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EXPERIMENTAL EVIDENCE FOR NUTRIENT LIMITATION OF SEAGRASS GROWTH IN A TROPICAL ESTUARY WITH RESTRICTED CIRCULATION

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ABSTRACT

We studied the impacts of additions of nutrients to a seagrass community on a carbonate mud bank in Florida Bay. Shallow mud banks dampen lunar tide in Florida Bay, and empoundment and channelization of the upland watershed (the Everglades) have reduced freshwater imput, resulting in restricted circulation and reduced nutrient availability. Nutrients were supplied by seabirds defecating from experimental roosts. Seabirds used the roosts 87% of the time so the input of nutrients was constant and quantifiable. The birds delivered approximately 2–4 g of excrement per day, resulting in an average loading rate of 0.052 gN and 0.009 $gP \cdot m^{-2} \cdot d^{-1}$. Only a portion of the excrement is immediately released as inorganic NH_3 and PO_4; about 80% reaches the sediment surface in a relatively insoluble form. There was a significant buildup of phosphate and ammonium in the pore water at the enriched. sites. The ammonium profile of low concentrations at the surface and then increasing with a steep slope through 20 cm suggests a rapid uptake and demand for mineralized nitrogen. Phosphorus in contrast had relatively high levels at the surface. Nutrient addition significantly increased areal leaf production and standing crop of *Thalassia testudinum* and *Halodule wrightii*. Above ground biomass at enriched sites averaged twice controls while below ground biomass was not significantly different between fertilized and control plots. Increased standing crop was produced primarily through longer, wider blades by *Thalassia* and longer blades and increased short shoot density by *Halodule*. *Thalassia* areal leaf production was 60% greater at enriched sites than at controls. *Halodule* areal leaf production increased by three orders of magnitude at enriched sites. Tissue nutrient content and nitrogen fixation assays suggest that phosphorus availability limits seagrass growth in unenriched conditions, but that nitrogen becomes limiting with the addition of bird excrement.

Marine angiosperms are among the most important primary producers in shallow water habitats (Zieman and Wetzel, 1980). In spite of their prominence, factors controlling the growth of seagrasses are only partially understood. Parameters that have been shown to be important to the development and persistence of seagrass meadows include: sediment depth (Zieman, 1972); water temperature (Bulthuis, 1987); salinity (McRoy and McMillan, 1977); water clarity (Dennison, 1987) and water motion (Fonseca and Kenworthy, 1987). Uncertainty still remains as to what extent nutrients limit the growth and development of seagrass meadows.

The leaves of seagrasses, especially those of tropical species, are usually bathed in low nutrient waters, while their roots occur in the enriched medium of sediment interstitial water (Patriquin, 1972; Kenworthy et al., 1982; Short, 1983; 1987; Short et al., 1985). Patriquin (1972) concluded from estimates of nitrogen (N) and phosphorus (P) requirements for *Thalassia* growth that quantities of those nutrients generally available in marine sediments would not restrict their growth. His conclusion was based in part on the hypothesis that nitrogen was fixed by anaerobic bacteria associated with seagrass roots and in the sediments of the rhizosphere. The occurrence of nitrogen fixation was later demonstrated for several seagrass species (Patriquin and Knowles, 1972; Capone and Taylor, 1980; Smith and Hyasaka, 1982; Capone, 1983). While the high rates of nitrogen fixation and relatively large concentrations of ammonium seem to suggest that seagrass growth

is not restricted by nitrogen, there are conditions where a combination of high plant density and low organic matter can result in nitrogen limitation (Short, 1983; Short and McRoy, 1984).

Studies of phosphorus and its availability in the sediment have been equivocal. Sufficiently high levels of phosphorus are often present in marine sediments (McRoy and McMillan, 1977; Entsch et al., 1983; Short, 1987); however, they tend to become adsorbed to carbonates (deKanel and Morse, 1978; Rosenfeld, 1979; Krom and Berner, 1980). Phosphorus tightly adsorbed to sediments is believed to be unavailable to marine angiosperms and this adsorption is likely to be a particularly important mechanism for nutrient limitation where carbonate mud sediments predominate (Hines and Lyons, 1982).

To test the role of nutrients as determinants of seagrass growth, several approaches have been used including: the assessment of nutrient reservoirs and measures of plant tissue concentration (Patriquin, 1972; Kenworthy et al., 1982; Atkinson and Smith, 1983; Short, 1983; Short et al., 1985); nutrient regeneration rates (Iizumi et al., 1982; Short et al., 1985); nitrogen fixation assays (Patriquin and Knowles, 1972; Smith and Hyasaka, 1982; Capone, 1983), fertilization studies (Raymont, 1947; Orth, 1977; Bulthuis and Woelkerling, 1981; Harlin and Thorne-Miller, 1981; Orth and Moore, 1982; Roberts et al., 1984; Pulich, 1985; Fonseca et al., 1986; Williams, 1987); and plant nutrient utilization (McRoy et al., 1972; Penhale and Thayer, 1980; Short, 1983; 1987). Despite some difficult interpretation problems, these studies point to nutrient availability, especially of nitrogen, as a major factor controlling seagrass growth in temperate zone environments. In contrast, initial studies in tropical environments suggest that nitrogen levels are likely to meet plant growth demands and phosphorus is likely to be limiting due to its tendency to become adsorbed to carbonate sediments (Short et al., 1985).

In this study we used nutrient additions to examine whether the production and standing crop of tropical seagrasses growing in carbonate sediments in northeastern Florida Bay are limited by nutrient availability. Nutrients were provided in the form of bird excrement on a shallow mud bank populated by two seagrasses, *Thalassia testudinum* and *Halodule wrightii*. Excrement additions were accomplished by encouraging seabirds to roost at specific locations. Nitrogen to phosphorus ratios of the bird excrement and plant tissue were examined in order to assess the relative importance of nitrogen and phosphorus additions. The implications of our findings are discussed in terms of the Florida Bay ecosystem, current water management practices and future nutrient inputs into the bay.

METHODS

Study Site.—Florida Bay is a large estuary bordered on the north by the tip of the Florida peninsula and on the south and east by the Florida Keys. An extensive network of anastomosing mud banks restricts tidal flow within the bay to such an extent that the interior area, including Cross Bank, is basically non-tidal (Powell et al., 1987). The mean range in daily fluctuations in water level on Cross Bank is only 3.9 ± 1.1 cm (Holmquist et al., 1989). The lack of freshwater input and exchange of water with the open ocean in eastern Florida Bay is further demonstrated by the tendency towards hypersalinity, with salinities reaching as high as 70‰ (Tabb et al., 1962; M. B. Robblee, unpubl.). Salinity measurements made intermittently on Cross Bank throughout the 4 years of this study ranged between 28 and 42‰ (Holmquist et al., 1989). The low levels of both tidal exchange and freshwater runoff at the Cross Bank study site minimized the importance of water exchange as a source of nutrient input. In the absence of significant water exchange, the major potential source of nutrients for seagrasses is the sediment by way of the sediment pore water. Sediment depths on Cross Bank average 2 m and are composed primarily of fine carbonate sediment (8–31 μm; Fleece, 1962). Water depth on Cross Bank varied between 9 and 35 cm during the years 1983 and 1985 (Powell et al., 1987). The principal seagrass species on the study area is *Thalassia*, with extremely sparse amounts of *Halodule* (Powell et al., 1987).

