*</sup>

<sup>1</sup> Department of Environmental Sciences, Clark Hall, University of Virginia, Charlottesville, Virginia 22903, USA

<sup>2</sup> National Audubon Society, 115 Indian Mound Trail, Tavernier, Florida 33070, USA

Date of final manuscript acceptance: April 10, 1992. Communicated by J. M. Lawrence, Tampa

**Abstract.** The primary source of nutrients for seagrass growth is considered to be the sediment porewater. Porewater nutrient concentrations were measured in 18 seagrass beds across Florida Bay, USA, a shallow, seagrass-dominated subtropical embayment, during the summers of 1987 and 1988. Concentrations of nutrients in porewater varied widely, with median values of 0.34  $\mu\text{M}$  for soluble reactive phosphorus (SRP) and 78.6  $\mu\text{M}$  for  $\text{NH}_4^+$ . SRP and  $\text{NH}_4^+$  concentrations were positively correlated. Due to spatial heterogeneity, there were no apparent trends with sediment depth (down to 40 cm) in the porewater nutrient concentrations. The SRP concentration of the porewater was highest in areas supporting *Halodule wrightii*, intermediate in areas of *Thalassia testudinum*, and lowest in sediments without seagrasses. There was no similar relationship with  $\text{NH}_4^+$ . Porewater SRP, but not  $\text{NH}_4^+$ , was significantly correlated with total seagrass standing crop. Elemental content (both N and P) of green leaves of *T. testudinum* was a function of the concentration of the nutrients in the porewater. Standing crop of *T. testudinum* was correlated with phosphorus content, but not with N content, of the seagrass leaves. The results support the hypothesis that sediment porewaters are the most important source of nutrients for seagrass growth. In this subtropical carbonate environment, the availability of phosphorus in the porewater limits the development, and controls the species composition, of seagrass beds.

### Introduction

Nutrient and light availability are considered two of the primary physical factors limiting seagrass distribution (see Dennison 1987 and Short 1987 for reviews). Sea-

grasses are faced with a paradox in their environmental requirements: as autotrophs, they need light to survive, but they are rooted under water, a medium that attenuates light much more strongly than air. In addition to light, they require mineral nutrients to photosynthesize and build tissue. Increases in nutrients in the overlying water column increase the attenuation of light in the water column as a result of plankton growth, often leading to extirpation of seagrass beds (Zieman 1975, Orth and Moore 1983, Cambridge and McComb 1984, Giesen et al. 1990, Larkum and West 1990, and others). Seagrasses are therefore usually found in areas with relatively low nutrient concentrations in the surface water.

Seagrasses may take up nutrients through their leaves, which are bathed in this relatively nutrient-poor surface water (McRoy and Bardsdate 1970), but leaf uptake is likely to be of secondary importance, since seagrass roots penetrate the more nutrient-rich medium of the sediments. Unlike macroalgae, submerged vascular plants have true roots, evolutionarily descendant from the roots of terrestrial plants, which have retained the functions of the roots of terrestrial plants, including nutrient absorption (Agami and Waisel 1986). Root uptake of nutrients from the sediments is considered to be the most important source of nutrients for seagrasses (see Short 1987 for review).

Short (1987) suggested a regional dichotomy as to which nutrient limits seagrass growth. With few exceptions (Orth 1977, Harlin and Thorne-Miller 1981), seagrasses growing in temperate climates and terrigenous sediments are nitrogen-limited (Short 1987, Dennison et al. 1987). Seagrasses growing in tropical climates and biogenic carbonate sediments, on the other hand, are often phosphorus-limited (Short et al. 1985, 1990, Powell et al. 1989, Fourqurean et al. 1992). This difference may be a result of the geochemistry of phosphate and carbonate minerals (Short 1987), since biogenic carbonate sediments commonly bind inorganic phosphate (Berner 1974, DeKanel and Morse 1978).

Measuring the availability of nutrients to macrophytes is not easy (Chambers and Fourqurean 1991).

\* Present address: Tiburon Center for Environmental Studies, San Francisco State University, P.O. Box 855, Tiburon, California 94920, USA

\*\* Present address: RARE Center for Tropical Conservation, 1529 Walnut Street, Philadelphia, Pennsylvania 19102, USA

