

PROCEEDINGS
OF
THE FIRST SYMPOSIUM
ON
THE BOTANY OF THE BAHAMAS

JUNE 11-14, 1985

College Center of the Finger Lakes
Bahamian Field Station
San Salvador, Bahamas

Editor

Robert R. Smith

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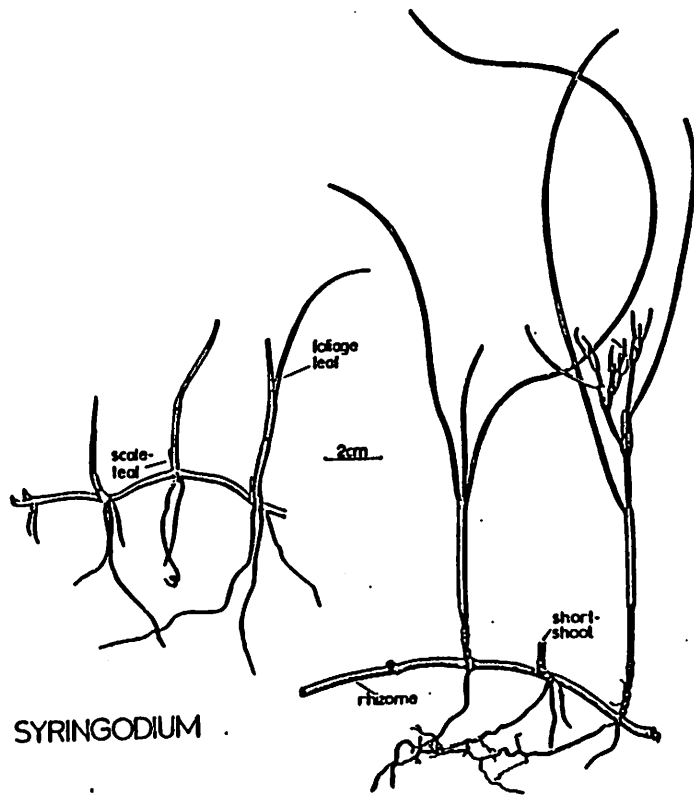
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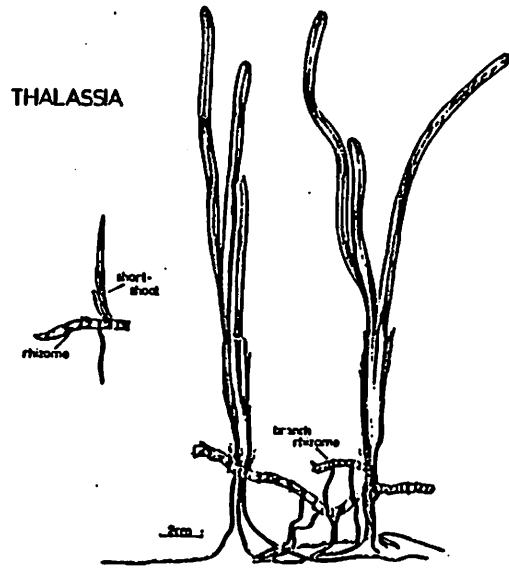
NUTRIENT ECOLOGY OF BAHAMIAN SEAGRASSES

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Seagrasses comprise a group of submerged marine angiosperms found worldwide in shallow tropical and temperate oceans (Hartog, 1970). Two seagrass species, Thalassia testudinum Banks ex König, and Syringodium filiforme Kützing dominate the tropical western North Atlantic and Caribbean coastal environments. Both species represent significant primary production of biomass (Table 1), Thalassia often dominating within the upper 10m, while Syringodium is abundant from shallow water to 25m (El-Sayed et al., 1972). Thalassia is the most widely researched of the tropical seagrasses (McRoy and McMillan, 1977), even though it has a more complex vegetative morphology than Syringodium (Tomlinson, 1974). Rates of production for Syringodium are high, $2.0 \text{ g C m}^{-2} \text{ d}^{-1}$, in the Bahamas (Table 1), although higher rates have been reported for Thalassia (Zieman and Wetzel, 1980). However, Syringodium shoot production exceeds that of Thalassia (Short, 1985). Studies of leaf loss have demonstrated that dead leaves and leaf sheaths of Thalassia (Fig. 1) are deposited near vegetative shoots, while detached leaf material of Syringodium is exported from seagrass beds (Zieman et al., 1979; Short, pers. obs.). Therefore, the organic input into the sediments of a Thalassia bed includes dead detrital leaf material in addition to root and rhizome material, while in Syringodium beds the only organic seagrass input is below the sediment surface. Rates of root and rhizome growth and



SYRINGODIUM



THALASSIA

FIGURE 1. The seagrasses *Syringodium filiforme* and *Thalassia testudium* (from Tomlinson, 1974) showing the attached old leaf sheaths around each short shoot of *Thalassia* and the absence of old sheaths on *Syringodium* short shoots. The absence of decomposing leaf material around the shoot of *Syringodium* results in less complex sediment nutrient cycles.