Experimental Design.—As part of a separate study, location markers constructed of PVC pipes (1.2 cm dia.) with wooden blocks (5 cm·10 cm·10 cm) on top had been set out at 100 m intervals along Cross Bank (Powell et al., 1987). These stakes were used as roosting sites by two species of seabirds, Royal Terns, *Sterna maxima,* and Double-crested Cormorants, *Phalacrocorax auritus,* 84% of the time (Powell et al., in prep.)[1]. This meant that the area around each stake was receiving supplementary nutrients in the form of excrement at a relatively consistent rate. The fact that seagrasses were observed to be much denser around these stakes led to our hypothesis that seagrasses on Cross Bank were nutrient limited.

Five of the pre-existing location markers, spaced at 600-m intervals (600, 1,200, 1,800, 2,400, and 3,100) were selected as experimental stations. At the beginning of the present experiment (November 1983), the markers had been in place for 28 months (since July 1981). At each station the original transect markers were pushed down to substrate level so that they continued to serve as site markers, but birds could no longer roost on them. A new identical stake with wooden top (hereafter termed enriched site) was inserted 5 m from the old marker. For controls, PVC pipe (1.2 cm dia.) with no wooden top was cut to a point and placed 5 m from each of the five original markers in the opposite direction along the bank from the enriched site. Design of the control stakes prevented the birds from landing at the control site, but provided the same presence of pipe in the water as the enriched sites.

Data Collection.—NUTRIENT INPUTS. The quantity of nutrients in the form of bird excrement delivered to the five stations was quantified by placing platform collectors (about 60 cm·60 cm) covered with removable clear sheets below the enriched stakes and removing collected excrement at 24-h intervals within 2 h after sunrise. Collections were made in March 1985, and April and November 1986. All samples of excrement were dried, weighed to a constant weight (±1 mg) and analyzed for total phosphorus and total nitrogen. Total phosphorus was determined by extracting phosphorus with persulfate digestion (Menzel and Corwin, 1965) and inorganic phosphorus was determined by the method of Strickland and Parsons (1972). Estimates of extraction efficiencies were determined from persulfate digestion of commercial fertilizers (Osmocote, Sierra Chemical Co.) and National Bureau of Standards (NBS) reference orchard leaves. Total nitrogen was obtained by oxidation using a Carlo Erba Model 1106 CHN analyzer standardized with NBS orchard leaves.

The solubility of the relatively solid phase of the bird excrement and release of inorganic PO_4-P and NH_4-N was determined on samples collected in November 1986. Two solubility experiments were conducted in which 16 (experiment 1) or 14 (experiment 2) portions of excrement (50–100 mg wet weight each) were placed in 20 ml of filtered, microwave-sterilized water collected 10 km offshore. The experiment was designed so that the solubility and nutrient release (PO_4^{3-} and NH_4^+) of two replicates of excrement and a control could be quantified in a time series. Sampling times in experiment 1 were 5, 10, 15, 30 min, 1, 3, and 24 h. Sampling times in experiment 2 were 5, 15, 30 min, 1, 6, 17 h. At each sampling time, two of the vials were removed from the experiment, and the inorganic PO_4^{3-} and NH_4^+ concentrations in the water were determined using the indophenol method of Koroleff (1983) for ammonium and the molybdate blue method for soluble inorganic phosphorus modified from Parsons et al. (1984). In addition to quantifying the release of inorganic nitrogen and phosphorus the remaining contents of each vial were filtered onto predried and tared glass fiber filters. The filters and their contents were dried to a constant weight (±1 mg) and the amount of insoluble excrement was determined at the termination of each incubation.

PORE WATER NUTRIENTS. Interstitial pore water and surface water was collected from the enriched and control treatments at station 1,800 in October 1986 after 3 years of enrichment. Surface water was collected from within the seagrass canopy, and filtered through 0.45-μm membrane filters into acid-washed vacutainers in the field. Tension lysimeters, modified from the design of Short et al. (1985), were placed at depths of −10, −20, −30, and −40 cm in the sediment at the four corners of a square approximately 1 m on a side around the central stake of each treatment. This allowed for sampling of water through and below the root zone of the grass beds. Samples were withdrawn on three successive days from these lysimeters under an argon atmosphere and filtered through 0.45-μm membrane filters into acid-washed vacutainers in the field. Samples of water from the slurry at the sediment-water interface were collected by inserting a capped, acid-washed flask into the sediment so that the mouth of the flask was flush with the sediment-water interface. This flask was then uncapped, and slurry was drawn into the container by the escaping air. All samples were stored on ice and returned to the lab, where all analyses were completed within 3 h of collection. Sediment-water interface samples were filtered through 0.45-μm filters in the lab. Nutrient determinations for all samples were done colorimetrically with the methods of Parsons et al. (1984) for phosphate and Koroleff (1983) for ammonia.

SEAGRASS BIOMASS. Standing crop (aboveground biomass) of each species was quantified at enriched

[1] Powell, G. V. N., J. W. Fourqurean and W. J. Kenworthy. The interrelationships between seabirds and seagrasses in a subtropical lagoon. In preparation.

and control sites in four replicate 10-cm by 10-cm quadrats. These replicate quadrats were placed 30 cm and 50 cm from the marker stakes along a transect parallel to the predominant direction of water flow. At the initiation of the experiment, standing crop measurements were made at three sites (600, 1,200 and 3,100). Thereafter, standing crops were collected annually in November at each of the five stations. The plant material was washed in 10% HCl to remove carbonates, rinsed and dried to a constant weight (±1 mg). To test for differences between enriched and unenriched, we used Paired *t*-tests on log-transformed data.

Samples for below ground biomass were collected once in April of 1986. One sample was obtained at both the control and enriched sites at each of the five stations. Samples were obtained with a 15-cm diameter coring device inserted approximately 25 cm into the sediment. The entire contents of the core were extracted, washed free of sediments and sorted by species and by plant component. The plant material was washed in 10% HCl and dried to a constant weight (±1 mg). Mann-Whitney *U*-tests were used to test for differences in below ground biomass for both *Halodule* and *Thalassia*.

ABOVEGROUND STRUCTURE. After the second year of enrichment all *Thalassia* collected for standing crop determinations were measured (length and width) and blades per short shoot counted to determine the impact of enrichment on the structure of the seagrass canopy. Analysis of variance (ANOVA) was used to test for differences in these measures of the aboveground structure of the meadow.

LEAF PRODUCTIVITY MEASUREMENTS. *Thalassia* productivity was measured in May and October 1986 using the stapling method of Zieman (1974). Five 10-cm·20-cm quadrats were placed at the enriched and control sites at three stations (600, 1,800 and 3,100). All *Thalassia* blades within the quadrats were marked with staples at the sediment surface. After 10 to 16 days the *Thalassia* was collected, new and old growth was separated at the staple, measured (length and width), washed in 10% HCl and oven dried to constant weight (±1 mg). Analysis of variance with time and site as repeated factors was used to analyze the data. Due to heteroscedasticity, values were log-transformed before the analysis.