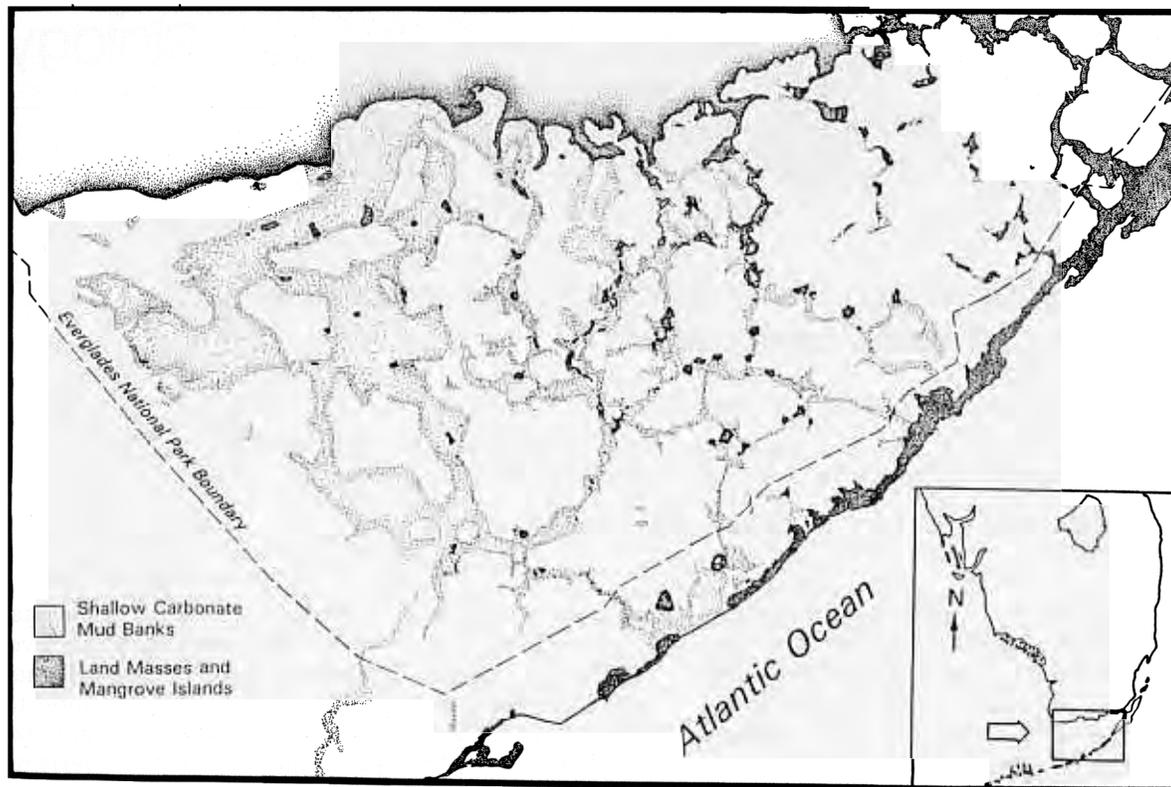


Fig. 1. Map of Florida Bay, Florida, USA

Simple measures of nutrient concentrations in sediments or porewaters may not accurately represent availability, since they do not take into account the turnover times of the nutrient pools (Howarth 1988). The ratio of C:N:P in aquatic plant tissue is an indicator of the availability of nutrients to the plant (Gerloff and Krombholz 1966), and seagrass species from nutrient-poor areas have substantially higher ratios than those from nutrient-rich areas (Atkinson and Smith 1983). Further, the C:N:P ratio of aquatic plant tissues varies with nutrient availability within a single species, as documented both in fertilization studies (Short 1987, Short et al. 1990) and in studies of spatial variation with respect to nutrient sources (Fourqurean et al. 1992).

Different seagrass species may have different nutrient requirements, but little work has been done on the relative nutrient requirements of seagrasses since most of the seagrasses-nutrient studies have been conducted in areas of *Zostera marina* monoculture. In south Florida, where there is a more diverse seagrass flora, Powell et al. (1991) documented concentric zones of seagrass dominated by different species around a point-source of nutrients, and suggested that the zonation is caused by the variation in the nutrient loading rate as distance from the point-source increases and the different nutrient requirements of the seagrass species. That study also documented shifts in the dominance of seagrass species following fertilization of experimental plots.

The present study examines the relationships among sediment nutrient supplies, seagrass standing crop, spe-

cies composition of seagrass beds, and elemental composition of seagrass tissue in a nutrient-limited, seagrass-dominated subtropical embayment. Since the sediments are hypothesized to be the primary source of nutrients for seagrasses, we expected there would be a correlation between seagrass standing crop and porewater nutrient supply. Further, because the elemental composition of seagrasses may indicate their nutrient supply (Gerloff and Krombholz 1966), we hypothesized that porewater nutrients and the C:N:P ratios of seagrasses are related. Because of observed zonation of seagrass species surrounding point-sources of nutrients (Powell et al. 1991), we also hypothesized that areas supporting different species of seagrass differ in the nutrient characteristics of their porewater.

## Materials and methods

### Study site

This study was conducted in Florida Bay, a large (1800 km<sup>2</sup>), shallow (< 3 m) embayment at the southern tip of the Florida peninsula, Florida, USA (~25°N; 81°W; Fig. 1) during the summer months of 1987 and 1988. The seagrass communities of Florida Bay have been described by Zieman et al. (1989). Florida Bay is carpeted with seagrasses, which range in density from very sparse in the northeastern end of the bay to very dense along the western edge of the bay. *Thalassia testudinum* is the dominant seagrass across the bay, but local areas are dominated by *Halodule wrightii* and/or *Syringodium filiforme*. Seagrass beds in Florida Bay are nutrient-limited (Powell

et al. 1989, Fourqurean et al. 1992). The sediments in which these seagrasses are rooted are composed of biogenic calcium carbonate from algal and animal skeletal fragments (see Bosence 1989 for review).

The 18 sampling locations chosen for study represented the ranges of seagrass density and meadow composition found in Florida Bay. Each of the sites from which porewater was collected was assigned a seagrass cover class, defined as: (1) areas with no seagrass; (2) areas with monotypic stands of *Thalassia testudinum*, or (3) areas that supported *Halodule wrightii*. In this last cover class, *T. testudinum* and *Syringodium filiforme* were sometimes present.

### Porewater collection and analysis

Porewater was collected using in situ suction lysimeters, or "sediment sippers" (Fig. 2), modified from the design of Montgomery et al. (1979) and Chambers and Odum (1990). The sippers were constructed of a top piece of 4.0 cm i.d. and bottom piece of 1.6 cm i.d. (1 1/2" and 1/2" U.S. Schedule 40, respectively) PVC pipe connected with a slip-fit reducer bushing. Any corners in the bushing that could trap and hold water were filled with polyester resin. The length of the 1.6 cm pipe section determined the sampling depth of the sipper, and the bottom of the 1.6 cm pipe was covered with a cap of fritted polyethylene (30  $\mu$ m pore size). A #9 two-hole rubber stopper plugged the top of the 4.0 cm pipe section. A sampling port was made by extending a length of plastic tubing through one of the holes to the fritted cap. The second hole served as a gas port. Both holes in the stopper were fitted with luer-lock stopcocks.

At each sampling location, five sippers each at sediment depths of 10, 20, 30 and 40 cm were randomly distributed in a 10 m  $\times$  10 m square. These depths allowed the sampling of porewater throughout the rhizosphere of *Thalassia testudinum* meadows. Sippers were pushed into the sediment until the reducer bushing was flush with the sediment, and argon gas was used to force all of the water out of the sipper through the sampling port. With the sampling port closed, suction was applied to the gas port using a line running to a battery-operated vacuum pump on the boat. This suction slowly drew porewater in through the fritted cap. After about 4 h, the porewater sample was collected using argon-gas pressure to force the sample out through the sampling port into a 60 ml syringe. Samples were filtered through 0.45  $\mu$ m membrane filters into evacuated collection tubes, and transported back to the laboratory on ice in the dark for chemical analysis.

In the laboratory, the sample vials were uncapped, acidified to pH = 2 using 6 N HCl, and sparged with argon to drive off H<sub>2</sub>S. Further analysis was done on these sparged samples. Dissolved inorganic nutrient concentrations of these sparged samples were determined colorimetrically using the ascorbate method for soluble reactive phosphate (SRP) and the indo-phenol blue method for ammonium (NH<sub>4</sub><sup>+</sup>) given in Parsons et al. (1984). All nutrient analyses were completed within 6 h of sample collection.