Table 1 . Leaf biomass and production of seagrass species in the Bahamas

Species	Biomass (g dry m ⁻²)	Production (g C m ⁻² d ⁻¹)	Reference
<u>Thalassia</u>	5.3		Patriquin, 1972
<u>testudinum</u>	200.	2.10	Capone, et al. 1979
	75.4	0.14	Jensen and Gibson unpubl.
<u>Syringodium</u>	159.	2.00	Short, et al. 1985
<u>filiforme</u>	7.6	0.01	Jensen and Gibson unpubl.
<u>Halodule</u>	5.9	0.004	Jensen and Gibson unpubl.
<u>wrightii</u>			

decomposition (Kenworthy, pers. com.) appear to be much faster for Syringodium than for Thalassia. It could be said that Syringodium beds are more dynamic and less complex tropical seagrass systems than those of Thalassia.

The chemical composition of seagrasses in tropical and temperate environments indicates a wide range of carbon to nitrogen to phosphorous ratios (C:N:P) (Table 2). Comparison of benthic plant samples from a variety of locations shows a significant difference between samples from low- and high-nutrient environments (Atkinson and Smith, 1983). Measurements of C:N:P for the seagrass Syringodium filiforme (Table 3) from terrigenous sediments in Florida and from carbonate sediments in the Bahamas also indicate depletion of N

Table 2. Comparative C:N:P Atomic Ratios for Seagrasses From
Around the World.

SEAGRASS	C:N:P ¹ ATOMIC RATIO	REFERENCE ²	
LEAVES			
<u>Enhalus acoroides</u> (Palau)	1000:48:1	Short <u>et al.</u> , 1985	
<u>Syringodium filiforme</u> (Bahamas)	1390:47:1		
<u>Zostera marina</u> (Virginia)	584:41:1		
<u>Posidonia oceanica</u> (Corsica)	956:39:1	Birch 1975	
<u>Thalassia testudinum</u> (Barbados)	:32:1		
<u>Posidonia ostenfeldia</u> (W. Australia)	1070:29:1		
<u>Thalassia hemprichii</u> (N. Queensland)	599:27:1		
<u>Phyllospadix scouleri</u> (California)	509:24:1		
<u>Amphibolis griffithii</u> (W. Australia)	535:20:1		
<u>Cymodocea serrulata</u> (N. Queensland)	:19:1		
<u>Halodule univervis</u> (N. Queensland)	623:18:1		
<u>Syringodium isoetifolium</u> (N. Queensland)	:17:1		
<u>Zostera capricorni</u> (N. Queensland)	:17:1		
<u>Posidonia sinuosa</u> (W. Australia)	512:16:1	Birch 1975	
<u>Cymodocea nodosa</u> (Corsica)	408:15:1	Birch 1975	
RHIZOME			
<u>Syringodium filiforme</u> (Bahamas)	3550:49:1	Short <u>et al.</u> , 1985	
<u>Posidonia oceanica</u> (Corsica)	1749:40:1		
<u>Thalassia testudinum</u> (Barbados)	:20:1	Birch 1975	
<u>Enhalus acoroides</u> (Palau)	659:16:1		
<u>Halodule univervis</u> (N. Queensland)	388:14:1		
<u>Cymodocea serrulata</u> (N. Queensland)	872:13:1		
<u>Syringodium isoetifolium</u> (N. Queensland)	:10:1		
<u>Zostera capricorni</u> (N. Queensland)	: 8:1		
ROOTS			
<u>Posidonia oceanica</u> (Corsica)	3550:61:1		Short <u>et al.</u> , 1985
<u>Syringodium filiforme</u> (Bahamas)	2080:44:1		
<u>Posidonia sinuosa</u> (W. Australia)	809:18:1		

¹Highest reported N:P known for each seagrass species.

²Values from Atkinson and Smith (1983) unless otherwise noted.

Table 3. Atomic ratios for carbon, nitrogen and phosphorus for the seagrass Syringodium filiforme.

<u>Syringodium filiforme</u>	Indian River, FL C:N:P	San Salvador, Bahamas C:N:P
Leaves	388:24:1	1390:47:1
Rhizome	450:17:1	3550:49:1
Roots	429:13:1	2080:44:1

and P relative to carbon in the low-nutrient Bahamian environment (Short et al., 1985; Short et al., in prep.). A high N:P for plants growing in carbonate environments has been observed repeatedly, suggesting sparse available P resources (Entsch et al., 1983; Atkinson and Smith, 1983; Short et al., 1985).