Halodule leaf productivity was measured in October 1986 using a modified leaf-marking technique. At two sites (600 and 1,800), all *Halodule* blades on 4–10 short shoots in six replicate 10-cm·10-cm quadrats were marked at the intersection of the sheath and leaf with number 00 stainless steel insect pins at both the enriched and control treatments. All of the replicates were placed within one meter of the stake at the enriched treatment, but the scarcity of *Halodule* at the control treatments necessitated our searching out short shoots for marking within a 10-m radius of the control stake. After 10 days, the *Halodule* blades were harvested and processed using the same procedure described for *Thalassia*. Areal productivity for *Halodule* was estimated by calculating the amount of productivity per short shoot and multiplying this value by the average number of short shoots·m^{-2} in the permanent quadrats.

SEAGRASS NUTRIENT CONTENT. Total nitrogen and phosphorus were determined for *Thalassia* and *Halodule* leaves and rhizomes from samples collected in April 1986 at enriched and control sites at each of the five stations. Total nitrogen and phosphorus were determined as described for bird excrement on triplicate subsamples of each plant component for both species. A Mann-Whitney *U*-test was used to test for differences in N and P content of plant tissues from enriched and control sites.

NITROGEN FIXATION. Rates of nitrogen fixation associated with *Thalassia* and *Halodule* leaf tissues were estimated using the acetylene reduction activity (ARA) technique of Stewart et al. (1967) and Hardy et al. (1968) as modified by Smith and Hyasaka (1982). Incubations were performed in clean, capped 50-cm^3 syringes from which 5 cm^3 of gas were removed and replaced with acetylene. Approximately 10 g wet weight of *Thalassia* or *Halodule* leaves were placed into 3 replicate syringes. At 3 and 6 h after the start of the incubations 10 ml of gas were removed from each syringe and stored in a vacutainer for transportation back to the lab. In the lab an aliquot (0.3 ml) of each vacutainer was removed and ethylene and acetylene were quantified with a gas chromatograph (Shimadzu GC-9a) equipped with a flame ionization detector. After each incubation the entire contents of each syringe were dried to a constant weight (±1 mg). Two replicates were conducted on material from enriched and control sites from station 1,800.

RESULTS

NUTRIENT INPUTS. The range of the average amounts of bird excrement deposited at each collection site was 2.76 g dw·d^{-1} in May 1985, to 4.1 g dw·d^{-1} in November. The daily variability in deposition rates was measured during a week-long intensive sampling period in October and November 1986; the standard error was approximately 30% of the daily mean. The daily input of bird feces at each site, calculated as the average of the daily means from the three sampling periods, was 3.50 ± 0.436 g dw (±1 SE).

Bird feces collected on Cross Bank averaged 3.63 ± 0.25 (N = 8) percent phosphorus and 19.32 ± 1.06 (N = 8) percent nitrogen by weight. The mean N/P

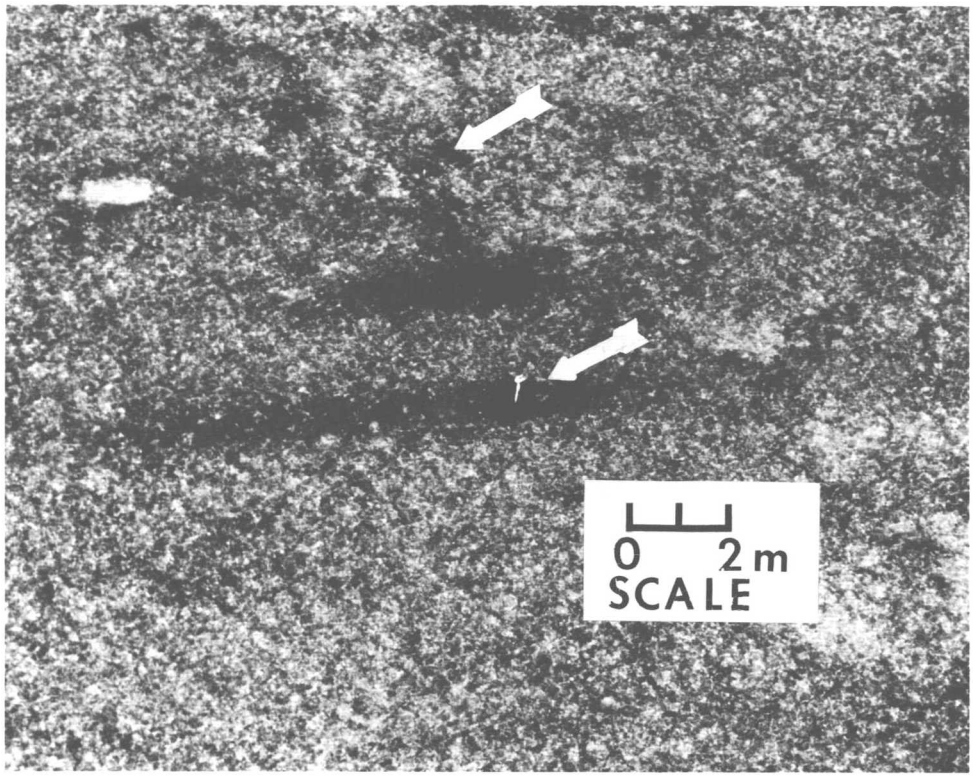

Figure 1. Aerial photograph showing dense seagrass growth around bird-enriched stakes. The upper arrow points to the control site; the lower arrow points to the enriched site (a Royal Tern is present on the perch); the enriched area (dark) between the two sites is the old enriched area that existed before the study began.

ratio (WT:WT) of the samples was 5.38 ± 0.56 (N = 8). These figures give a loading rate of 0.678 g nitrogen and 0.127 g phosphorus per day (246 g nitrogen and 46.3 g phosphorus per year) at each site. The area receiving these nutrients was estimated as the area of the obvious enriched patch surrounding each stake (Fig. 1). These enriched areas were generally elliptical, with the long axis of the ellipse parallel to the direction of current flow averaging 5.44 m. The minor axis was perpendicular to the current flow with an average length of 2.65 m for an enriched area of 12.8 m^2. The average daily areal input of excrement was 0.273 g $dw \cdot m^{-2}$, which supplied 0.052 $gN \cdot m^{-2}$ and 0.009 $gP \cdot m^{-2}$.

Over a 24-h period, 28–30% of the relatively solid phase of the bird excrement was dissolved in seawater. A small fraction of the total nitrogen and phosphorus was released almost immediately as inorganic PO_4^{3-} and NH_4^+ (Fig. 2), and approximately 50% of the original phosphorus and 9% of the original nitrogen in the excrement was released as phosphate and ammonia after 17–24 h of immersion. This results in 17.5 mg phosphorus and 16.6 mg nitrogen being added to the water column for each gram of excrement, or 61.2 mg PO_4-$P \cdot d^{-1}$ and 58.1 mg NH_4-$N \cdot d^{-1}$ at each bird roosting stake.

