McGill University

THE ORIGIN OF NITROGEN AND PHOSPHORUS FOR GROWTH OF THE MARINE ANGIOSPERM THALASSIA TESTUDINUM KÖNIG

by

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APPENDIX B. A GENERAL DESCRIPTION OF THE *THALASSIA* BEDS AND ADDITIONAL DATA ON PRODUCTION

REGIONAL SETTING

Barbados (Fig. 15) is a small island of non-volcanic origin lying in the trade wind belt and region of equatorial currents at 13°10' N, 59°30' W. Most of the island is covered by Pleistocene coral limestone; outcroppings of poorly indurated Tertiary sediments occur in the Scotland district in the NE section of the island. The coastline is regular, there are no offshore islands, and living reefs are limited to small fringing reefs on the west coast (Lewis, 1960a). Rubble banks, supporting only sparse coral growth, occur close to shore on the south coast and at a distance of approximately 0.7 km off the SE coast. Rainfall averages about 50 cm/yr, winds are predominantly from the eastern sector and mean annual wind speed is 11.0 m.p.h. (Rouse, 1966). Lewis (1960b) reported observations on tidal, water temperature and wave conditions at Barbados. The mean tidal range is approximately 0.7 m, and the diurnal range, 1.1 m. Surface temperatures of coastal water varied between 25.2 and 28.5°C over a one year period. Wave amplitudes are four to eight times greater on the east coast than on the west coast. Because Barbados lacks large lagoons and semiprotected bays, *Thalassia* beds there are not extensive. The largest beds occur at Bath and at St. Lawrence, where most of the nutrient studies were carried out. A general survey of the substrate types, sea grasses and associated flora and fauna in these beds was carried out prior to initiation of the nutrient studies.

Data on production and some sedimentary characteristics were also obtained from *Thalassia* beds at Carriacou. This is a small island of volcanic origin, lying approximately 200 km SW of Barbados (Fig. 15). *Thalassia* beds are more extensive at Carriacou than at Barbados, and can probably be

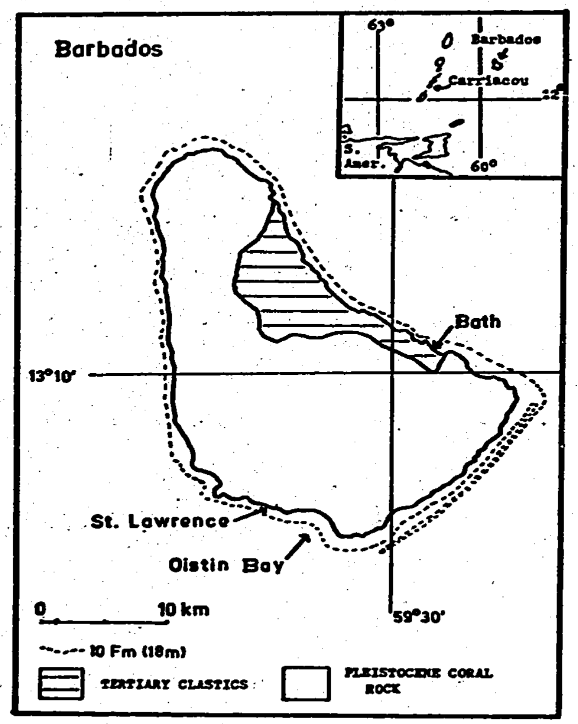

Fig. 15. Index map of Barbados.

considered representative of typical *Thalassia* growth in the southern Caribbean.

MATERIALS AND METHODS

For the purpose of mapping the Bath and St. Lawrence *Thalassia* beds, base maps were prepared from aerial photographs (Hunting Surveys Ltd., taken in 1964). A series of transects were swum out from positions on shore located on the base maps; orientation was maintained by lining up two targets on shore. Distances and depths along the transects were measured with a 2 m pole, and these were recorded on an underwater slate together with observations on the substrate type and flora and fauna. Observations of sea level were made at ½ hour intervals at fixed reference points during the periods of transect observations, and observations were adjusted to a common tidal level which is approximately mean low water (accurate tidal data for Barbados are lacking). Maps of the hydrography, distribution of sea grasses and bottom types were prepared by making use of details which could be distinguished in the aerial photographs together with data of the transect observations. Surveys of the macro-infauna, sea grasses and sediments were carried out by sampling 20 randomly located positions at Bath, and 27 positions at St. Lawrence. At each position, a 3/16 m^2 sample of the sea grasses was obtained. This was made up of cuttings from three separate 1/16 m^2 areas, positions of which were selected by throwing a quadrat within a total area of approximately 100 m^2. If the *Thalassia* stand was not reasonably uniform with respect to length of the leaves--this was the case for only one stand, at Bath--then the area was subjectively subdivided into uniform stands, and the subdivisions were sampled separately. To sample the macro-infauna, the substrate was dug up under a surface area of approximately 0.15 m^2, and immediately washed through a 2 mm mesh sieve. Sediment samples were taken from all positions but only selected samples were analyzed. The proportions of coarse material (> 5.2 mm) in substrates which had been subjectively classified as predominantly sand, cobble-sand and Porites rubble flats were estimated by digging up a measured volume of substrate, sieving the sample through a 5.2 mm mesh sieve, and determining the volume of water displaced by the coarse material. This was done for several positions in each of the above substrates. The proportion of coarse material in substrates which had been subjectively classified as cobble framework or cobble-cobble-sand was estimated from visual observations at erosional scarps. Observations of Thalassia beds in Oistin Bay were made during the course of nutrient investigations.

A map of sea grass distribution at Carriacou was prepared by examination of aerial photographs (United Kingdom, Directorate of Overseas Surveys, Contract 85, taken in 1966). Approximate depths were taken from Admiralty Chart 2872, and 27 positions were selected for sampling such that Thalassia beds from various depths and degrees of exposure to wave action were represented. At each position, observations were made on flora and fauna, substrate type, and samples of sea grass and sediment were taken as at Barbados. Depths were measured by use of a 'venturi' type depth gauge.

For each of the 3/16 m^2 samples, the Thalassia and Syringodium leaves were separated, and then the wet weight of each determined. For the Thalassia leaves, the lengths of the 10 longest leaves and widths of 30+ leaves were measured. L_{10} was used as a measure of the maximum length (L_m), except in samples of few leaves in which the average length of the three longest leaves was used as a measure of maximum leaf length. P_s and P_m, and the number of erect shoots per m^2 were estimated from these data by the relations given in Appendix A.