The kinetics of P and N uptake have not been published for any of the tropical seagrass species. Thus, my discussion of nutrient acquisition by seagrasses must rely on what is known about nutrient uptake by the temperate seagrass Zostera marina and similar freshwater angiosperms. Rates of phosphate uptake have been measured of both leaves and roots of Zostera at concentrations ranging from 0.06-8.9 μM P (Penhale and Thayer, 1980). Their study indicated that uptake rates for both the roots and leaves depended on P concentration. Measurement of P uptake in several freshwater angiosperms supports this finding and shows that these species obtain most of the P for growth from

the sediments (Carignan and Kalff, 1980). The kinetics of N uptake in Zostera have received considerable attention recently (Iizumi and Hattori, 1982; Thursby and Harlin, 1982; Short and McRoy, 1984), with somewhat divergent results. The evidence does show, however, that measured rates of N uptake are a function of concentration for both roots and leaves. Rates of N depletion from flowing seawater by a tropical seagrass community (Halodule wrightii) suggest a similar concentration-dependent uptake (Short and Short, 1984).

The significance of concentration-dependent nutrient uptake in tropical seagrass leaves becomes obvious when considering the oligotrophic conditions in tropical and subtropical oceans (Ryther, 1963). In addition, the relatively low concentrations of P and N reported for the pore water of carbonate sediments in seagrass beds (Patriquin, 1972; Short et al., 1985) illustrate the need for examination of nutrient uptake by seagrass roots at low concentrations. This is particularly true for P uptake. Studies indicate that dissolved phosphate concentrations are maintained at low levels (0-10 μM P) due to the rapid removal of phosphate onto carbonate sediments (Berner, 1974; DeKanel and Morse, 1978; Kitano et al., 1978; Gaudette and Lyons, 1980). Thus, even where there are large amounts of P in the sediments, P is in an adsorbed form and may not be directly available to the plants.

The role of seagrasses in influencing sediment redox conditions and nutrient pool sizes is an important consideration in the evaluation of P and N cycling (Short, 1986). In fact, these considerations may be intricately connected to the status

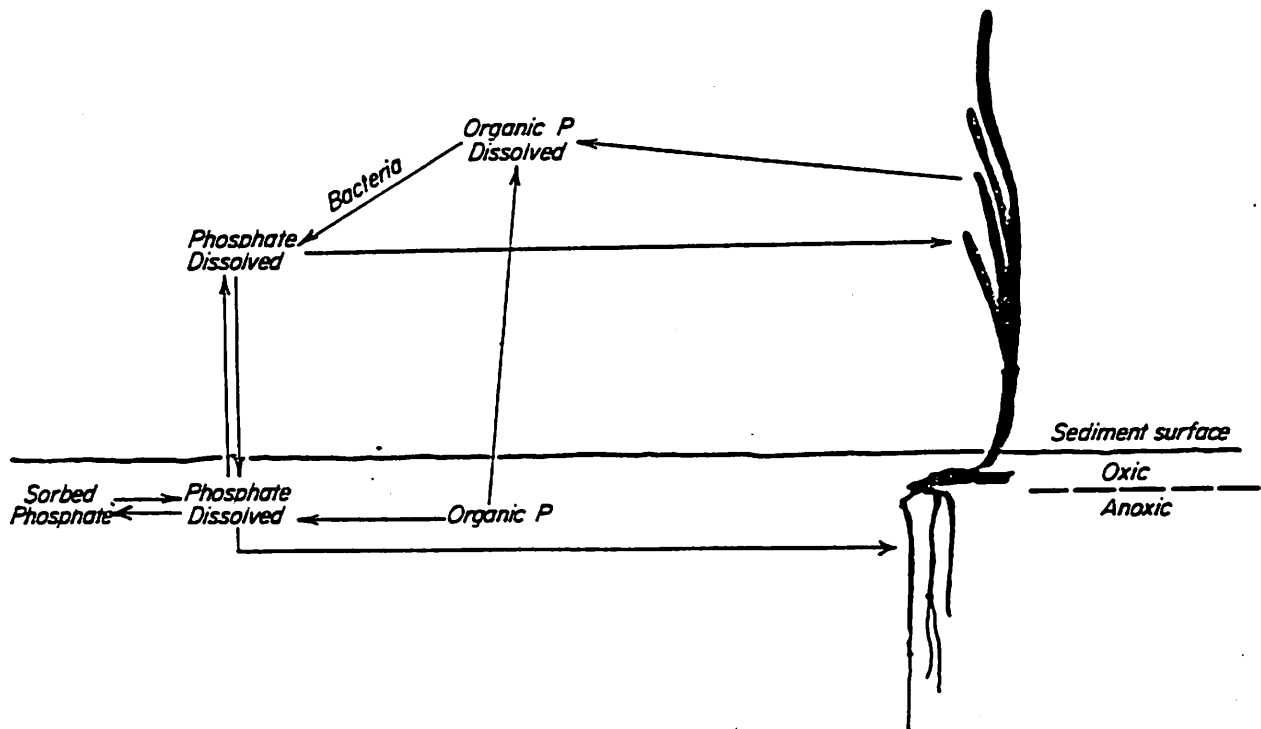


Figure 2: Major flows of phosphorus in the carbonate seagrass environments. Pathways include: phosphate uptake; regeneration; geochemical sorption; diffusive flux.

of P limitation in carbonate seagrass environments. Recent evidence has established the significance of ammonium regeneration in temperate *Zostera* sediment (Iizumi et al., 1982). The importance of anaerobic oxidation and nutrient regeneration is virtually unknown for tropical seagrass sediments (Short et al., 1985).