### Plant collection and processing

Core tubes (15 cm diam) were used to collect three replicate subsamples from each sampling location. Seagrass biomass was separated by species, and green leaf tissue was separated from the non-photosynthetic biomass in the core. The leaves were gently scraped and washed in flowing tap water to remove epibionts and sediments that had adhered to the leaves. These washed samples were lyophilized to a constant weight. Standing crop was calculated as the dry weight of green leaves per area of Florida Bay bottom, expressed as g (dry wt) m<sup>-2</sup>.

For determination of the elemental content of seagrass leaves, the dried leaves were first homogenized by milling them to a fine powder. Carbon and nitrogen content was determined for duplicate subsamples of each sample by oxidation in a Carlo Erba Model 1500 CHN analyzer. Phosphorus content was measured using a

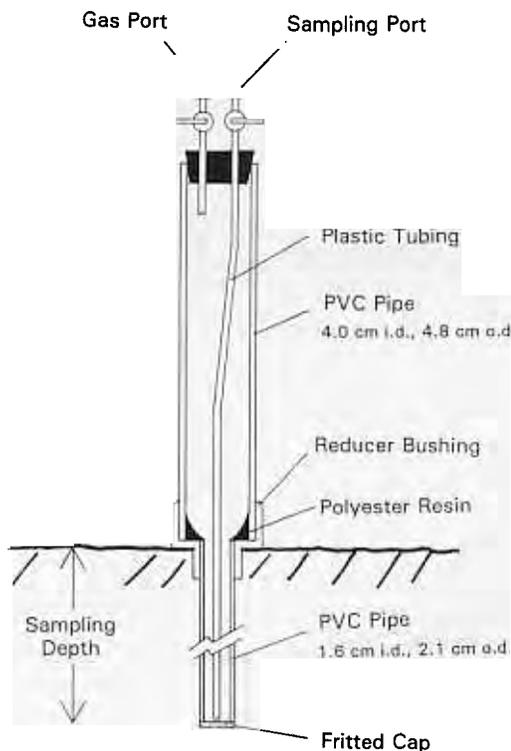


Fig. 2. Diagram of inexpensive, in-situ "sediment sippers" (suction lysimeters) used to collect porewater from seagrass beds of Florida Bay

modification of the method presented in Solórzano and Sharp (1980) for particulate total phosphorus determination. Duplicate subsamples of each sample were weighed (5 to 20 mg) into tared glass scintillation vials. 0.5 ml of 0.17 M Na<sub>2</sub>SO<sub>4</sub> and 2.0 ml of 0.017 M MgSO<sub>4</sub> were added to each vial, and the vials were dried in an oven at 90°C. Standards were treated identically. Dry vials containing samples and standards were ashed at 500°C for 3 h. After cooling, 5.0 ml of 0.2 N HCl was added to each vial, the vials were capped and placed in an oven at 80°C for 30 min. Each vial was diluted with 10.0 ml of deionized water, shaken, and allowed to stand overnight to allow the ash to settle. The SRP concentration of the solution in the vials was determined colorimetrically as described above. This method yielded 95 to 103% of the reported phosphorus content of NBS (National Bureau of Standards)-standard orchard leaves. The elemental ratios C:P, C:N and N:P were calculated on a mol:mol basis.

### Results

There was large variation in nutrient concentrations of porewater from Florida Bay sediments. For individual sippers, SRP concentrations ranged from below detection (0.05  $\mu$ M) to 33.8  $\mu$ M and NH<sub>4</sub><sup>+</sup> concentrations ranged between 6.3 and 2400  $\mu$ M. The values were not normally distributed, but showed extreme positive skewness towards low values (Fig. 3). The median concentrations were 0.34  $\mu$ M for SRP and 78.6  $\mu$ M for NH<sub>4</sub><sup>+</sup>. Due to the extreme positive skewness of the distributions, statistical comparisons of porewater data were done using log transformations for the ammonium data and log ([SRP] + 1) transformations for the SRP data.

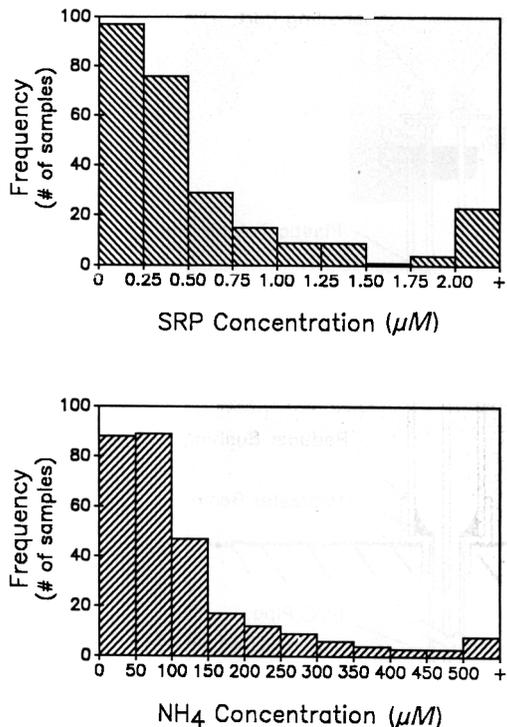


Fig. 3. Frequency distributions of concentrations of soluble reactive phosphorus (SRP) and ammonium ( $\text{NH}_4^+$ ) in individual sediment sipper samples. Note that values are skewed towards low values

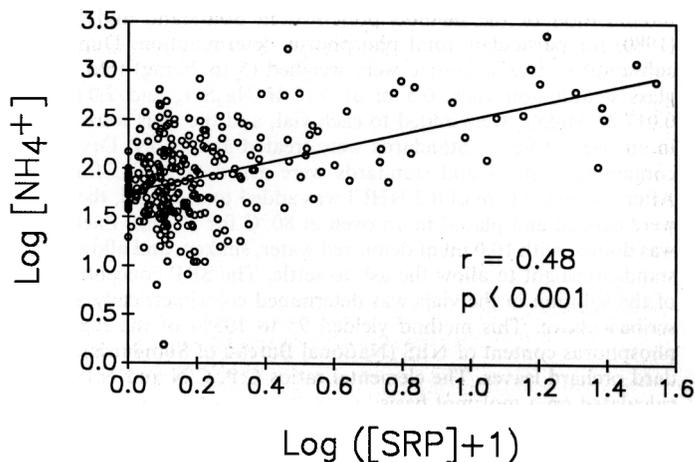


Fig. 4. Scatterplot of transformed nutrient concentrations of porewater from individual sediment sippers, showing positive correlation between SRP and  $\text{NH}_4^+$

Individual sipper samples that had high SRP concentrations also tended to have high  $\text{NH}_4^+$  concentrations (Fig. 4). Transformed porewater SRP and  $\text{NH}_4^+$  concentrations were significantly correlated, with a Pearson's correlation coefficient of 0.48 ( $n=286$ ,  $p<0.001$ ). The median porewater molar  $\text{NH}_4^+:\text{SRP}$  ratio of all individual sipper samples was 217.