Particle size analyses were made on 50 to 100 g splits of the sediment samples. The samples (or splits of) were oxidized in commercial bleach and washed several times with distilled water using centrifugation to remove water after each wash. Each sample was then shaken in distilled water and wet sieved through a 300 mesh (47 μ) sieve. Material passing through the sieve was flocculated by adding 5 ml saturated potassium alum solution, centrifuged to remove excess water, and then dried in a tarred beaker. The clay content of two samples was determined by pipette analysis (Day, 1965). Coarse material was dry sieved by means of a mechanical shaker through sieves of the following mesh sizes: 5.16 mm, 3.35 mm, 2.46 mm, 1.52 mm, 0.98 mm, 0.52 mm, 0.28 mm, 0.14 mm, 0.074 mm and 0.047 mm. Results were plotted as cumulative curves on probability paper using 'phi' units of grain size. From these curves the graphic mean (M_z) and inclusive graphic standard deviation (σ_I), measures of average size and sorting, were determined (Folk, 1965). M_z is reported in units of millimeters. σ_I values are reported according to the verbal classification scale of Folk (1965) which is as follows.

σ_I	under .35ϕ, very well sorted
	.35-.50ϕ, well sorted
	.50-.71ϕ, moderately well sorted
	.71-1.0ϕ, moderately sorted
	1.0-2.0ϕ, poorly sorted
	2.0-4.0ϕ, very poorly sorted
	over 4.0ϕ, extremely poorly sorted

The percentage of each sediment sample in standard (U.S. Dept. of Agriculture) size intervals was interpolated from the cumulative frequency-grain size plot. For selected samples, the percentage of acid insoluble material in each of the coarse (> 47u) sieve separates was estimated as the percentage of grains in a sample of 300 to 500 grains which did not dissolve in hydrochloric acid (15% concentrated). The percentage of acid insoluble material in the silt and clay fraction (< 47u) was estimated from the loss of weight following treatment with hydrochloric acid. Values for the standard size intervals were interpolated from plots of percentage of size class acid insoluble versus size class median diameter (phi units). Observations were made on the constituent nature of both the acid soluble and acid insoluble fractions. For this purpose, and also for the purpose of examining ferrous sulfide formation in skeletal carbonate grains (Section II), selected size fractions were embedded in polyester resin, thin sectioned, and examined under a petrographic microscope. Mr. Noel James of the Geology Department, McGill University, prepared the thin sections, and aided in identification of sediment constituents.

RESULTS AND DISCUSSION

Substrate classification

On the basis of the proportion of coarse material in the substrates, Thalassia substrates at Barbados and Carriacou were classified into four types. A fifth substrate type was distinguished from the others because of its unique vertical position. The under 5.2 mm fraction of almost all sediments examined at Barbados and Carriacou contained less than 10% silt and clay (Table XVI). In the following descriptions, 'sandy sediment' refers to sediment of particle size diameters less than 5.2 mm, while 'cobble sized' refers to material coarser than 5.2 mm. The substrate types are characterized as follows.

Table XVI. Grain size characteristics of sediments.

NO.	SAMPLE SITE CHARACTERISTICS	% OF SAMPLE IN SIZE SEPARATES % OF SIZE SEPARATE ACID INSOLUBLE (in brackets) (GRAVEL) 5.2 -2.0 mm	VERY COARSE SAND 2.0 -1.0	COARSE SAND 1.0 -0.5	MEDIUM SAND 0.5 -0.25	FINE SAND 0.25 -0.10	VERY FINE SAND 0.10 -0.05	SILT & CLAY < 0.05	CLAY < 0.002	M_z (mm)	SORTING
	BATH										
1	PS substrate, 0.5m	0	0.9 (0)	1.1 (1)	3.2 (9)	78.8 (20)	13.7 (26)	2.3 (50)		0.13	well sorted
2	PS substrate, 0.3m	2.0	1.0	1.3	1.7	74.0	18.2	1.8		0.12	well sorted
3	PS substrate area, under blue-green mat, 0.5m	0	0	0.2	0.8	79.0	17.2	2.8		0.12	very well sorted
4	CS substrate, 0.7m	6.3	33.7	27.0	3.5	12.5	12.5	4.5		0.50	poorly sorted
5	CS substrate, 0.5m	5.0	6.0	7.0	6.0 (0)	49.0 (11)	25.0 (24)	8.0 (43)	3.2	0.18	poorly sorted
6	Adjacent to No. 5, but in grass-free area, 0.8m	10.0	37.0	33.0	6.2	12.0	1.8	0.01		0.78	poorly sorted
7	PF substrate, 0.2m	2.3	6.9	7.8	11.3	54.8	12.4	4.5		0.21	poorly sorted
8	CF substrate, 0.3m	5.5	11.0	14.0	9.5 (1)	26.0 (2)	19.0 (7)	15.0 (36)		0.20	very poorly sorted
9	CF substrate, 0.4m	0.9	2.5	12.6	22.0	46.0	12.9	3.1		0.21	poorly sorted
10	Adjacent to No. 9 , but in grass-free area, 0.5m	28.5	37.5	25.6	3.1	3.9	1.3	0.1		1.45	poorly sorted

Table XVI -- Continued

NO.	SAMPLE SITE CHARACTERISTICS	% OF SAMPLE IN SIZE SEPARATES % OF SIZE SEPARATE ACID INSOLUBLE (in brackets) (GRAVEL) 5.2 -2.0	VERY COARSE SAND 2.0 -1.0	COARSE SAND 1.0 -0.5	MEDIUM SAND 0.5 -0.25	FINE SAND 0.25 -0.10	VERY FINE SAND 0.10 -0.05	SILT & CLAY 0.05	CLAY 0.002	M_z (mm)	SORTING
	BATH (continued)										
11	Transient sand on coral-coralline algal bottom seaward of <u>Thalassia</u> bed	2.9	23.6	73.3	0.2	0	0	0		0.91	well sorted
	SOUTH COAST - ST. LAWRENCE										
12	Upstream of <u>Thalassia</u> bed, grass-free area, 0.5m	0	0.4	4.5	6.4	82.7	6.0	0		0.16	moderately well sorted
13	Upstream part of <u>Thalassia</u> bed, in mixed <u>Thalassia-Syringodium</u> stand, 0.5m	0	0	0	0.4	77.6	20.8	1.2		0.12	very well sorted
14	As for No. 13, but at 0.9m	0	0	0	0.5	51.5	45.0	3.0		0.10	well sorted
15	Central part of bed, pure <u>Thalassia</u>, rich fauna, 0.6m	3.7	6.3	10.4	14.6 (0)	49.5 (1)	11.8 (2)	3.7 (24)		0.23	poorly sorted
16	As for No. 15, but at 0.9m	3.7	4.8	9.5	16.0	49.8	12.7	3.5		0.21	poorly sorted
17	Downstream part of bed, 1.6m, mixed <u>Thalassia-Syringodium</u>	1.6	1.8	3.9	9.7	56.0	23.7	3.3		0.14	moderately sorted
18	In <u>Diplanthera</u> growth inshore of <u>Thalassia</u> bed	0	1.4	3.2	6.6	70.3	18.5	0		0.14	moderately well sorted

Table XVI. Concluded.