Pore Water Chemistry. There was no measurable inorganic phosphate in the surface water over any of the sites (sensitivity = 0.03 μM). Pore water PO_4^{3-} concentration at the enriched treatment was higher than at the control stake. Background pore water phosphate levels, as measured at the control stake, were

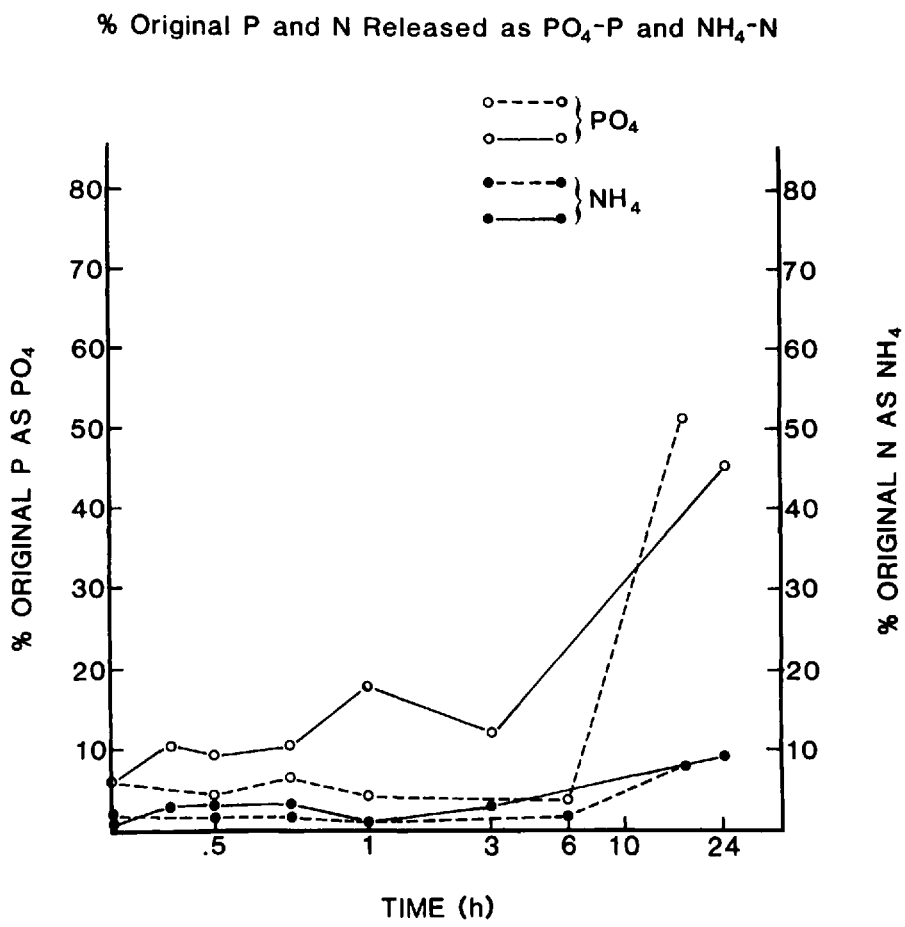

Figure 2. Release of dissolved inorganic PO_4-P and NH_4-N from bird excrement placed in filtered seawater. Shown are the results of two incubations; each point is the mean of two replicates.

between 0.1 and 3.0 μM PO_4^{3-}, and averaged 0.8 $\pm$ 0.3 μM PO_4^{3-} ($\bar{x} \pm 1$ SE) over all depths in the sediment. At the enriched site, phosphate concentrations were between 1.6 and 25.9 μM, with a depth-averaged (0–40 cm) value of 12.3 $\pm$ 2.5 μM. Phosphate levels showed little variation with depth in the sediment at the control site, but changed with depth at the enriched site (Fig. 3). Concentrations were enhanced over control values in the upper 20 cm of sediment, but returned to background levels at -30 cm in the sediment. The maximum PO_4^{3-} concentration was between 0–10 cm.

Interstitial pore water and surface water ammonium levels showed much greater variation than PO_4^{3-} levels (Fig. 3). Surface water samples ranged from 6.8 to 80.7 μM NH_4^+, with an average of 35.3 $\pm$ 9.0 μM. Depth-averaged pore water values showed more NH_4^+ at the enriched site (324.8 $\pm$ 84.9 μM) than at the control site (190.8 $\pm$ 59.5 μM). As with the PO_4^{3-} data, the ammonium levels seem to be enhanced only in the upper 20 cm of sediment at the enriched sites. Ammonium concentrations increase with depth throughout the profile at the control site, but show an increase with depth to 20 cm, followed by a decrease to background levels at lower depths at the enriched area.

SEAGRASS BIOMASS. There was no significant difference between control sites

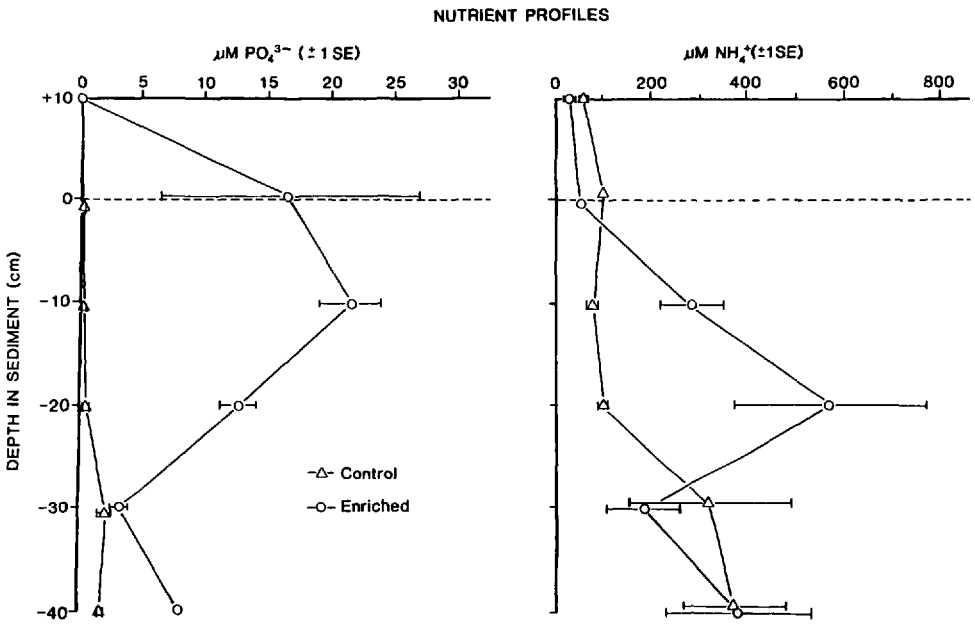

Figure 3. Sediment pore water nutrient profiles for control and enriched treatments in October 1986. Each point is the $\bar{x} \pm 1$ SE of three replicates.

and sites that were to be enriched at the beginning of the experiments (Table 1). After 1 year of enrichment, standing crops at enriched sites averaged more than twice the controls and all control and enrichment pairs were significantly different ($P < 0.01$, Table 1). Thereafter, *Thalassia* standing crop either remained constant (3,100) or declined through the next 2 years (Table 1). After 3 years of enrichment, there was no significant difference between enriched and unenriched *Thalassia* standing crop ($P = 0.3$). In contrast, *Halodule* standing crop increased slowly the first 2 years before increasing greatly between the second and third years (Table 1).

There was a substantial variation among stations for the below-ground biomass of *Thalassia* (Table 2). Variation was as great among treatments as between treatment and controls and there was no evident enhancement or reduction of *Thalassia* root and rhizome biomass at the enrichment sites ($\bar{x} = 829.0 \pm 81.3$ $g \cdot m^{-2}$ for enriched and 793.3 ± 66.0 $g \cdot m^{-2}$ for controls, $P > 0.10$). *Halodule* below-ground biomass was higher at enriched sites (33.9 ± 6.0) than at control sites (0.0 g, $P < 0.025$).