The biological cycle of P (Fig. 2) is simple in principle (Cosgrove, 1977). Unlike N, P usually does not undergo oxidation-reduction processes (for exceptions see Silverman and Ehrlich, 1964). In general, phosphate is taken up biologically, incorporated into organo-P and finally released as phosphate during decomposition (Fenchel and Blackburn, 1979). This cycle

is hampered by the tendency of phosphate to be adsorbed to clays and metal oxides and to form insoluble compounds such as apatite and vivianite. The stoichiometric regeneration of phosphate during sulfate reduction is well documented (i.e. Berner 1974, 1978, 1980; Goldhaber et al., 1977; Aller, 1977, Martens and Goldhaber, 1978). Reducing conditions are also responsible for the dissolution of FePO_4 , thereby releasing phosphate into solution. Although Smith et al. (1978) have demonstrated that the P in the mineral apatite is available to bacteria and algae, it does not appear that the form of adsorbed P in natural carbonates is available to seagrasses.

The apparent rapid regeneration of nutrients in anoxic carbonate sediments does not result in increased pore water concentrations (Berner, 1974; Rosenfeld, 1979b; Short et al., 1985). Low concentrations of phosphate relative to ammonium have been observed in a number of studies of carbonate sedimentary pore water (Rosenfeld, 1979b; Gaudette and Lyons, 1980; Hines and Lyons, 1982; Short et al., 1985). The low dissolved phosphate concentrations may be a result of adsorption of P on carbonate sediment grains and organic coatings, diagenetic formation of apatite, or replacement of calcium carbonate with a phosphate-rich phase (Seuss, 1970; Berner, 1974; DeKanel and Morse, 1978; Wilson, 1979; Gaudette and Lyons, 1980). Pore water samples from carbonate sediments of seagrass beds and coral reefs also contain low phosphate concentrations, although additional phosphate can be extracted with seawater from these sediments (Patriquin, 1972; Entsch et al., 1983; Short et al., 1985).