NO.	SAMPLE SITE CHARACTERISTICS	% OF SAMPLE IN SIZE SEPARATES % OF SIZE SEPARATES ACID INSOLUBLE (in brackets) (GRAVEL) 5.2 -2.0 mm	VERY COARSE SAND 2.0 -1.0	COARSE SAND 1.0 -0.5	MEDIUM SAND 0.5 -0.25	FINE SAND 0.25 -0.10	VERY FINE SAND 0.10 -0.05	SILT & CLAY 0.05	CLAY 0.002	M_z (mm)	SORTING
	SOUTH COAST - OISTIN BAY										
19	Oistin Bay west (stand A-1), 1.9 m	1.9	2.6	3.3	10.2 (0)	72.0 (1)	9.3 (6)	0.7		0.17	moderately sorted
20	Oistin B. south (A-7), 0.7m	1.6	3.9	7.0	20.0	66.9	0.5	0.1		0.23	moderately sorted
	CARRIACOU (all in Thal. beds)										
21	Watering B., 3m, strong current	0.3	3.4	12.8	23.5	52.0	5.8	2.2		0.25	moderately sorted
22	Watering Bay, 1.2m, in lee of patch reef	0.7	4.4	12.2	14.7	22.5	26.5	19.0	3.2	0.19	poorly sorted
23	Jew Bay, 66m from shore, 3m	1.2 (10)	6.8 (30)	20.3 (24)	32.7 (27)	22.1 (49)	9.0 (60)	7.9 (56)		0.28	poorly sorted
24	Jew Bay, 330m offshore, 4m, strong current	0.5	2.7	6.8	14.0	64.7 (0)	5.6 (8)	5.7 (26)		0.20	moderately sorted
25	Jew Bay, 8m, strong current	9.3	21.2	30.5	24.0	11.7	1.5	1.8		0.66	poorly sorted
26	Grand Bay, 5m, weak current	2.5	12.5	21.0	22.5	27.5	9.7	4.3		0.33	poorly sorted
27	Gt. Bretache Bay, 4.5m	0.3	2.3	15.4	38.0	42.8	0.4	0.8		0.30	moderately sorted
28	L'Esterre B., CF substrate, 1.2m	5.6	10.7	1.7	42.0	30.1	1.7	8.2		0.36	poorly sorted
29	Hillsborough Bay, 4m	0.4	8.1	21.5	22.0	41.0	4.6	2.4		0.30	poorly sorted

Cobble framework (CF) substrates

These are substrates in which cobble sized material forms a 'structural framework' and sandy sediment fills in the spaces (Plate IIc). The cobble sized material occupies approximately 70% and greater of the sediment volume. Exposures at erosional scarps indicate that the *Thalassia* root layer is usually restricted to the upper 15 to 20 cm of these substrates. These substrates are very strongly bound together, and are sampled only with considerable difficulty.

Predominantly sand (PS) substrates

These are substrates in which cobble sized material occupies less than about 5% of the substrate volume. At Barbados, the PS substrate overlies a coral rock basement or a layer of densely packed cobble sized coral rubble referred to here as the 'rubble layer'. The transition between the PS substrate and the rubble layer is generally abrupt, and the *Thalassia* rhizomes do not penetrate the rubble layer. The root layer in PS substrates at Barbados generally extends from the bottom of the PS substrate layer, at about 10 cm to 1 m below the sediment surface, to within 30 to 2 cm of the substrate surface. Where the root layer is spread out, erect shoots of *Thalassia* may be very long and largely unbranched (Plate IId). At most areas in Carriacou, the PS substrate is of undetermined thickness (but over 1 m), and the *Thalassia* root layer occurs within the top 75 cm of the PS substrate layer, and commonly within the top 20 cm.

Cobble-sand (CS) substrates

In these substrates, cobble sized material occupies approximately 5 to 45% of the substrate volume. At Barbados, CS substrates overlie a coral rock basement or rubble layer, as described for the PS substrates.

Cobble-Cobble-sand (CCS) substrates

This substrate type is intermediate between the CF and CS substrate types, with cobble sized material occupying approximately 50 to 70% of the substrate volume. This substrate type was encountered at only one position, in Oistin Bay. Here, a layer of sand overlies the CCS substrate, and a rubble layer occurs below the CCS substrate layer. *Thalassia* rhizomes are restricted to the CCS substrate layer.

Porites rubble flats (PF)

This substrate type occurs at Bath. In several near-shore areas at Bath, converging waves have caused piling up of skeletons of the coral *Porites furcata* to approximately 10 cm below mean low water. These areas are exposed at low water of spring tides. The skeletons of *Porites furcata* are irregularly branched cylindrical structures about 1 cm in diameter. The skeletons form a structural framework, and sandy sediment fills in the spaces. An estimated 50% of the substrate volume is occupied by *Porites* skeletons. *Thalassia* rhizomes are restricted to the upper 15 cm of these substrates.

The Bath *Thalassia* bed

General hydrography

The generalized bathymetry and distribution of sea grasses are shown in Fig. 16. The *Thalassia* bed lies partially in the lee of large rocks, the 'breaker zone rocks', which rise close to and above mean low water. Shallow areas bound the NW and SE regions of the bed. Because of the spaces between shallow areas seaward of the *Thalassia* bed, the shallowness of the *Thalassia* bed, and the generally high level of wave action of the east coast of Barbados, conditions in the *Thalassia* bed are generally turbulent and the