ABOVEGROUND STRUCTURE. The average length of *Thalassia* blades was significantly longer on enriched sites ($\bar{x} = 13.8$ cm) than controls ($\bar{x} = 11.1$ cm, $F = 34.7$, $P < 0.01$). Average blade width was also slightly wider for enriched blades ($\bar{x} = 0.637$ cm enriched, 0.598 cm for controls, $F = 5.1$, $P = 0.03$). The number of blades per short shoot was not significantly different between control and enriched sites ($P > 0.05$).

The effect of enrichment on *Halodule* was quantitatively evident in the structure of the canopy (Fig. 4). The average longest leaf and the total leaf length per short shoot were all greater than the controls. Since width of *Halodule* is so narrow (about 1 mm) we did not attempt to measure for differences in width of enriched and unenriched blades.

LEAF PRODUCTIVITY. Nutrient addition significantly increased areal production of *Thalassia* (Fig. 5, $F_{1,2} = 34.5$, $P = 0.028$). In May there was 55% more pro-

Table 1. Standing crop (g dw·m^{-2}) for *Thalassia* and *Halodule* at five paired bird-enriched and control sites (values in parentheses are 1 SE, N = 4)

	Pre-enrichment	Post-enrichment		
		1 year	2 years	3 years
Thalassia				
600				
Control	81.75 (35.16)	62.85 (12.10)	35.33 (3.69)	33.73 (8.05)
Enriched	45.00 (2.15)	133.15 (10.69)	66.03 (8.72)	3.90 (1.98)
1,200				
Control	90.75 (14.38)	61.15 (12.85)	38.70 (7.76)	48.93 (13.46)
Enriched	64.75 (15.28)	147.35 (6.54)	177.93 (29.07)	81.45 (20.03)
1,800				
Control	ND	42.68 (9.35)	61.50 (6.19)	51.85 (7.80)
Enriched	ND	127.50 (22.98)	98.80 (25.31)	31.83 (11.98)
2,400				
Control	ND	24.90 (10.99)	51.20 (15.59)	21.03 (5.73)
Enriched	ND	115.45 (28.43)	87.55 (14.41)	61.63 (21.17)
3,100				
Control	88.25 (24.99)	64.70 (14.07)	86.55 (13.97)	84.55 (7.65)
Enriched	72.25 (19.16)	169.78 (36.29)	191.50 (18.58)	192.50 (4.84)
Halodule				
600				
Control	0	0	0	0
Enriched	0	11.40 (3.24)	17.58 (4.09)	39.88 (8.76)
1,200				
Control	0	0	0	0
Enriched	0	0.18 (0.15)	28.35 (8.84)	49.88 (12.57)
1,800				
Control	ND	4.53 (3.52)	0.60 (0.52)	0
Enriched	ND	3.72 (3.23)	60.05 (23.62)	100.33 (5.52)
2,400				
Control	ND	0	0	0.22 (0.19)
Enriched	ND	16.85 (6.19)	114.68 (19.45)	151.93 (16.89)
3,100				
Control	0	0	0	0
Enriched	0	0	0	0

ductivity at the enriched sites; productivity at the control sites was 2.15 ± 0.52 g dw·m^{-2}·d^{-1} (±1 SE, N = 3), compared to 3.34 ± 0.82 g dw·m^{-2}·d^{-1} at the enriched sites. Similarly, in October, the enriched sites were 86% more productive than control sites (1.49 ± 0.75 g dw·m^{-2}·d^{-1} at controls, 2.78 ± 1.10 g dw·m^{-2}·d^{-1} at enriched). There was no significant difference between the areal productivity for the two sample periods ($F_{1,2} = 1.2$, $P = 0.385$). The mean areal productivity for time periods was 1.84 ± 0.43 g dw·m^{-2}·d^{-1} for the controls and 2.98 ± 0.62 g dw·m^{-2}·d^{-1} at the enriched sites. Enriched areas produced twice the new leaf area (length × width) ($\bar{x}$ = 430 ± 110 cm^2·m^{-2}·d^{-1}) as control sites ($\bar{x}$ = 225 ± 34 cm^2·m^{-2}·d^{-1}, *t*-test, $P = 0.04$).

Areal productivity of *Halodule* was strongly affected by the addition of nutrients. Productivity at enriched sites was three orders of magnitude higher than at control sites ($\bar{x}$ = 16.36 ± 5.74 g dw·m^{-2}·d^{-1} for enriched versus $\bar{x}$ = 0.013 ± 0.013 g dw·m^{-2}·d^{-1} for controls). *Halodule* short shoots in enriched sites put on twice as much new leaf length as shoots in control areas (Fig. 4).

SEAGRASS NUTRIENT CONTENT. Total phosphorus content (dry weight basis) was greater at enriched sites for leaf and rhizome tissue of both species ($P < 0.03$ for

Table 2. Dry weights (grams)·m^{-2} collected from Cross Bank bird stakes 4/26/86. Below ground biomass values include roots, rhizomes and shoots up to the base of the leaves

		Sample type			
Station	Treatment	*Thalassia* Standing crop	*Thalassia* Below ground	*Halodule* Standing crop	*Halodule* Below ground
600	Enriched	98.52	672.27	12.67	18.98
	Control	149.09	590.34	0.00	0.00
1,200	Enriched	417.04	1,181.64	47.56	58.52
	Control	90.00	1,162.50	0.00	0.00
1,800	Enriched	98.75	563.12	25.91	20.51
	Control	99.89	645.34	0.00	0.00
2,400	Enriched	53.86	395.57	58.35	71.76
	Control	10.06	440.91	0.00	0.00
3,100	Enriched	441.25	1,332.50	0.00	0.00
	Control	246.25	1,127.55	0.00	0.00
$\bar{x}$	Enriched	221.87	829.03	28.92	42.44
	Control	38.07	81.31	10.80	11.93
$\bar{x}$	Control	119.03	793.35	0.00	0.00
	SE	17.39	65.97	0.00	0.00

all comparisons, Fig. 6). The percent nitrogen (dry weight basis) of *Halodule* leaves was greater in the enriched sites ($P = 0.01$); however, *Thalassia* leaves had a similar nitrogen content at both controls and enriched sites ($P = 0.40$). *Thalassia* rhizomes at the control sites tended to have a greater nitrogen content than enriched sites ($P = 0.057$), while *Halodule* rhizomes tended to have a greater nitrogen content at enriched sites ($P = 0.057$, Fig. 6).

Acetylene Reduction Activity (ARA). Rates of nitrogen fixation associated with *Halodule* leaves estimated from ARA were substantially greater at enriched sites than at control sites in each of the incubations (Fig. 7). ARA for microbes associated with enriched *Thalassia* leaves were similar in both incubations and were generally higher than controls (Fig. 7).