At each site, the SRP and  $\text{NH}_4^+$  concentrations of all the individual sippers at each depth were averaged to-

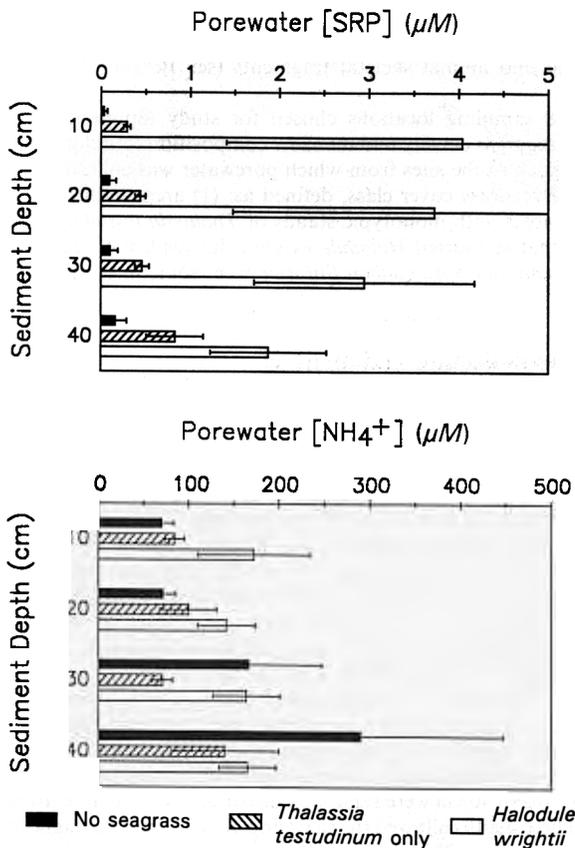
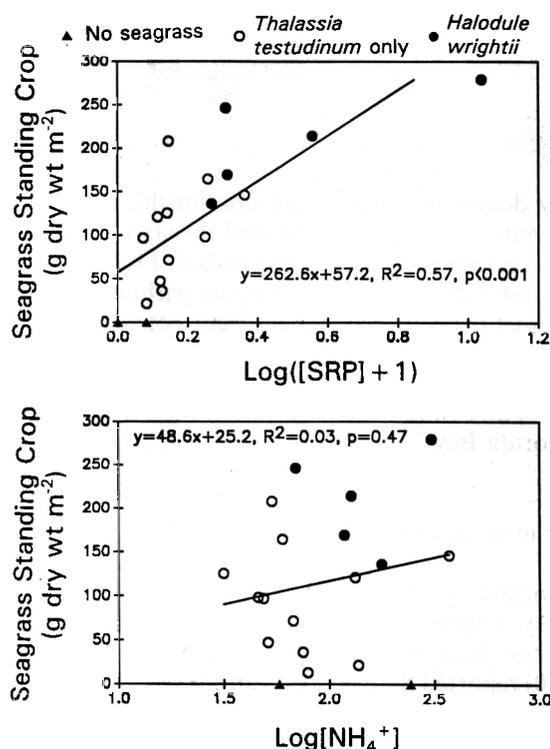


Fig. 5. Average depth profiles of SRP and  $\text{NH}_4^+$  in porewater. Error bars indicate  $\pm 1$  SE

gether to provide one estimate of the porewater nutrient concentrations at each depth. Average porewater depth profiles for SRP and  $\text{NH}_4^+$  for each seagrass cover class were then made by averaging these values across all stations in each cover class (Fig. 5). There were, however, no consistent trends evident with depth in either SRP or  $\text{NH}_4^+$  concentrations for all cover classes.

Because of the lack of discernable trends in nutrient concentrations with depth, a single depth-averaged value for porewater SRP and  $\text{NH}_4^+$  was determined at each porewater collection site by averaging the mean values for each depth. The molar ratio of  $\text{NH}_4^+:\text{SRP}$  for each site was determined using these depth-averaged values. There were significant differences in the depth-averaged porewater SRP concentrations between the cover classes (Table 1). Areas with no seagrass had the lowest porewater SRP ( $0.10 \pm 0.10 \mu\text{M}$ ), areas that supported *Thalassia testudinum* alone had intermediate SRP concentrations ( $0.49 \pm 0.10 \mu\text{M}$ ), and areas that supported *Halodule wrightii* had the highest SRP concentrations ( $3.09 \pm 1.74 \mu\text{M}$ ). In contrast, there were no significant differences in depth-averaged porewater  $\text{NH}_4^+$  concentrations between cover classes. Because of the significant differences in SRP, there were significant differences in the  $\text{NH}_4^+:\text{SRP}$  ratios among cover classes. The lowest ratios,  $93 \pm 31$ , were found in areas that supported *H. wrightii*, and the highest ratios,  $895 \pm 320$ , were found in areas with no seagrass. *T. testudinum*-only areas had intermediate ratios of  $232 \pm 54$ .

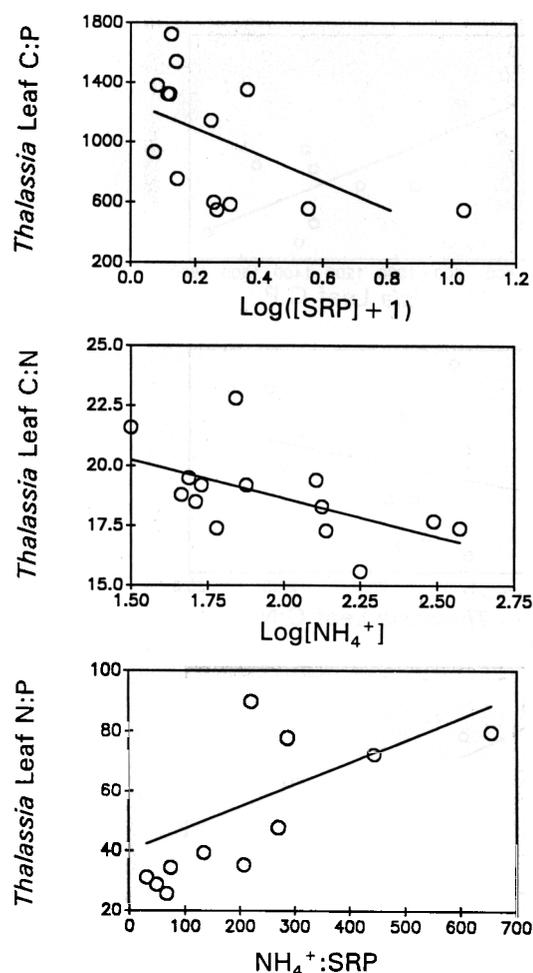


**Fig. 6.** Relationships between total seagrass standing crop and depth-averaged SRP and  $\text{NH}_4^+$  concentrations in porewater. Different cover-classes are represented by different symbols (top abscissa). Statistics for linear regression analyses are given inside graphs