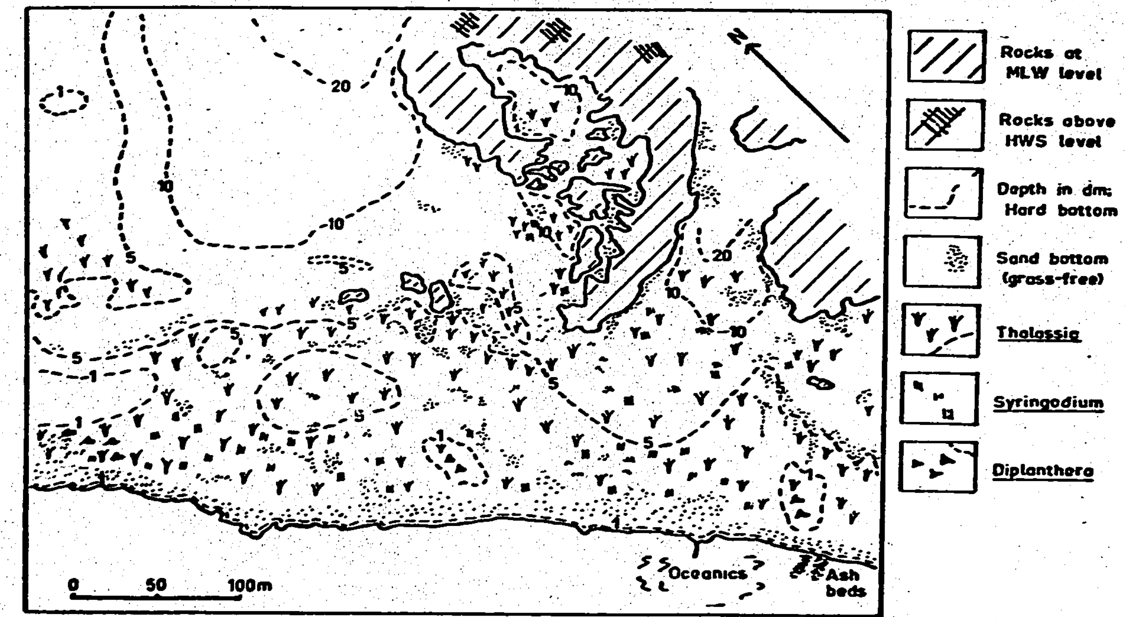

Fig. 16. Generalized bathymetry, and distribution of sea grasses at Bath.

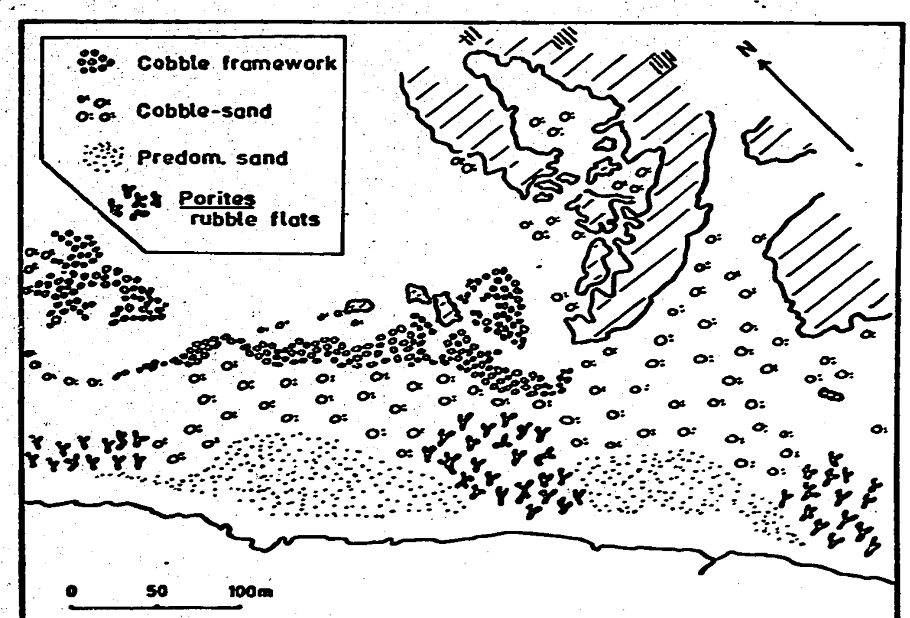

Fig. 17. Distribution of substrate types in sea grass beds at Bath.

water turbid from stirred up bottom sediment, except for a few hours at low water. Currents over the Thalassia bed are generally weak and irregular, but there is an overall flow of water towards the NW and currents are strong in channels cutting through the shallow areas at the NW and SE boundaries of the bed. Seaward of the Thalassia bed is a coral-coralline algal bottom with only transient sand cover.

Substrate types

The distribution of substrate types in the Thalassia bed is shown in Fig. 17. A CF substrate occurs at the seaward face of the Thalassia bed where wave action has caused piling up of coarse debris originating from the coral-coralline algal bottom. This material is piled up to about 25 cm below mean low water. The coarse debris consists largely of 'algal balls' 5 to 15 cm in diameter which were formed by growth of encrusting coralline algae around loose coral fragments; these algal balls were observed rolling about in pockets in the coral-coralline algal bottom. Plate IIc is a photograph of an erosional scarp in the CF substrate area. Skeletons of Porites furcata are piled up at several nearshore areas (Fig. 17) as described above. The upper limit of accumulation of the Porites skeletons is probably determined by factors limiting the growth of Thalassia, i.e. tidal level. In the shallowest areas of these flats, growths of Diplanthera occur, and associated with the Diplanthera is an accumulation of sandy sediment to about MLW level. PS substrates occur in inshore areas between the Porites rubble flats. CS substrates occur over most of the Thalassia bed area.

Sediment size and constituent characteristics

Grain size characteristics and the proportion of acid insoluble material of samples from the different substrates are given in Table XVI. There is some variation in the relative amounts of coarse, medium and fine sand, but all samples are characterized by small amounts of silt and clay. Samples from grass-free areas differ from samples from the *Thalassia* stabilized sediments in having much smaller proportions of grains smaller than 0.5 mm; this illustrates the effect of *Thalassia* in modifying sorting of sediments by waves. The good sorting and coarse grain size of sample 11 (Table XVI) from the coral-coralline algal bottom is indicative of the strong wave action in that area.

Sediments at Bath are derived from several sources, and this is reflected in the constituent composition. Skeletal carbonates constitute predominant class of sediment constituents, making up approximately 75 to 92% (equivalent to the acid soluble fraction) of the sediments. These are derived largely from molluscs, corals, *Halimeda* (green alga), foraminifera and red algae growing in the *Thalassia* beds and on the hard coral-coralline algal bottom. Minor amounts of debris derived from echinoderms, alcyonarians, crustacea and ostracods were recognized in examination of the sediments. A few composite grains, probably derived from the Pleistocene coral cap or rocks of the breaker zone, were also observed. The predominant minerals of the acid insoluble fractions of these samples are quartz, feldspar and horneblende, in that order. These may have been derived in part from outcroppings of volcanic ash beds in this area (Fig. 16). Radiolarian tests, derived from Tertiary Oceanic deposits on shore (Fig. 16) were also observed in the acid insoluble fraction. Soil erosion, which is severe in this part of the island, probably contributes silt and clay sized material to the Bath sediments.