Discussion

Fertilization Response.—Birds added a substantial amount of nutrients to the seagrass system of Cross Bank in this study. Some of this nutrient load is readily soluble, and becomes immediately available to plants in the water column. A large fraction (approximately 70%) of the bird excrement is composed of relatively insoluble organic compounds. Hutchinson (1950), for example, reports that ⅔ of the nitrogen in seabird excrement is in uric acid. At least a part of these more insoluble components of the excrement are deposited in the surficial sediments where thay are decomposed and inorganic nutrients are remineralized (Fig. 2). Higher concentrations of NH_4^+ and PO_4^{3-} in the sediment pore water from the enriched sites reveal the effect of these processes; they are more nutrient rich than the pore water at control sites (Fig. 3).

Both *Thalassia* and *Halodule* showed significant growth responses to nutrient additions indicating that, in this environment at least, both were nutrient limited. Most of the response by *Thalassia* was in increased length and width of blades of existing short shoots. It is noteworthy that the increase in *Thalassia* standing crop occurred during the first year of enrichment, and either remained constant

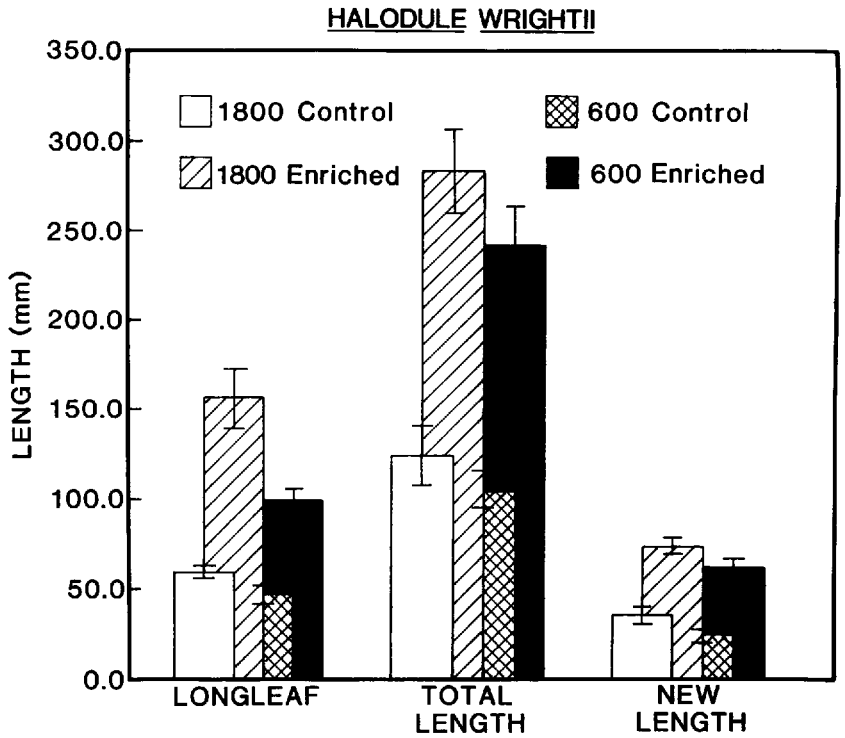

Figure 4. The effect of nutrient enrichment on leaf length of *Halodule wrightii*. Shown are the longest leaf per shoot, total length per shoot and new length per shoot at two of the five study stations in October 1986. Error bars indicate ± 1 SE.

or declined over the next two years. The elevated *Thalassia* standing crops were similar to levels typical of western Florida Bay (Zieman et al., 1989). In contrast to our study area, western Florida Bay is open to water exchange with the Gulf of Mexico, has a large semi-diurnal tidal flux (Holmquist et al., 1989) and is characterized by the highest seagrass biomass of anywhere in the bay (Powell et al. 1987; Zieman et al., 1989).

The response of *Halodule* to nutrient additions differed markedly from *Thalassia*. *Halodule* is virtually absent from banks in eastern Florida Bay in general and was absent from most of the pre-enrichment sites. After a single year of enrichment, *Halodule* had become established at low densities at three sites and was established at four of the five sites by the end of the second year. Over the four-year tenure of this study *Halodule* standing crop increased by an order of magnitude at the enriched sites without changing at the control sites (Table 1). As was the case with *Thalassia*, the only part of Florida Bay that has standing crops of *Halodule* that approach the enriched site standing crop is the Gulf area (Zieman and Fourqurean, 1985; Powell et al., 1987).

Nitrogen versus Phosphorus Limitation.—The proportion of phosphorus contained in the excrement that is solubilized in the first 24 h is much larger than the proportion of nitrogen, resulting in an N:P ratio of near unity for the soluble inorganic fraction immediately available to the plants (Fig. 2). This ratio is much higher than the normal N:P ratios for organic matter originating from seagrasses

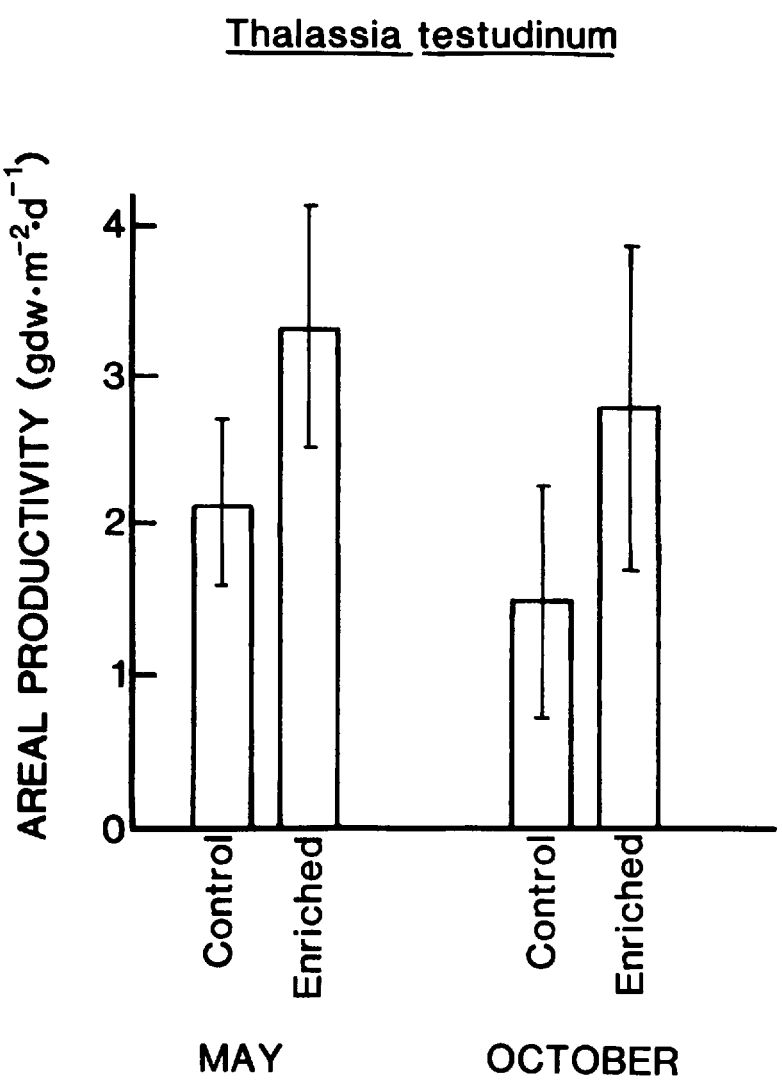

Figure 5. Areal productivity of *Thalassia testudinum* at control and enriched sites in May and October 1987. Values shown are $\bar{x} \pm 1$ SE for three replicates.