**Table 1.** Means  $\pm$  1 SE of depth-averaged soluble reactive phosphorus (SRP) and ammonium ( $\text{NH}_4^+$ ) concentrations in porewater and  $\text{NH}_4^+$ :SRP ratios of porewater in areas supporting no seagrasses, *Thalassia testudinum* alone, and areas with *Halodule wrightii*. Statistics for one-way ANOVAs for comparison between groups are also given. Due to positive skewness in data, ANOVAs were performed on  $\log([\text{SRP}] + 1)$  and  $\log[\text{NH}_4^+]$  transformations. Asterisks indicate comparison between groups significant at  $p \leq 0.05$

Seagrass cover class	(n)	Depth-averaged porewater nutrients		
		SRP ( $\mu\text{M}$ )	$\text{NH}_4^+$ ( $\mu\text{M}$ )	$\text{NH}_4^+$ :SRP
No seagrasses	(2)	$0.10 \pm 0.10$	$150.3 \pm 92.8$	$895 \pm 320$
<i>Thalassia testudinum</i> only	(11)	$0.49 \pm 0.10$	$98.0 \pm 29.5$	$232 \pm 54$
<i>Halodule wrightii</i>	(5)	$3.09 \pm 1.74$	$160.3 \pm 40.7$	$93 \pm 31$
ANOVA F		7.1	1.6	13.0
p		<0.01 *	0.23	<0.001 *

Seagrass standing crop at the 18 porewater sampling sites ranged from 0 to  $279.4 \text{ g dry wt m}^{-2}$ , with a mean of  $115.5 \pm 18.9 \text{ g dry wt m}^{-2}$  ( $\pm 1 \text{ SE}$ ). There was a statistically significant relationship between total seagrass standing crop at the sampling sites and the depth-averaged SRP concentration of porewater ( $R^2 = 0.57$ ,  $p < 0.001$ , Fig. 6). Note that the sampling sites in the *Thalassia testudinum*-only cover class tended to have a lower



**Fig. 7.** *Thalassia testudinum*. Relationships between elemental ratios of green leaf tissue and porewater SRP and  $\text{NH}_4^+$  and  $\text{NH}_4^+$ :SRP ratio. Statistics of linear regression analyses are given in Table 2

standing crop than areas that supported *Halodule wrightii*. There was no significant relationship between seagrass standing crop and the depth-averaged  $\text{NH}_4^+$  concentration of porewater ( $R^2 = 0.03$ ,  $p = 0.47$ , Fig. 6).

Relationships between the nutrient content of leaves of *Thalassia testudinum* and the concentration of nutrients in the porewater were statistically significant (Fig. 7, Table 2). High concentrations of P in the porewater, as indicated by SRP, were associated with low C:P ratios of leaves of *T. testudinum*. A low C:P corresponds to a high phosphorus content of the leaves. Similarly, high concentrations of nitrogen in the porewater were associated with high concentrations of nitrogen in the leaves of *T. testudinum*. There was a much greater range in leaf C:P than C:N. C:P values ranged from 549 to 1725, a difference of 3.1-fold, while there was only a 1.5-fold difference in the maximum (22.8) and minimum (15.6) C:N ratios. There was a positive relationship between the ratios of N to P in the leaves and porewater: high  $\text{NH}_4^+$ :SRP ratios in the porewater were associated with high N:P ratios of the leaves (Fig. 7 and Table 2).

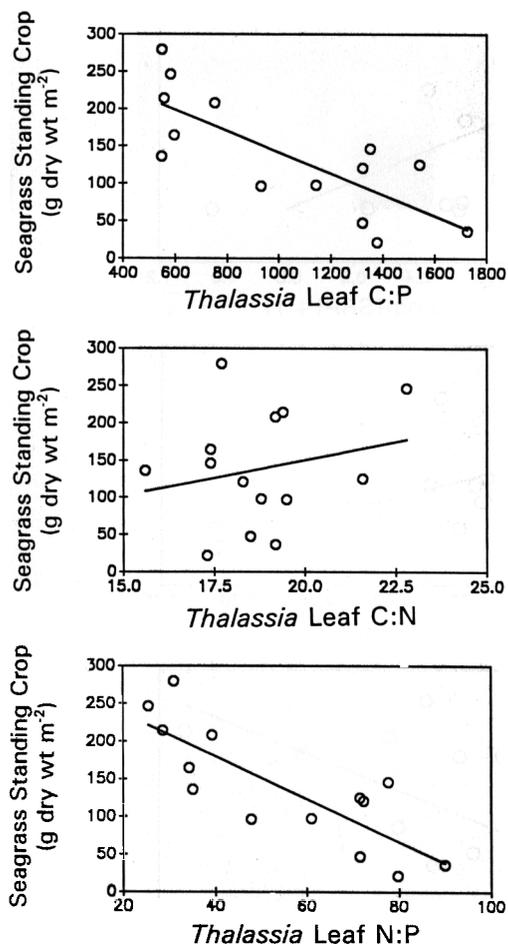


Fig. 8. Total seagrass standing crop (all species) as a function of the C:P, C:N and N:P ratios of green leaf tissue of *Thalassia testudinum*. Statistics for linear regression analyses are given in Table 2

Table 2. Results of linear regression analysis for relationships between depth-averaged concentration of nutrients in porewater, elemental ratios of *Thalassia testudinum* leaves, and total seagrass standing crop (all species combined). Asterisks indicate relationships significant at  $p < 0.05$

Dependent variable	Independent variable	Slope	Intercept	$R^2$	F	p
Leaf C:P ratio	$\text{Log}([\text{SRP}] + 1)$	-881.3	1 264.2	0.29	4.8	0.05*
Leaf C:N ratio	$\text{Log}[\text{NH}_4^+]$	-3.2	25.1	0.33	5.8	0.03*
Leaf N:P ratio	$\text{NH}_4^+:\text{SRP}$	0.1	40.3	0.34	6.1	0.03*
Standing crop	Leaf C:P ratio	-0.1	284.2	0.59	17.5	0.001*
Standing crop	Leaf C:N ratio	9.6	-42.5	0.05	0.6	0.44
Standard crop	Leaf N:P ratio	-2.8	294.1	0.66	23.2	0.001*

The concentration of phosphorus in *Thalassia testudinum* leaves was significantly related to the total standing crop of seagrass at a site (Fig. 8 and Table 2). At high phosphorus content, or low C:P, standing crop was high. There was no similar relationship between nitrogen content of leaves and standing crop. Since standing crop was positively correlated with leaf phosphorus content and

independent of leaf nitrogen content, there was a strong relation between leaf N:P ratio and standing crop.