Substrate stability

Sediments are stabilized by growth of *Thalassia*, as was pointed out by Ginsburg and Lowenstam (1958), both through the binding effect of rhizomes, and through the slowing down of water motions at the sediment surface associated with the presence of leaves. In addition, growths of sessile organisms of all sorts (see 'Epifauna and flora' below) help stabilize the sediment surface, and in a _Thalassia_ stand with a well developed epifauna and flora, there is very little disturbance of the sediment surface even under conditions of strong wave action. However, once rhizomes are exposed, then erosion, directed horizontally from the place of exposure, may take place fairly rapidly and under conditions of only moderate wave action. Grass-free, depressed areas or 'blowouts' similar to those described by Hoskin (1963) occur throughout the PS and CS substrate areas at Bath. Hoskin (1963) noted that the steep, seaward edges of these depressed areas expose a well developed root system of _Thalassia_ (see Plate IId, this thesis), and he believed that the blowouts are produced by wave erosion during storms. This may be so, but it is also apparent that once formed, erosion at the seaward face (erosional scarp) of the blowout may continue for some time. Measurements of erosion at two such areas at Bath were carried out over a one year period; the seaward faces of the grass-free areas were eroded 1.2 and 1.6 m during this period and rates of erosion did not vary much from month to month. At the same time as erosion took place at the seaward face of the grass-free areas, _Syringodium_ advanced into the leeward regions, restabilizing the sediments. Irregularly oriented erosional scarps and depressed grass-free areas also occur in the CF and PF substrate areas. Erosion in these areas is probably slower. The Bath _Thalassia_ bed thus appears to be subject to continuous erosion-succession processes, erosion occurring in some areas, and growth of _Syringodium_ and subsequent development of _Thalassia_ and associated epifauna and flora in other areas. Emery et al. (1957) remarked that graded bedding would be expected in shallow lagoon areas subject to continuous erosion and deposition of sediments by tidal currents. It is probable that the occurrence of a rubble layer below the CS and PS substrates at Bath is a result of recurrent erosion-succession processes.

Marine angiosperms

Diplanthera is restricted in occurrence to the shallowest parts of the *Porites* rubble flats, and occasional narrow bands at the landward border of *Thalassia* and *Syringodium* growth. *Syringodium* occurs in the PS and CS substrates, mainly in mixed stands with *Thalassia*; pure stands occur bordering the grass-free depressed areas, and *Syringodium* rhizomes can be observed growing into these areas. *Thalassia* occurs in pure stands in the CF substrates, mainly in pure stands in the *Porites* rubble flats (mixed with *Diplanthera* in some of the shallower areas), in pure and mixed (with *Syringodium*) stands in the CS substrates, and in mixed stands only in the PS substrates. In the absence of recurrent erosion processes at Bath, *Syringodium* would probably be completely replaced by *Thalassia*.

Epifauna and flora

A rich epifauna and flora occurs in the Bath *Thalassia* bed. The most abundant and conspicuous organisms are (substrate types in brackets): the corals *Porites furcata* and *Siderastrea radians* (CS); a sponge *Anthosigmella varians* ? (PF,CF,CS); the anemone *Homostichanthus duerdeni* (PS,CS); the sabellid polychaete *Branchiomma nigromaculata* (PF,PS,CS); the Queen conch *Strombus gigas* (PS,CS) and a number of small gastropods such as *Columbella mercatoria* and *Smaragdia viridis viridemaris* which feed on *Thalassia* or its epiphytes; hermit crabs *Calcinus tubicen* (all substrates) and *Clibanarius tricolor* (PF), a number of spider crabs including *Pitho aculeata* and *Microphyrs bicornutus* (all substrates); the spiny lobster *Panulirus argus*

(PF,CS,PS); the sea urchin Tripneustes esculentus (PS,CS); the large ophiuran Ophiocoma echinata; the green algae Caulerpa spp. (CS,CF,PS), Avrainvillea nigricans (CS,CF), Avrainvillea rawsonii (CF,CS), Udotea spp. (CS,PS), and Halimeda opuntia (CF,CS); red algae Amphiroa spp.; and a number of blue-green algae. Blue-green algae (Microcoleus sp?) form extensive mats in some of the PS and CS substrate areas, and appear to trap fine sand (sample no. 3, Table XVI) as described by Sharp (1969). Blue-green algal growths were examined for the presence of heterocystous (N_2-fixing; Stewart, 1966) forms, but none were observed. In some CS substrate areas, Halimeda opuntia, Porites furcata and Avrainvillea rawsonii have completely overgrown the substrate, causing a reduction in the number of Thalassia shoots. Growths of Avrainvillea rawsonii in the CF substrate areas have the same effect (Plate IIb and Table XVII below).

Infauna

With the exception of a maldanid polychaete and a jawfish, infaunal organisms are very sparsely distributed at Bath. Tubes of about 5 cm length of a small maldanid polychaete (Clymenella torquata ?) number in the thousands per square meter in some PS and CS substrate areas. They are most common in areas of Syringodium growth where the sediment consists predominantly of fine sand (such as for sample 1, Table XVI). Burrows of a jawfish (probably Opistognathus aurifrons) number several per square meter in a few restricted CS substrate areas of rather sparse Thalassia growth. With the exception of these organisms, which may cause some overturning of the top 10 cm of sediment, there was no evidence of significant overturning of the Bath sediments by infaunal organisms. No bivalves other than the occasional Atrina seminuda were observed. A terrebellid was common on the undersides of algal balls in the surface layer of CF substrates. Other than these organisms, in twenty-one 0.15 m^2 infaunal samples, only 4 polychaetes, 3 sipunculoids, 5 enteropneusts (Ptychodera bahamensis), and 1 callianasid were collected.

The St. Lawrence Thalassia bed

General hydrography

The general hydrography and distribution of sea grasses at St. Lawrence is shown in Fig. 18. A rubble reef borders the shore at distances of 70 to 170 m from shore. Sand covers the bottom in the lee of the reef, and the sea grasses Thalassia, Syringodium and Diplanthera are all common in the leeward area. The 'Thalassia bed' refers to the largest, central sea grass bed in Fig. 18. Wave action over the leeward area is generally gentle, but at high tide is usually sufficient to cause stirring up of the sediment surface. A continual current flows westward over the leeward area, presumably resulting from the easterly component in wave approach on this coast; velocities of 4.7 and 10.7 cm/sec were observed at low and high tide on a day of moderate sea conditions.