(Atkinson and Smith, 1983) or for that matter most other sources (Redfield et al., 1963). In this study, both nitrogen and phosphorus were added by the bird excrement so it is not possible to unequivocally determine their relative contribution to increased productivity. However, indirect evidence points to phosphorus as the limiting nutrient under unenriched conditions.

Concurrent with this study, a 6-month nutrient-enrichment study conducted on a *Thalassia*-dominated mud bank in northeast Florida Bay showed that nitrogen enrichment stimulated a significant growth of brown algae but no significant changes in seagrass standing crop or productivity (Powell et al., 1987). The results contrast with the more than doubling of *Thalassia* standing crop within 1 year of bird enrichment. The contrasting results of the two studies point to phosphorus as the nutrient limiting *Thalassia* biomass at the bird-enrichment sites. Because

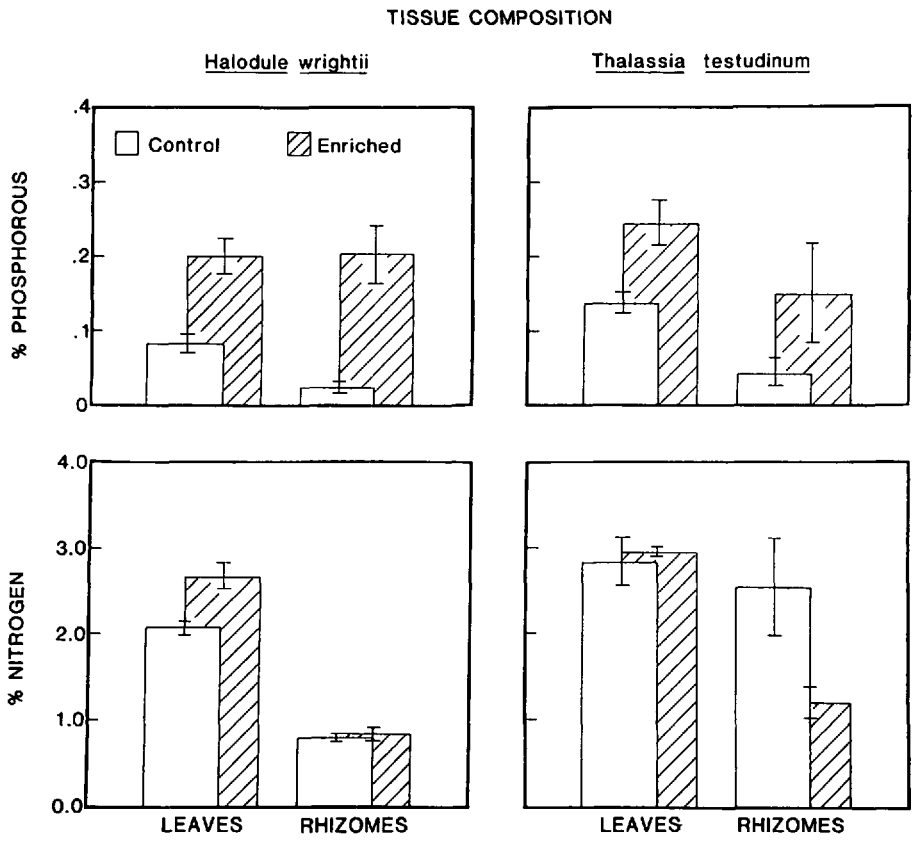

Figure 6. Total nitrogen and total phosphorus content of *Halodule wrightii* and *Thalassia testudinum* leaves and rhizomes in April 1986. Values are $\bar{x} \pm 1$ SE of five replicates. Percentages were calculated on a dry weight basis.

the response of *Halodule* to nutrient additions at the bird-enriched sites was not strongly evident until the second year, the 6-month experiment by Powell et al. (1987) may have been too short to test for the effect of nitrogen additions on that species.

Another line of evidence that points to phosphorus as the limiting nutrient, at least at the initiation of the nutrient additions, is the nitrogen-to-phosphorus ratio of the seagrasses from these experiments. Our data show that phosphorus has accumulated in the plant tissues at the enriched sites. Assuming that the concentration of an element in plant tissue is a reliable indicator of the availability of that element in the environment (Gerloff and Krombholz, 1966; Atkinson and Smith, 1983; Barko and Smart, 1986), we conclude that the availability of phosphorus had increased relative to the availability of nitrogen from pre-enrichment levels; therefore, P was probably limiting prior to enrichment. Phosphorus content for seagrasses from enriched sites is among the highest ever reported for either *Thalassia* or *Halodule* and results in depleted N:P ratios compared to other seagrasses (Atkinson and Smith, 1983; Short et al., 1985).

Under bird-enriched conditions, the control on seagrass productivity appears to shift from phosphorus to nitrogen limitation. While large amounts of nitrogen were added by the birds, a substantial fraction of the nitrogen was introduced as

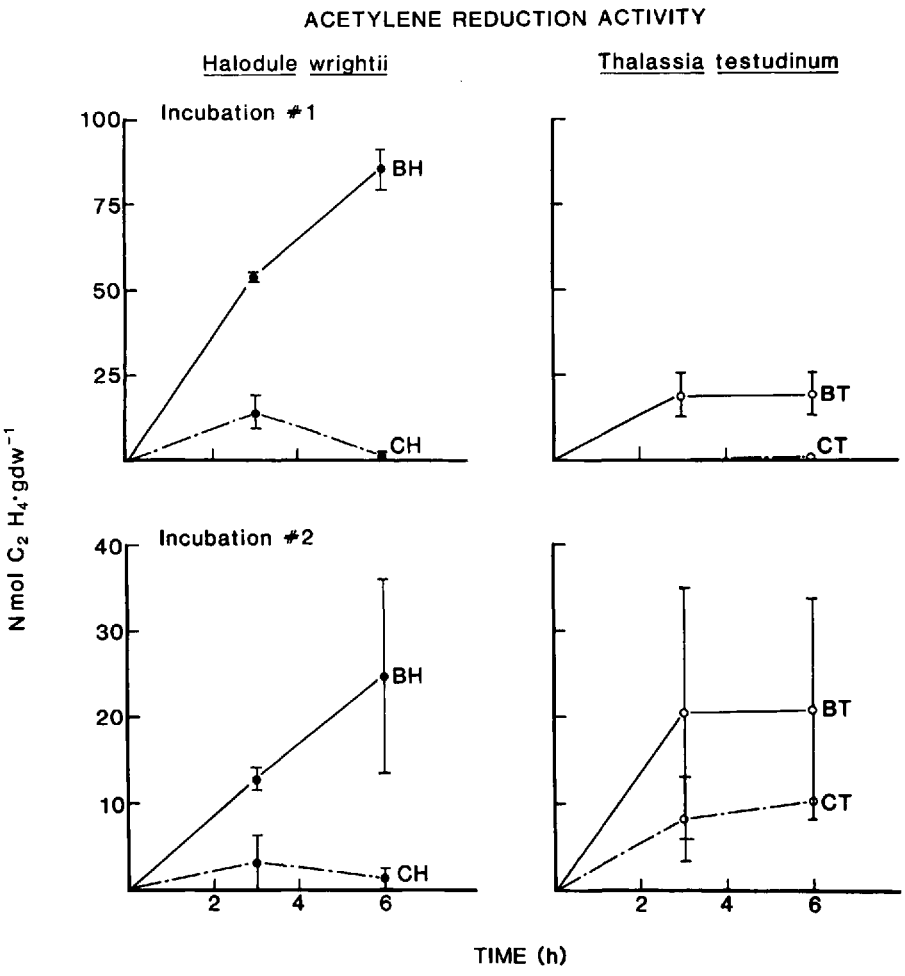

Figure 7. Acetylene reduction activity associated with leaves of two seagrasses, *Halodule wrightii* and *Thalassia testudinum*. Values are $\bar{x} \pm 1$ SE for two replicates at each sampling time.

uric acid, which has a low solubility in seawater (CRC Handbook of Chemistry and Physics) and is therefore likely to be initially unavailable to the plants. Some of this relatively insoluble excrement will be incorporated into the sediment, but a substantial fraction is likely to be moved away by currents before it can be buried and remineralized by microbial action.