## Discussion

This study documents the strong relationship between porewater nutrient concentrations and the standing crop and species composition of seagrass beds in Florida Bay. The elemental composition of seagrasses within the beds is also a function of porewater nutrient concentration. These relationships indicate that concentrations of phosphorus, not nitrogen, in the porewater limit the development and control the species composition of seagrass beds in Florida Bay.

## Porewater nutrient concentrations

The concentrations of SRP and  $\text{NH}_4^+$  in the porewater of Florida Bay seagrass beds were similar to values from other seagrass beds in carbonate sediments. Short et al. (1985, 1990) reported SRP concentrations of  $< 2 \mu\text{M}$  and  $\text{NH}_4^+$  concentrations of  $\sim 100 \mu\text{M}$  in beds of *Syringodium filiforme* in the Bahamas. In a seagrass bed composed of *Thalassia testudinum* and *S. filiforme* in St. Croix, US Virgin Islands,  $\text{NH}_4^+$  concentrations were between 10 and  $100 \mu\text{M}$  (Williams 1990). Our results differ significantly from one previous measure of porewater SRP in Florida Bay, however. Using core squeezers, Rosenfeld (1979) reported SRP concentrations of 5 to  $30 \mu\text{M}$  from a bare mud area on a shallow bank in Florida Bay. The only places we encountered SRP values this high in Florida Bay were immediately adjacent to bird rookery/nesting islands, which are large point-sources of nutrients in the system (Powell et al. 1991). One explanation for this difference may lie in the different techniques used to collect the porewater.

Studies of porewater nutrient concentrations from seagrass beds in carbonate sediments show general increases in concentration with depth (Short et al. 1985, Williams 1990). The lack of this trend in our data may be a function of the spatial heterogeneity of seagrass beds. When porewater nutrient profiles were measured at particular spots within seagrass beds in Florida Bay using vertical arrays of porewater equilibrator chambers, concentrations of both SRP and  $\text{NH}_4^+$  increased with depth (Fourqurean and Carlson unpublished data). The variation within the  $10 \text{ m} \times 10 \text{ m}$  plots in which sediment sippers were deployed in this study generally eradicated any signal of increasing porewater nutrient concentrations with depth.

## Porewater nutrient concentrations and seagrass standing crop

The seagrass beds of one bank dominated by *Thalassia testudinum* in eastern Florida Bay have been shown experimentally to be phosphorus-limited (Powell et al. 1989). The positive relationship between total seagrass

standing crop and porewater SRP observed in the present study suggests that unperturbed seagrass beds are phosphorus-limited across Florida Bay. Correlation between porewater nutrient concentration and plant standing crop does not automatically prove that a causal relationship exists between the factors (Chambers and Fourqurean 1991). For instance, increased input and diagenesis of organic matter in dense seagrass beds would lead to increased nutrient concentrations in the porewater as a function of the density of the seagrass bed; high porewater nutrient concentrations could be a consequence, not a cause, of high seagrass standing crop. In addition to the possibly ambiguous correlation between porewater SRP concentration and seagrass standing crop in Florida Bay, other evidence supports a conclusion of phosphorus limitation. The correlations between (1) porewater nutrients and the nutrient content of seagrass leaves, and (2) the nutrient content of seagrass leaves and seagrass standing crop suggest phosphorus limitation of seagrass standing crop.

This work supports the generalization that seagrasses in biogenic carbonate sediments are phosphorus-limited, in contrast to the nitrogen limitation of temperate eelgrass beds in terrigenously derived sandy and muddy sediments (Short 1987). The relationship between relative eelgrass (*Zostera marina*) growth and sediment ammonium concentration suggests that eelgrass is nitrogen-limited in areas of sediment ammonium concentration of  $<100 \mu\text{mol NH}_4^+$  per liter of sediment, and nitrogen-saturated at  $>100 \mu\text{mol l}^{-1}$  (Dennison et al. 1987). Our data suggest a similar relationship between porewater SRP concentration and Florida Bay seagrass beds composed of *Thalassia testudinum* and *Halodule wrightii*, with phosphorus limitation occurring in areas where porewater SRP is  $<2 \mu\text{M}$ , and phosphorus saturation in areas where SRP is  $>2 \mu\text{M}$ .

### Seagrass elemental ratios

The C:N:P ratios of plants has been used to assess the nutrient status of phytoplankton (Redfield 1958) and macrophytes (Gerloff and Krombholz 1966). The amount of nitrogen or phosphorus, relative to carbon, in plant tissues is a function of the availability of N or P in the environment. The C:P and C:N of leaves of *Thalassia testudinum* decreased with increasing porewater SRP and  $\text{NH}_4^+$ , respectively, implying that the measures of porewater nutrient concentration made in this study can be considered measures of nutrient availability. Moreover, the N:P ratio of seagrass leaf tissue reflected the relative availability of N and P in the environment.

Seagrass standing crop in Florida Bay was a function of the C:P ratio, but not the C:N ratio, of the leaves of *Thalassia testudinum*. This indicates that the seagrass standing crop was associated with high phosphorus availability (as measured by C:P). Standing crop was independent of nitrogen availability, even though there was a significant positive relationship between the N content of the leaves and the N concentration in the porewater. This relationship may have been due to 'luxury consump-

tion' of N; i.e., the assimilation of nutrients, above a critical concentration, which has no effect on plant growth (Gerloff and Krombholz 1966). Seagrasses in Florida Bay appeared to be saturated with respect to N. For the ranges of N and P content of seagrass leaves encountered in this study, the ratio of N:P in seagrass tissue was also a good predictor of seagrass standing crop: as P became more available with respect to N, seagrass standing crop increased.