Substrate types

Thalassia grows in a CF substrate at the inner borders of the rubble reef. The cobble framework is made up of flattened and rounded coral debris. PS substrates occur over the entire leeward area. A rubble layer occurs at a depth of 10 cm to 1 m or more below the substrate surface.

Sediment size and constituent characteristics

Grain size characteristics of sediment samples from St. Lawrence are given in Table XVI. All samples are characterized by a predominance of fine sand sized sediment, and less than 5% silt and clay. South coast sediments

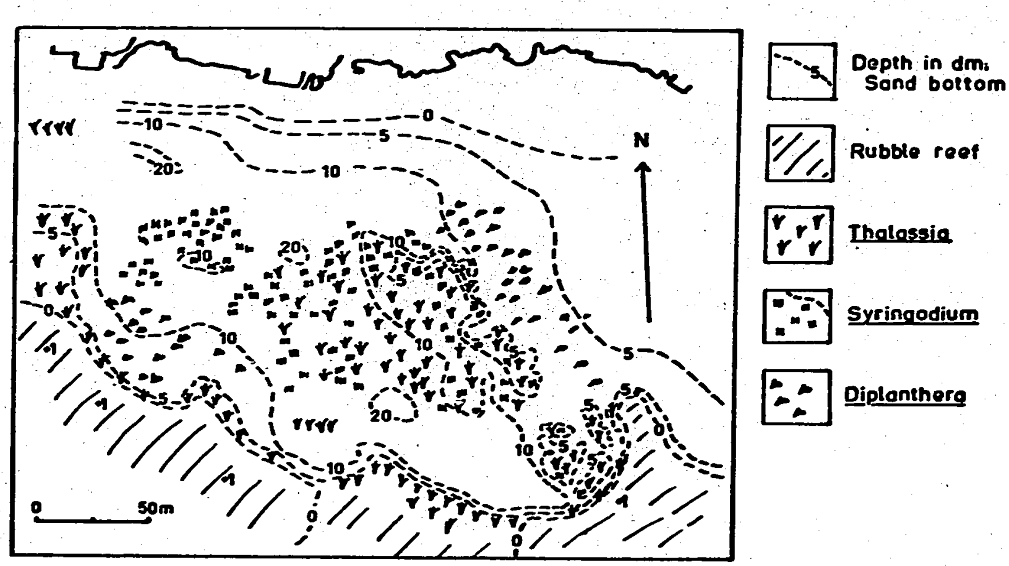

Fig. 18. Generalized bathymetry and distribution of sea grasses at St. Lawrence.

contain very little (less than 2%) non-carbonate material. The carbonate fraction of St. Lawrence sediments is similar in constituent composition to that described for Bath.

Substrate stability

Noticeable changes in substrate level in the grass-free sandy areas over periods of several weeks indicate significant motion of the sediment in these areas. Considerations based on settling velocity, threshold velocity and roughness velocity indicate that particles of about 0.18 mm in diameter require the least disturbance to be moved in comparison to both larger and smaller particles (Inman, 1949). The St. Lawrence sediments are in general well sorted and have median diameters close to this value. Thus even though wave action is not particularly strong in this area, the sediments are easily moved. There was little change in substrate level noted within the *Thalassia* bed, but, at high tide, there was usually noticeable disturbance of the surface sediments in most areas where the surface was not stabilized by blue-green algae or other organisms. Erosional scarps border much of the leeward margin of the bed, and large changes in the limits of the bed occurred subsequent to mapping of the *Thalassia* bed in July, 1968, erosion occurring in some areas, and extension of *Syringodium* into grass-free areas elsewhere.

Marine angiosperms

Thalassia occurs in pure stands at the leeward edge of the rubble reef, and in pure stands and mixed *Thalassia-Syringodium* stands in PS substrates. *Syringodium* occurs in pure stands and mixed stands. *Diplanthera* is restricted to small pure stands outside the main *Thalassia* bed. The substrate in areas where *Diplanthera* grows is noticeably unstable, and *Diplanthera* is alternately covered by sand (including leaves) and then exposed (including rhizomes) with no apparent ill effect. Recurrent erosion of Thalassia-Syringodium stands apparently favors maintenance of Syringodium at St. Lawrence, and shallower areas, because of the instability of the substrates, are suitable only for Diplanthera.

Epifauna and flora

The epifauna and flora are best developed in the pure Thalassia stands in the central part of the Thalassia bed. In other areas the sediment surface is largely bare. The most abundant and conspicuous elements of the epifauna and flora are the corals Porites furcata and Siderastrea radians; sponges (Haliclona spp. and others); the anemone Homostichanthus duerdeni, the sea urchin Tripneustes esculentus, the ophiuran Ophiothrix orstedii, the queen conch Strombus gigas and small gastropods as at Bath; spider crabs as at Bath; the bivalve Atrina seminuda and the ascidian Microsomus helleri are are partially buried in the sediment; blue-green algal mats as at Bath; and several species of Caulerpa are common. In some areas, sponges have overgrown the substrate, apparently 'choking out' Thalassia (Table XVII, below).

Infauna

Macro-infauna are abundant in comparison with the infauna at Bath, but not abundant in comparison with temperate water infauna. Infaunal organisms are more or less uniformly distributed in the Thalassia bed, and are limited largely to the top 10 cm of substrate. The more abundant organisms, and the approximate numbers per square meter are: bivalves Codakia orbiculata (4.4), C. pectinella (26), C. orbicularis (15), Chione pygmaea (8.5); gastropods Bulla striata (1.5), Olivella nivea (2.3) and Jaspidella jaspidea (3.6); the the sipunculoid Siphonosoma cumanense (5.1); the holothurian

Thyoneria cognata (3.9); the enteropneust Ptychodera bahamensis (4.4); polychaetes all species (9.1) of which the most abundant are Glycera sp. (1.5) and two Capitellid spp. (2.4).

The Oistin Bay Thalassia beds

Two Thalassia beds at Oistin Bay were sampled in the nutrient studies. There are no offshore reefs in Oistin Bay, and the area is subject to strong wave action. Thalassia is the only sea grass occurring in Oistin Bay. Stands A-1 and B-2 are adjacent stands in a small patch of Thalassia close to shore at the western extremity of Oistin Bay. Stand A-7 is in a small, near-shore patch of Thalassia at the southern extremity of Oistin Bay. The CCS substrate at the former position is described above under 'Substrate classification'. The substrate at the Oistin Bay S position is a PS substrate overlying a coral rock basement. At both areas the substrate surface is disturbed by wave action, and is devoid of attached epifauna and flora. The infaunal populations are similar to that described for St. Lawrence. Sediments (samples 19, 20, Table XVI) consist predominantly of fine sand sized skeletal carbonates.