Based on the %N and %P composition of control *Thalassia* tissue we estimate nitrogen and phosphorus demands under typical conditions (*Thalassia* production = 1 g C·m^{-2}·d^{-1}) of approximately 0.0595 g N·m^{-2}·d^{-1} and 0.00321 g P·m^{-2}·d^{-1}. Under these idealized conditions the demand for nitrogen would be nearly equivalent to the estimated daily areal input of the birds. However, the input of phosphorus from the birds exceeds the estimated plant demand by a factor of three. In contrast to unenriched sites, this would suggest that at bird-enriched sites the plants would face a deficit of nitrogen if they were capable of utilizing all of the allochthonous phosphorus unless other nitrogen sources were available. Other nitrogen resources are available, especially in the decomposing pool of

organic matter in the sediments (Patriquin, 1972; Kenworthy et al., 1982; Short et al., 1985; Short, 1987), but these may not be sufficient to match a nearly 3× load of phosphorus without supplemental nitrogen sources.

Further evidence for nitrogen limitation under enriched conditions is derived from the pore water analyses. Nutrient concentrations in pore waters of enriched sites were much higher than controls but the relatively steep slope of the nitrogen profile in the upper 20 cm at the enriched site suggests more rapid uptake and demand for mineralized nitrogen at these sites (Fig. 3).

Increased nitrogen fixation of associated microorganisms, as evidenced by the incubation experiments, could provide supplemental nitrogen to meet at least a portion of the excessive phosphorus delivered by the birds (Capone, 1983). In both incubation experiments (Fig. 7), ARA for *Halodule* was substantially and consistently greater for leaves from enriched sites than at the controls, while *Thalassia* leaf ARA at enriched sites was higher but more variable. The substantially elevated ARA for *Halodule* leaves at enriched sites corresponds to a significantly greater leaf nitrogen content. *Syringodium filiforme* beds in San Salvador, Bahamas, responded to phosphorus fertilizer additions in a similar manner with the enhancement of nitrogen fixation attributed to release of labile organic carbon during elevated levels of seagrass leaf production (Fred Short, pers. comm.).

Nitrogen content was similar for *Thalassia* leaves from enriched and control sites but showed a tendency to be depleted in the rhizomes of plants analyzed from the enrichment sites ($\bar{x}$ enriched = 1.17% ± 0.17%, $\bar{x}$ control = 2.49% ± 0.56%, Fig. 6). The relative depletion of nitrogen in *Thalassia* rhizomes at the enriched sites may be due in part to a large demand for nitrogen in the leaves that are experiencing elevated productivities stimulated by phosphorus enrichment. To match the elevated levels of phosphorus, nitrogen may be diverted from accumulating in the rhizomes just as occurs during a typical seasonal cycle of *Thalassia* production (Dawes and Lawrence, 1980). *Halodule* leaves from enriched sites had more nitrogen yet, unlike *Thalassia,* there was no difference in nitrogen content of *Halodule* rhizomes at enriched and control sites ($\bar{x}$ enriched = 0.82% + 0.070%, $\bar{x}$ control = 0.79% ± 0.024%, Fig. 6). These differences between the species suggest fundamental differences in physiology and growth relative to the acquisition, accumulation, and storage of the major macronutrients.

Nutrients and Seagrass Distribution.—Our results clearly show that over a 3-km section of bank, seagrass productivity and standing crop were nutrient limited. Quantitative studies of seagrass meadows in Florida Bay have shown a sharp gradient in *Thalassia* and *Halodule* standing crops from the depauperate northeast-interior part of the bay to the more luxuriant growth in the open southwestern section of the bay (Powell et al., 1987; Zieman et al., 1989). This trend typifies bank vegetation even though the banks have relatively deep sediments (>1 m) throughout the bay (Davies, 1980). The amount of exchange of water with open waters, as well as the movement of water across seagrass beds by tidal flushing, also increases along the same transect, from low in the northeast to high in the southwest (Holmquist et al., 1989). The results of our study taken in conjunction with this natural seagrass cline within the bay lead us to hypothesize that water circulation plays a major role in providing nutrients (especially phosphorus) for seagrass growth. The occurrence of similar seagrass standing crops in the western part of the bay, where circulation is high, and in our enriched plots suggests that the western area has sufficient circulation to provide required nutrients. In contrast, more interior parts of the bay have restricted circulation and therefore

limited sources of nutrient input. The exception to this generalization of restricted circulation and low standing crops in the eastern bay is the small breaks within banks that allow passage of water between basins. In these cuts, which have shallow sediments (5–15 cm) and relatively high current velocities, seagrasses tend to be robust with standing crops higher than adjacent banks or basins (Thayer et al., 1989). These elevated standing crops are presumably a response to exposure to a greater volume of water and consequently more dissolved nutrients.

Management Implications of Nutrient Limitation.—Restricted exchange of water with the open ocean and low circulation in northeastern Florida Bay result in very little nutrient input from oceanic sources; overland freshwater input into northeastern Florida Bay may therefore be an important source of nutrients for seagrass productivity in that area. The likelihood that water management practices in the Everglades, and especially the east Everglades, have decreased overland flow into northeastern Florida Bay and therefore decreased nutrient supply leads us to predict that northeast Florida Bay has experienced decreasing seagrass productivities over the last several decades. This lack of nutrient input from decreased freshwater runoff would have been exacerbated during the last 2 decades by an atypically long interval between hurricanes, another force that likely increases nutrient availability in this area (Zieman and Fourqurean, 1985). There are no past quantitative measures of Florida Bay seagrasses to test for a decline in seagrass productivity. However, Zieman (1982) notes that muddy, sparse *Halodule* beds that were present in northeast Florida Bay in the mid 1960's had been replaced by *Thalassia* beds in 1979. We have shown that increased nutrient levels stimulate *Halodule* growth, so the decline in *Halodule* in northeast Florida Bay may be an indication of lower nutrient availability in that area.

There is general agreement that northeast Florida Bay has always been an area of relatively low productivity compared to the rest of Florida Bay (Robert Ginsberg, Durbin Tabb, Joseph Zieman, pers. comm.). However, it seems clear, in view of the response of *Thalassia* and particularly *Halodule* to nutrient additions, that the area is highly sensitive to nutrient availability and that any alterations of nutrient input, either through natural or man-induced changes to the system will have dramatic effects on the seagrass community.

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