The potential pathways of N in seagrass systems are

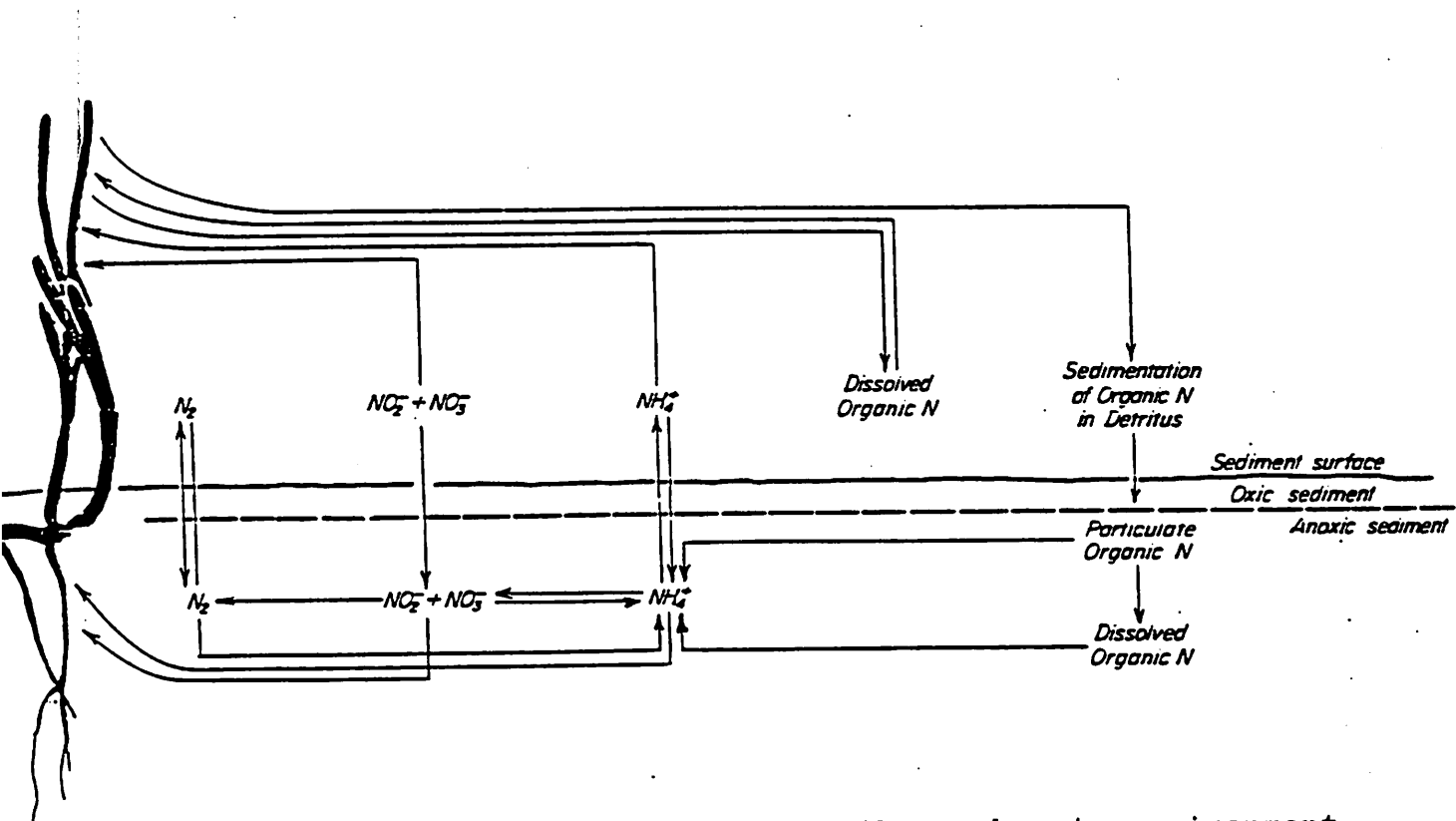


Figure 3: Major flows of nitrogen in the carbonate environment. Pathways include: uptake; denitrification; N fixation; nitrification; dissimilatory nitrate reduction; ammonification; diffusive flux.

numerous (Fig. 3). N_2 fixation, denitrification, nitrification, ammonification, and dissimilatory nitrate reduction to ammonium have all been found to occur in various seagrass sediments. Each process interacts with the ambient pools of nitrogen. Coupling between processes is likely, as the products of one pathway are the substrates of another. Various factors affect the nature and extent of the transformations of N that occur in a particular sediment, including sediment grain size, organic loading, infaunal activity, temperature, and O_2 availability.

Seagrass sediments are favorable and, in fact, very important sites of N_2 fixation (Capone and Carpenter, 1982; Capone, 1983a,b). Additionally, ammonium is present in

interstitial and adsorbed forms in carbonate sediments (Rosenfeld, 1979a, b; Short et al., 1985). These results suggest that one-third to one-half of the ammonium in these sediments is extractable. Rosenfeld (1979b) found that less ammonium was extractable from carbonate than terrigenous sediments of comparable dissolved ammonium concentrations and that the adsorbed ammonium in carbonate sediments was predominately associated with organic matter.

In 1982 I studied a seagrass bed of Syringodium filiforme in Graham's Harbor, a shallow semi-enclosed lagoon at the north end of San Salvador Island, Bahamas (Fig. 4). This lagoon averages 1-2 meters in depth and is protected from oceanic swells and storms by fringing islands and coral reefs, a configuration that allows extensive flushing of the seagrass bed with oligotrophic Atlantic Ocean water while dissipating most of the wave energy. A S. filiforme bed located on the west side of Cut Cay was selected for study because it represented a monospecific stand of seagrass in an area of uniform environmental conditions, i.e., constant water depth, relatively uniform current flow, and fine-grained carbonate mud.

Abundant S. filiforme was found in a pure stand having average maximum biomass of 816g dry m^{-2} (Table 4) and a relatively high leaf growth rate ($2.0g\ C\ m^{-2}d^{-1}$) for late October. This is in the range of other reported rates for this species and comparable to production rates for other seagrasses (Zieman and Wetzel, 1980; Fry, 1983) although this is only a portion of whole plant growth. Plant biomass represents a pool of $0.10g\ P\ m^{-2}$ and $2.05g\ N\ m^{-2}$ in the leaves, $0.10g\ P\ m^{-2}$ and