### Porewater nutrients and species composition

The areas classified in the *Halodule wrightii* cover class had higher porewater SRP concentrations than either of the other two cover classes. This is consistent with the observed zonation of these species around a point-source of nutrients in eastern Florida Bay, where *H. wrightii* was dominant in an area close to the nutrient source and *Thalassia testudinum* was dominant further from the nutrient source (Powell et al. 1991). Changing the nutrient regime of existing seagrass beds may affect the species composition of the seagrass bed. Shifts in species dominance, from *T. testudinum* to *H. wrightii*, occurred when areas of *T. testudinum* were fertilized (Powell et al. 1991). Two alternative hypotheses are consistent with these observations: (1) *H. wrightii* can survive in areas of higher nutrient concentration than *T. testudinum*, or (2) *H. wrightii* requires a greater nutrient supply than *T. testudinum* in order to develop into the dominant seagrass in a bed. From this study, the clearly positive relationship between porewater SRP concentrations and the standing crop of *T. testudinum* suggests that higher SRP concentrations benefited *T. testudinum*. Because *H. wrightii* was never found in areas of low porewater SRP concentration, we conclude that growth of *H. wrightii* requires a greater nutrient supply than *T. testudinum*.

The relative nutrient requirements of *Thalassia testudinum* and *Halodule wrightii* provide a possible explanation of the predominance of *T. testudinum* in low-nutrient environments and *H. wrightii* in high-nutrient environments. Estimates of the nutrient demands may be made using production rates and the concentration of nitrogen and phosphorus in the plant tissue. *H. wrightii* has a much higher production rate than *T. testudinum*: previous work in Florida Bay has estimated leaf production of  $47 \text{ mg g}^{-1} \text{ d}^{-1}$  for *H. wrightii* (Powell et al. 1989) and  $22 \text{ mg g}^{-1} \text{ d}^{-1}$  for *T. testudinum* (Zieman et al. 1989). On a dry weight basis, leaves of *T. testudinum* from the area average 2.24% N and 0.09% P (Fourqurean et al. 1992), and leaves of *H. wrightii* average 2.75% N and 0.2% P (Powell et al. 1989). From these figures, we estimate the P required to support daily production of new leaves (on a per gram dry leaf basis) to be  $94 \mu\text{g P g}^{-1}$  for *H. wrightii* and  $20 \mu\text{g P g}^{-1}$  for *T. testudinum*. Similarly, the daily N demand of *H. wrightii* ( $1.3 \text{ mg N g}^{-1}$ ) is much higher than that of *T. testudinum* ( $0.5 \text{ mg N g}^{-1}$ ). These estimates are of the demand for new leaf production only, and neglect the nutrients required for producing other plant tissues. *H. wrightii*, which was only found in areas with high nutrient concentrations, had a 4.7-fold

higher P demand, and a 2.6-fold higher N demand, than *T. testudinum*, which was the dominant species in areas of low nutrient concentration. This suggests that *H. wrightii* is less efficient than *T. testudinum* at utilizing nutrients when availability is low.

*Halodule wrightii* is considered to be the pioneering species in seagrass beds of Florida and the Caribbean, and *Thalassia testudinum* dominates the "climax" seagrass community (Zieman 1982). During recolonization of mechanically disturbed seagrass beds, *H. wrightii* is often the first seagrass to become established due to its rapid rate of sexual and vegetative reproduction. Over the course of 5 to 15 yr, *T. testudinum* slowly recolonizes these areas and replaces the other seagrasses (Patriquin 1975). In the present study, we did not investigate porewater nutrient concentrations in any "pioneering" *H. wrightii* beds.

One of the generalized patterns in changes in plant physiological ecology during succession is a change from species with high nutrient demands to those with low demands (Bazaaz 1979, Tilman and Wedin 1991 a, b). Florida Bay seagrasses are no exception: *Halodule wrightii*, the early successional species, has a higher nutrient demand than *Thalassia testudinum*, the late successional species. However, in most successional sequences, nutrient pools are lowest in early succession and increase through time (e.g. Tilman 1982). Early successional species exploit relatively nutrient-poor areas early in succession, despite their higher nutrient demand, due to their rapid colonization rates compared to late successional species (Platt 1975, Connell and Slayter 1977, Bazaaz 1979, Tilman and Wedin 1991 b). Early succession in Florida Bay seagrass beds also fits this model. *H. wrightii*, the normal early successional species, has a higher demand for sediment nutrients than *T. testudinum*, the later successional species, but a much faster colonization rate than *T. testudinum* (Fonseca et al. 1987). This rapid colonization rate enables *H. wrightii* to colonize relatively nutrient-poor bare sediments in Florida Bay.

In the context of resource competition theory (Tilman 1982), the replacement of *Halodule wrightii* by *Thalassia testudinum* in the secondary successional sequence may be explained by the relative efficiencies of the species in utilizing a limiting resource, in this case sedimentary phosphorus supply. If nutrient-use efficiency is an inverse function of the nutrient demands of the species as calculated above, then *T. testudinum* should be able to survive at lower P availability than *H. wrightii*. If the total supply of P remains constant in an area during secondary succession, then as P is incorporated into plant tissue during increases in biomass, P will become less available in the environment. The minimum level to which P availability can be lowered is a function of the nutrient-use efficiency of the plants and the rates of remineralization of fixed P. As biomass of *T. testudinum* increases in a bed of *H. wrightii*, P availability will decrease, shifting the competitive edge to *T. testudinum*. Stable coexistence of the two species will only occur if some other factor, such as light, limits the ability of *T. testudinum* to diminish the amount of environmentally available P below the critical level required by *H. wrightii*.

**Acknowledgements.** The authors would like to thank D. L. Childers, M. H. Fourqurean, K. J. Halama, A. H. Powell and J. Prentice for field assistance and D. Yozzo for laboratory assistance. J. M. Lawrence, R. M. Price, D. T. Osgood, P. R. Carlson, R. M. Chambers and an anonymous reviewer read and commented on drafts of this paper. Funds for the support of this research were supplied by a John D. and Catherine T. MacArthur Foundation grant to the National Audubon Society and a cooperative agreement between the U.S. National Park Service and the University of Virginia (Contract #CA-5280-0-9009).