The Carriacou Thalassia beds

The distribution of sea grasses at Carriacou is shown in Fig. 19. On the east, windward coast of Carriacou, a N-S oriented reef lies at distances of 750 to 1850 m offshore. The lagoonal areas behind the reef have a maximum depth of about 14 m. An almost continuous Thalassia (Thalassia-Syringodium) bed fringes the shore from the northern part of Watering Bay to the southern edge of Grand Bay, extending seaward 200 to 300 m. Thalassia beds are irregularly distributed through the remainder of the lagoonal area. Some of these areas are subject to strong tidal currents. Thalassia beds on

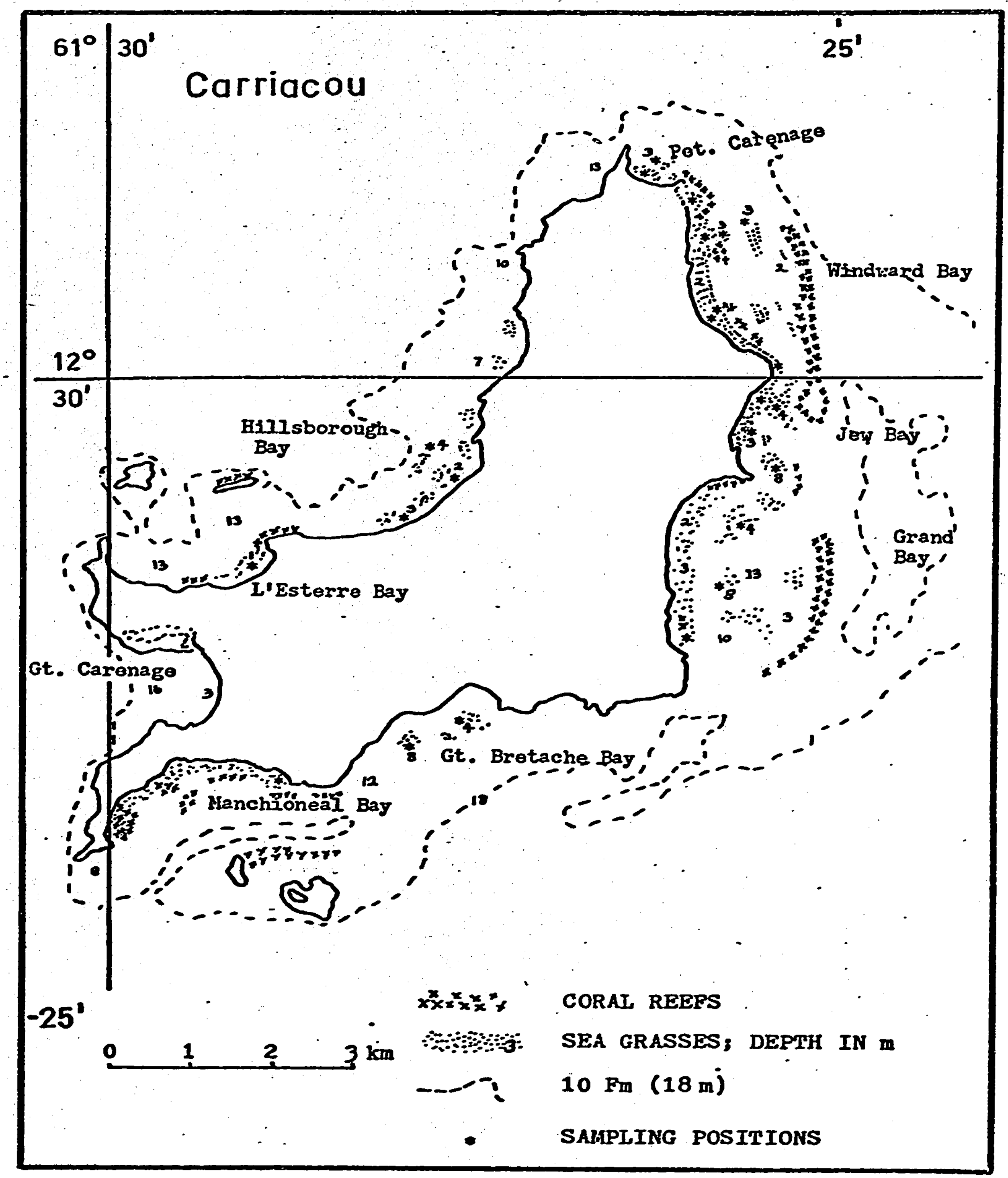

Fig. 19. Distribution of sea grasses at Carriacou.

other coasts are less extensive than on the east coast. Diplanthera is not common at Carriacou, occurring in a few shallow near-shore areas, and in some areas of Grand Bay at about 6 m depth. Halophila baillonis occurs in Thalassia-Syringodium stands in some of the deeper beds. Almost all beds at depths greater than 6 m are mixed Thalassia-Syringodium beds; Moore (1963) also noted that deep beds are usually mixed Thalassia-Syringodium. Substrates are most commonly the PS type, with less than 1% cobble sized material. CS substrates occur in some patch reef-Thalassia complexes. CF substrates occur in L'Esterre Bay, an area generally subject to turbulent conditions, and a CF substrate also occurs at a near-shore position in Hillsboro Bay. Sediment size characteristics (Table XVI) are similar to those for Barbados Thalassia sediments, with a predominance of sand sized material, and generally small amounts of silt and clay. Except in immediate near-shore areas where a large proportion of the sediments consists of non-carbonate material (Sample no. 23, Table XVI), the sediments consist predominantly of skeletal carbonates (sample no. 24, Table XVI). The epifauna and flora include many of the organisms observed at Barbados, such as Porites furcata, Siderastrea radians, Haliclona spp., Strombus gigas, Atrina seminuda, Tripneustes esculentus, various spider crabs and small gastropods, Caulerpa spp., Avrainvillea nigricans, Halimeda opuntia, Udotea spp., Amphiroa spp. and blue-green algae. In addition, organisms characteristic of Thalassia beds elsewhere in the Caribbean but not observed in Barbados Thalassia beds, occur in the Carriacou Thalassia beds. These include the coral Manicina areolata, the loggerhead sponge Spheciospongia vesparia, the basket star Oreaster reticulatus, many sponges and alcyonarians, and the green algae Halimeda simulans, Halimeda incrassata, and Penicillus dumetosus. Infaunal organisms were in general surprisingly sparse, with only the tube-dwelling polychaete Onuphis erimata being commonly observed. In a few shallow water areas there was some evidence of overturning of Thalassia sediments by Callianassa, but there was little evidence of biogenic overturning of Thalassia sediments elsewhere.