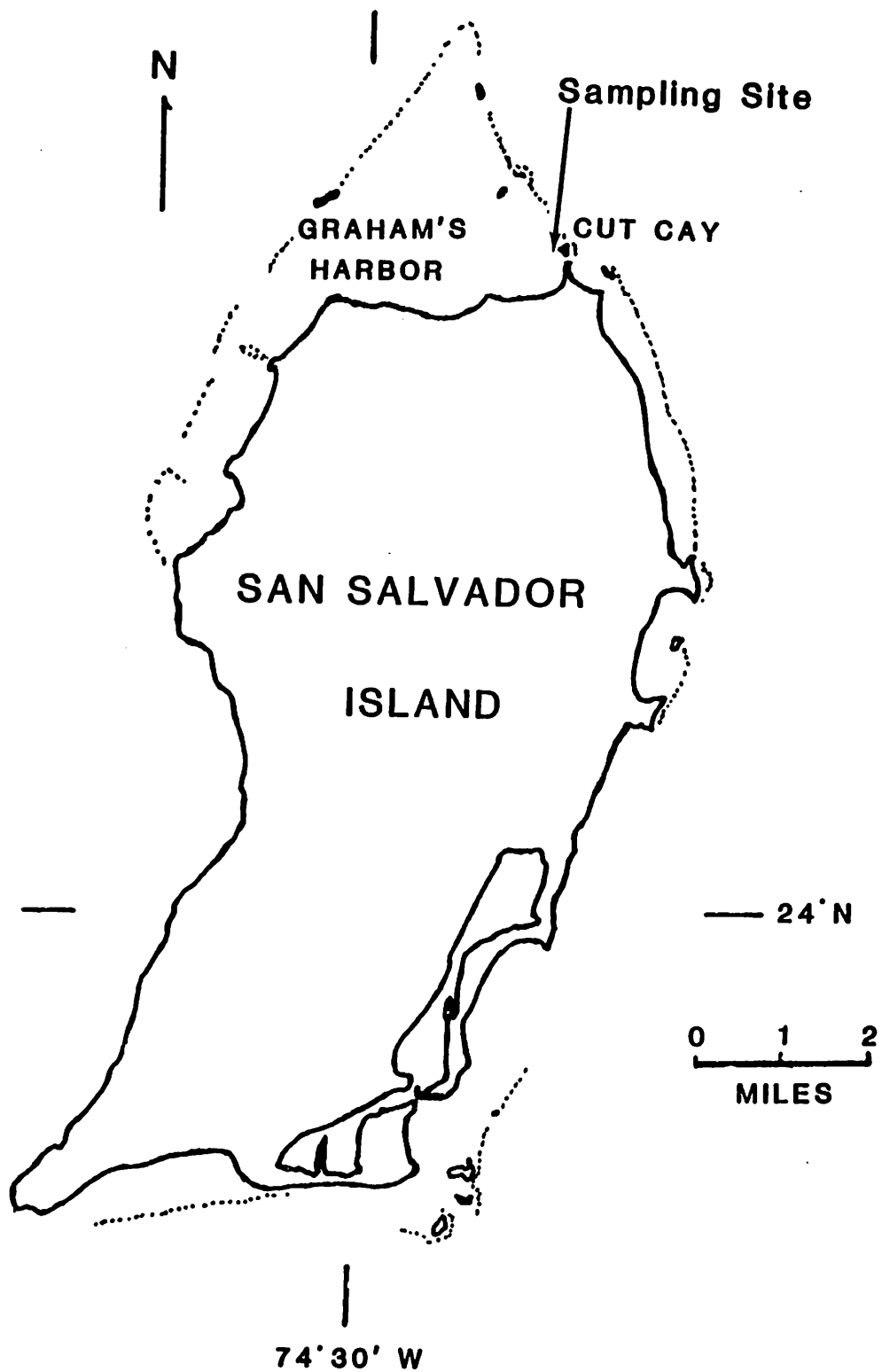


Figure 4. San Salvador Island, Bahamas, showing the location of the study site west of Cut Cay in Graham's Harbor.

Table 4: Syringodium filiforme abundance at Cut Cay, San Salvador Island, Bahamas.
 Samples were collected with a 1/16 m² frame (21 Oct.) and 16 cm diameter core sampler (24 Oct.).

Sample Date	Shoot Density #m ⁻²	Leaf Biomass g dry m ⁻²	Rhizome Biomass g dry m ⁻²	Root Biomass g dry m ⁻²	Rhizome Length m m ⁻²	Shoot Height cm
21 Oct 82	9020	151	ND	ND	ND	19
21 Oct 82	10824	191	ND	ND	ND	18
24 Oct 82	7905	130	376	460	220	15
24 Oct 82	12444	171	426	214	261	20
24 Oct 82	8568	154	260	234	233	18
Average	9752	159	354	303	238	18

ND - indicates no data

2.09g N m⁻² in the roots, producing a total seagrass pool of 0.32g P m⁻² and 6.50g N m⁻² or a N:P of 20:1. Root biomass in this S. filiforme bed accounts for more than one-third of the total plant biomass (Table 4). The large portion of nitrogen and phosphorus in these roots (Table 2) is not typical for seagrasses (Birch, 1975; Aioi and Mukai, 1980; Atkinson and Smith, 1983). Similarly, the C:N:P for S. filiforme rhizome is greater than that reported for other seagrasses (Table 2). The atomic ratio for leaves (N:P=47) is higher than any value reported for marine or freshwater spermatophytes, which range from 5 to 41 except for one value of 48 for Enhalus acoroides from Palau (Raven, 1981; Atkinson and Smith, 1983). Phosphorus depletion is not considered the typical situation in marine ecosystems where the atomic ratio, C:N:P, for marine plankton has been established at 106:16:1 (Redfield et al., 1963). The equivalent ratio for the photosynthetic portion of many seagrass species averages 507:21:1 (Atkinson and Smith, 1983). Comparison to the ratio for S. filiforme leaves, C:N:P=1390:47:1, suggests depletion of both phosphorus and nitrogen relative to carbon.

The low nitrogen and phosphorus content of these plants indicates that the plant system has adapted to conditions of scarce primary nutrient resources. The average N:P of 47 for S. filiforme tissue content in San Salvador is similar to that of interstitial water from core samples (Short et al., 1985).