## Literature cited

- Agami, M., Waisel, Y. (1986). The ecophysiology of roots of submerged vascular plants. *Physiologie vég.* 24: 607–624
- Atkinson, M. J., Smith, S. V. (1983). C:N:P ratios of benthic marine plants. *Limnol. Oceanogr.* 28: 568–574
- Bazaaz, F. A. (1979). The physiological ecology of plant succession. *A. Rev. Ecol. Syst.* 10: 351–371
- Berner, R. A. (1974). Kinetic models for the early diagenesis of nitrogen, sulfur, phosphorus and silicon in anoxic marine sediments. In: Golberg, E. D. (ed.) *The sea*. Wiley, New York, p. 427–450
- Bosence, D. (1989). Surface sublittoral sediments of Florida Bay. *Bull. mar. Sci.* 44: 434–453
- Cambridge, M. L., McComb, A. J. (1984). The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquat. Bot.* 20: 229–243
- Chambers, R. M., Fourqurean, J. W. (1991). Alternative criteria for assessing nutrient limitation of a wetland macrophyte (*Peltandra virginica* (L.) Kunth). *Aquat. Bot.* 40: 305–320
- Chambers, R. M., Odum, W. E. (1990). Porewater oxidation, dissolved phosphate and the iron curtain: Iron – phosphorus relations in tidal freshwater marshes. *Biogeochemistry* (Dordrecht) 10: 37–52
- Connell, J. H., Slayter, R. O. (1977). Mechanism of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119–1144
- DeKanel, J., Morse, J. W. (1978). The chemistry of orthophosphate uptake from seawater on to calcite and aragonite. *Geochim. cosmochim. Acta* 42: 1335–1340
- Dennison, W. C. (1987). Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquat. Bot.* 27: 15–26
- Dennison, W. C., Aller, R. C., Alberte, R. S. (1987). Sediment ammonium availability and eelgrass (*Zostera marina*) growth. *Mar. Biol.* 94: 469–477
- Fonseca, M. S., Thayer, G. W., Kenworthy, W. J. (1987). The use of ecological data in the implementation and management of seagrass restorations. In: Durako, M. J., Phillips, R. C., Lewis, R. R., III (eds.) *Proceedings of Symposium on Subtropical Seagrasses of the Southeastern United States Marine Research Laboratory, St. Petersburg, Fla.*, p. 175–187 (Fla. mar. Res. Publs No. 42)
- Fourqurean, J. W., Zieman, J. C., Powell, G. V. N. (1992). Phosphorus limitation of primary production in Florida Bay: evidence from the C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnol. Oceanogr.* 37: 162–171
- Gerloff, G. C., Krombholtz, P. H. (1966). Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. *Limnol. Oceanogr.* 11: 529–537
- Giesen, W. B. J. T., van Katwijk, M. M., den Hartog, C. (1990). Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquat. Bot.* 37: 71–85
- Harlin, M. M., Thorne-Miller, B. (1981). Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. *Mar. Biol.* 65: 221–229
- Howarth, R. W. (1988). Nutrient limitation of net primary production in marine ecosystems. *A. Rev. Ecol. Syst.* 19: 89–110

- Larkum, A. W. D., West, R. J. (1990). Long-term changes of seagrasses in Botany Bay, Australia. *Aquat. Bot.* 37: 55–70
- McRoy, C. P., Barsdate, R. J. (1970). Phosphate adsorption in eelgrass. *Limnol. Oceanogr.* 15: 14–20
- Montgomery, J. R., Zimmerman, C. F., Price, M. T. (1979). The collection, analysis and variation of nutrients in estuarine pore water. *Estuar., cstl mar. Sci.* 9: 203–214
- Orth, R. J. (1977). Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. *Mar. Biol.* 44: 187–194
- Orth, R. J., Moore, K. J. (1983). Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science, N.Y.* 222: 51–53
- Parsons, T. R., Maita, Y., Lalli, C. M. (1984). A manual of chemical and biological methods of seawater analysis. Pergamon Press, New York
- Patriquin, D. G. (1975). "Migration" of blowouts in seagrass beds at Barbados and Carriacou, West Indies, and its ecological and geological implications. *Aquat. Bot.* 1: 163–189
- Platt, W. J. (1975). The colonization and formation of equilibrium plant series associations on badger mounds in a tall-grass prairie. *Ecol. Monogr.* 45: 285–305
- Powell, G. V. N., Fourqurean, J. W., Kenworthy, W. J., Zieman, J. C. (1991). Bird colonies cause seagrass enrichment in a subtropical estuary: observational and experimental evidence. *Estuar., cstl Shelf Sci.* 32: 567–579
- Powell, G. V. N., Kenworthy, W. J., Fourqurean, J. W. (1989). Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bull. mar. Sci.* 44: 324–340
- Redfield, A. C. (1958). The biological control of chemical factors in the environment. *Am. Scient.* 46: 561–600
- Rosenfeld, J. K. (1979). Interstitial water and sediment chemistry of two cores from Florida Bay. *J. sedim. Petrol.* 49: 989–994
- Short, F. T. (1987). Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquat. Bot.* 27: 41–57
- Short, F. T., Davis, M. W., Gibson, R. A., Zimmermann, C. F. (1985). Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. *Estuar., cstl Shelf Sci.* 20: 419–430
- Short, F. T., Dennison, W. C., Capone, D. G. (1990). Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Mar. Ecol. Prog. Ser.* 62: 169–174
- Solórzano, L., Sharp, J. H. (1980). Determination of total dissolved phosphorus and particulate phosphorus in natural waters. *Limnol. Oceanogr.* 25: 754–758
- Tilman, D. (1982). Resource competition and community structure. Princeton University Press, Princeton, New Jersey
- Tilman, D., Wedin, D. (1991 a). Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72: 685–670
- Tilman, D., Wedin, D. (1991 b). Dynamics of nitrogen competition between successional grasses. *Ecology* 72: 1038–1049
- Williams, S. L. (1990). Experimental studies of Caribbean seagrass bed development. *Ecol. Monogr.* 60: 449–469
- Zieman, J. C. (1975). Tropical sea grass ecosystems and pollution. In: Wood, E. J. F., Johannes, R. E. (eds.) *Tropical marine pollution*. Elsevier, New York, p. 63–74 (Elsevier Oceanogr. Ser. No. 12)
- Zieman, J. C. (1982). The ecology of the seagrasses of south Florida: a community profile, U.S. Fish & Wildlife Services, Office of Biological Services, Washington, D.C. (FWS/OBS-82/25)
- Zieman, J. C., Fourqurean, J. W., Iverson, R. L. (1989). Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bull. mar. Sci.* 44: 292–311