Since the uptake of phosphate by roots of the temperate seagrass Zostera marina is concentration-dependent (Penhale and Thayer, 1980) it is expected that the rate of nutrient uptake by tropical seagrass roots in sediments of low phosphate

concentration will be slow. This slow phosphate uptake rate appears to be the major obstacle to the accumulation of phosphate in S. filiforme tissue. In contrast, the ammonium concentration in the sediment interstitial water provides a large supply of nitrogen to the seagrass roots. The rate-limiting step of phosphate uptake by S. filiforme roots may explain the inordinately high root biomass observed for these sediments (Table 4). Increasing the root surface area is an effective morphological mechanism for increasing nutrient uptake at low concentrations (Short, 1983a). Thus the acquisition of phosphate by S. filiforme is limited by both the sparse supply in the water column and the plants' inability to rapidly take up phosphate from the sediments.

REFERENCES

- Aioi, K. and Mukai, H. 1980. On the distribution of organic contents in a plant of eelgrass (Zostera marina L.). Japanese Journal of Ecology 30: 189-192.
- Aller, R. C. 1977. The influence of macrobenthos on chemical diagenesis of marine sediments. Ph.D. thesis. Yale University, New Haven.
- Atkinson, M. J. and Smith, S. V. 1983. C:N:P ratios of benthic marine plants. Limnol. Oceanogr. 28:568-574.
- Berner, R. A. 1974. Kinetic models for anoxic marine sediments, In: Goldberg, E. D., (Ed.), The Sea, Vol. 5, New York: John Wiley and Sons. pp. 427-450.
- Berner, R. A. 1978. Sulfate reduction and the rate of deposition of marine sediments. Earth Planet. Sci. Lett. 37:492-498.
- Berner, R. A. 1980. Early Diagenesis: A Theoretical Approach. Princeton, New Jersey: Princeton University Press, 241 pp.
- Birch, W. R. 1975. Some chemical and calorific properties of

- tropical marine angiosperms compared with those of other plants. Journal of Applied Ecology 12: 201-212.
- Capone, D. G., Penhale, P. A., Oremland, R. S. and Taylor, B. F. 1979. Relationship between productivity and N_2 (C_2H_2) fixation in a Thalassia testudinum community. Limnol. and Oceanogr. 24(1): 117-125.
- Capone, D. G. 1983a. N_2 fixation in seagrass communities. Marine Technology Society Journal 17:32-37.
- Capone, D. G. 1983b. Benthic nitrogen fixation. In: E. J. Carpenter and D. G. Capone (Eds.) Nitrogen in the Marine Environment. New York: Academic Press, pp. 105-137.
- Capone, D. G. and Carpenter, E. J. 1982. Nitrogen fixation in the marine environment. Science 217: 1140-1142.
- Carignan, R. and Kalff, J. 1980. Phosphorous sources for aquatic weeds: water or sediment? Science 207:987-989.
- Cosgrove, D. J. 1977. Microbial transformations in the phosphorous cycle. Adv. Microbial Ecol. 1: 95-134.
- DeKanel, J. and Morse, J. W. 1978. The chemistry of orthophosphate uptake from seawater on to calcite and aragonite. Geochim. Cosmochim Acta 42:1335-1340.
- El-Sayed, S. Z., Sackett, W. M., Jeffrey, L. M., Fredericks, A. D., Saunders, R. P., Conger, R. S., Fryxell, G. A., Steidinger, K. A., and Earle S. A., 1972. Chemistry, Primary Productivity, and Benthic Algae of the Gulf of Mexico. Am. Geographical Society Publ. 22 pp.
- Entsch, B., Boto, K. G., Sim, R. G. and Wellington, J. T., 1983. Phosphorus and nitrogen in coral reef sediments. Limnol. Oceanogr. 28: 465-476.
- Fenchel, T. and Blackburn, T., 1979. Bacteria and Mineral Cycling. New York: Academic Press, 225 pp.
- Fry, B. 1983. Leaf growth of the seagrass Syringodium filiforme Kutz. Aquat. Bot 16: 361-368.
- Gaudette, H. E. and Lyons, W. B., 1980. Phosphate geochemistry in nearshore carbonate sediments: a suggestion of apatite formation. Soc. Econ. Paleon. Min. Spec. Publ. 29: 215-225.
- Goldhaber, M. B., Aller, R. C., Cochran, J. K., Rosenfeld, J. K., Martens, C. S. and Berner, R. A., 1977. Sulfate reduction, diffusion and bioturbation in Long Island Sound sediments. Report of the FOAM group. Am Jour. Sci. 277:193-237.

- Hartog, C. Den. 1970. The Seagrasses of the World. North Holland Publ. Co., Amsterdam.
- Hines, M. E. and Lyons, W. B., 1982. Biogeochemistry of nearshore Bermuda sediments. I. Sulfate reduction rates and nutrient generation. Mar. Ecol. Prog. Ser. 8: 87-94.
- Iizumi, H. and Hattori, A., 1982. Growth and organic production of eelgrass (Zostera marina L.) in temperate waters of the Pacific coast of Japan. III. The kinetics of nitrogen uptake. Aquat. Bot. 23: 245-256.
- Iizumi, H., Hattori, A. and McRoy, C. P., 1982. Ammonium regeneration and assimilation in eelgrass (Zostera marina) beds. Mar. Biol. 66: 59-65.
- Kitano, Y., Okumura, M. and Idogaki, M., 1978. Uptake of phosphate ions by calcium carbonate. Geochem. J. 12: 29-37.
- Martens, C. S. and Goldhaber, M. B., 1978. Early diagenesis in transitional sedimentary environments of the White Oak River Estuary, North Carolina. Limnol. Oceanogr. 23: 428-441.
- McRoy, C. P. and McMillan, C., 1977. Production ecology and physiology of seagrass. In: C. P. McRoy and C. Helfferich (Eds.) Seagrass Ecosystems. New York: Marcel Dekker, Inc., pp. 53-87.
- Patriquin, D. G. 1972. The origin of nitrogen and phosphorus for growth of the marine angiosperm Thalassia testudinum. Mar. Biol. 15: 35-46.
- Penhale, P. A. and Thayer, G. W., 1980. Uptake and transfer of carbon and phosphorus by eelgrass (Zostera marina L.) and its epiphytes. J. Exp. Mar. Biol. Ecol. 42: 113-123.
- Raven, J. A. 1981. Nutritional strategies of submerged benthic plants: the acquisition of C, N, and P by hizophytes and haptophytes. New Phytol. 88: 1-30.
- Redfield, A. C., Ketchum, B. H. and Richards, F. A., 1963. The influence of organisms on the composition of seawater. In: M. N. Hill (Ed.) The Sea, Vol. 2, New York: John Wiley and Sons, pp. 26-77.
- Rosenfeld, J. K. 1979a. Ammonium adsorption in nearshore anoxic sediments. Limnol. Oceanogr. 24: 356-364.
- Rosenfeld, J. K. 1979b. Interstitial water and sediment chemistry of two cores from Florida Bay. J. Sedim. Petr. 49: 989-994.
- Ryther, J. H. 1963. Geographic variations in productivity.

In: The Sea, vol. 2, M. N. Hill (Ed.), New York: John Wiley and Sons, pp. 347-380.

- Short, F. T. 1983a. The seagrass Zostera marina L.: plant morphology and bed structure in relation to sediment ammonium in Izambek Lagoon, Alaska. Aquat. Bot. 16: 149-161.
- Short, F. T. 1985. A method for the culture of tropical seagrasses. Aquat. Bot. 22:187-193.
- Short, F. T. 1986. The effects of sediment nutrients on seagrass growth and abundance. Aquat. Bot. (in press).
- Short, F. T. and McRoy, C. P., 1984. Nitrogen uptake by leaves and roots of the seagrass Zostera marina L. Bot. Mar. 27: 547-555.
- Short, F. T. and Short, C. A., 1984. The seagrass filter: purification of coastal waters. In: V. S. Kennedy (Ed.) The Estuary as a Filter. Academic Press pp. 395-413.
- Short, F. T., Davis, M. W., Gibson, R. A. and Zimmerman, C. F., 1985. Evidence for phosphorus limitation in carbonate sediments of the seagrass Syringodium filiforme. Est. Coast. Shelf Sci. 20:419-430.
- Short, F. T., Montgomery, J. R. and Zimmermann, C. F., In prep. Seasonal seagrass abundance and nutrient dynamics of a Syringodium filiforme Kutz bed in Indian River Lagoon, FL., USA.
- Silverman, M. P. and Ehrlich, H. L., 1964. Microbial formation and degradation of minerals. Adv. Appl. Microbiol. 6: 153-206.
- Smith, E. A., Mayfield, C. I. and Wong, P. T. S., 1978. Naturally occurring apatite as a source of orthophosphate for growth of bacteria and algae. Microb. Ecol. 4: 105-117.
- Suess, E. 1970. Interaction of organic compounds with calcium carbonate - I. Association phenomena and geochemical implications. Geochim. Cosmochim. Acta 34:157-168.
- Thursby, G. B. and Harlin, M. M. 1982. Leaf-root interaction in the uptake of ammonium by Zostera marina. Mar. Bio. 72: 109-112.
- Tomlinson, P. B. 1974. Vegetative morphology and meristem dependence - the foundation of productivity in seagrasses. Aquaculture 4: 107-130.
- Wilson, K. M. 1979. Diagenesis of phosphorus in carbonate sediments from Bermuda. M. S. thesis, University of New Hampshire, Durham.

- Zieman, J. C. and Wetzel, R. G., 1980. Productivity in seagrasses: methods and rates. Chp. 7 In: Handbook of Seagrass Biology: An Ecosystem Perspective. New York: Garland STPM Press, pp. 87-116.
- Zieman, J. C., Thayer, G. W., Robblee, M. B. and Zieman, R. T., 1979. Production and export of seagrasses from a tropical bay. In: R. J. Livingston (Ed.). Ecological Processes in Coastal and Marine Systems. New York: Plenum Press, pp. 21-34.