Production data

Production data from surveys of Thalassia beds at Bath, St. Lawrence and Carriacou are given in summarized form in Table XVII. Except where stated, the following remarks are based on these data.

1. At depths less than 0.2 to 0.3 m below mean low water at Barbados, leaf length, and thus growth rate and P_s are limited by depth of water (see remarks, p. 41, 156).
2. The mean values of L_m, P_s, P_m and the no. shoots/m^2 of PS and CS substrate stands at Bath, St. Lawrence and Carriacou are remarkably similar.
3. Examination of the original data for individual Thalassia stands at Carriacou revealed no significant trends of change in production parameters with depth. However, data were obtained for only 7 stands in the depth range 4 to 9 m. Further, it may not be reliable to use the relations of Appendix A to estimate production of stands at depths much greater than 2 m.
4. P_s of CF substrate stands is, on the whole, significantly higher than P_s of CS and PS substrate stands. However, the maximum values on each substrate type are approximately the same. The maximum P_s observed for a CF stand was 17.5 mg/shoot per day (Stand A-2, Table II), while the maximum P_s for a PS substrate was 17.0 mg/shoot per day (Series 2 St. Lawrence stand, Table XI). These values are similar to those observed for the CCS substrate in Oistin Bay (Table III),

Table XVII. Production data of Barbados and Carriacou *Thalassia* beds.

SAMPLE GROUP CHARACTERISTICS	ALL STANDS										THALASSIA STANDS ONLY						
		L_m (cm)			P_s (mg/shoot per day)			MAXIMUM STANDING CROP (g wet wt/m²)				P_m (g/m² per day)			SHOOTS (no./m²)		
	n	$\bar{x}$	SD	RANGE	$\bar{x}$	SD	RANGE	*Thalassia*	*Syring.*	*Thalassia* + *Syring.*	n	$\bar{x}$	SD	RANGE	$\bar{x}$	SD	RANGE
1. St. Lawrence																	
PS substrate	25	21.9	3.2	17.0-27.0	6.8	1.9	4.2-12.6	1510[p]	1570[p]	1822	5	4.1		1.7-5.6	650		340-800
Overgrown by sponges	1	26.3			9.2			407[p]			1	1.5			160		
2. Bath																	
OS substrate 0.3m+	10	21.3	4.6	14.3-29.3	6.5	2.7	3.2-11.4	1360[p]	815[m]	1600	5	3.2		2.6-5.0	550		470-680
OS substrate 0.25m	2	21.6		21.0-22.1	4.5		4.4-4.6	468[m]	1358[m]	1660	0						
OS substrate 0.25m stunted growth	1	10.2			1.5			272[m]	60[m]	332							
PS substrate 0.25m	1	18.4			3.6			330[m]	468[m]	800							
PF substrate 0.2m-	2	10.8		9.3-12.3	1.7		1.0-2.3	340[p]			2	1.0		0.7-1.3	800		300-1300

Table XVII. Concluded.

SAMPLE GROUP CHARACTERISTICS	ALL STANDS										*THALASSIA* STANDS ONLY						
		L_m			P_s			MAXIMUM STANDING CROP				P_m			SHOOTS		
	n	$\bar{x}$	SD (cm)	RANGE	$\bar{x}$	SD (mg/shoot per day)	RANGE	*Thalassia*	*Syring.*	*Thalassia* + *Syring.* (g wet wt/m^2)	n	$\bar{x}$	SD (g/m^2 per day)	RANGE	$\bar{x}$	SD (no./m^2)	RANGE
2. Bath (continued)																	
CP substrate 0.4m+	3	27.9		25.0-31.7	10.5		8.8-12.5	1207[p]			3	3.6		3.0-4.5	340		290-360
CP substrate 0.3m	2	21.2		19.7-22.6	5.4		5.3-5.4	1177[p]			2	2.8		1.1-4.4	520		210-820
CP substrate 0.25m (overgrown by *Avrainvillea*)	1	16.7			4.3						1	0.16			37		
3. Carriacou																	
PS substrate	22	22.5	4.1	16.5-32.3	5.9	1.9	3.0-8.9	1615[p]	1066[m]	1700	10	3.8	1.6	2.0-6.0	650	245	310-930
OS substrate	4	20.4		18.0-23.7	5.9		4.7-7.2	1238[p]			4	2.3		0.8-4.6	450		170-640
CP substrate	2	29.3		29.1-29.5	10.6		9.9-11.3	1811[p]			2	5.6		4.4-6.7	540		390-680

[p]Pure stand, [m]Mixed stand

18.2 and 15.4 mg/shoot per day.

5. Routine observations were not made of the thickness of the root layer in the surveys represented in Table XVII. However, examination of a number of areas in which long erect shoots occurred, and of a number of CS and PS substrate areas in which long leaves occurred, indicate that high P_s in PS and CS substrates is invariably associated with long erect shoots, and vice versa, that long erect shoots invariably have high P_s. Similar observations indicate that P_s in the range 3 to 4 mg/shoot per day in PS and CS substrate stands is associated with shallow, presumably partially aerated (see p. 62) root layers. 'Stunted' Thalassia growths, i.e. stands with very short leaves and low P_s (less than about 3 mg/shoot per day) not in depths less than 0.3 m and for which the nutrient studies indicate growth is not limited by availability of nitrogen, are unusual at Barbados, and were not observed at Carriacou. The question of what limits growth at these particular stands is the question which led to the approach used in this study for investigating the origin of nitrogen and phosphorus for growth of Thalassia. It remains unanswered.

6. There is a roughly inverse relation between standing crop of Thalassia and standing crop of Syringodium. This is shown by the plot of the standing crop of Thalassia versus standing crop of Syringodium at St. Lawrence (Fig. 20), and is also suggested by the similar maximum standing crops of Thalassia and Syringodium on PS and CS substrates (Table XVII). It is tempting to suggest that this indicates similar P/SC ratios for Thalassia and Syringodium. However, it is not clear why the maximum P_m observed for the Barbados-Carriacou Thalassia stands, 7.6 g/m^2 per day (Stand A-1, Table II), should be

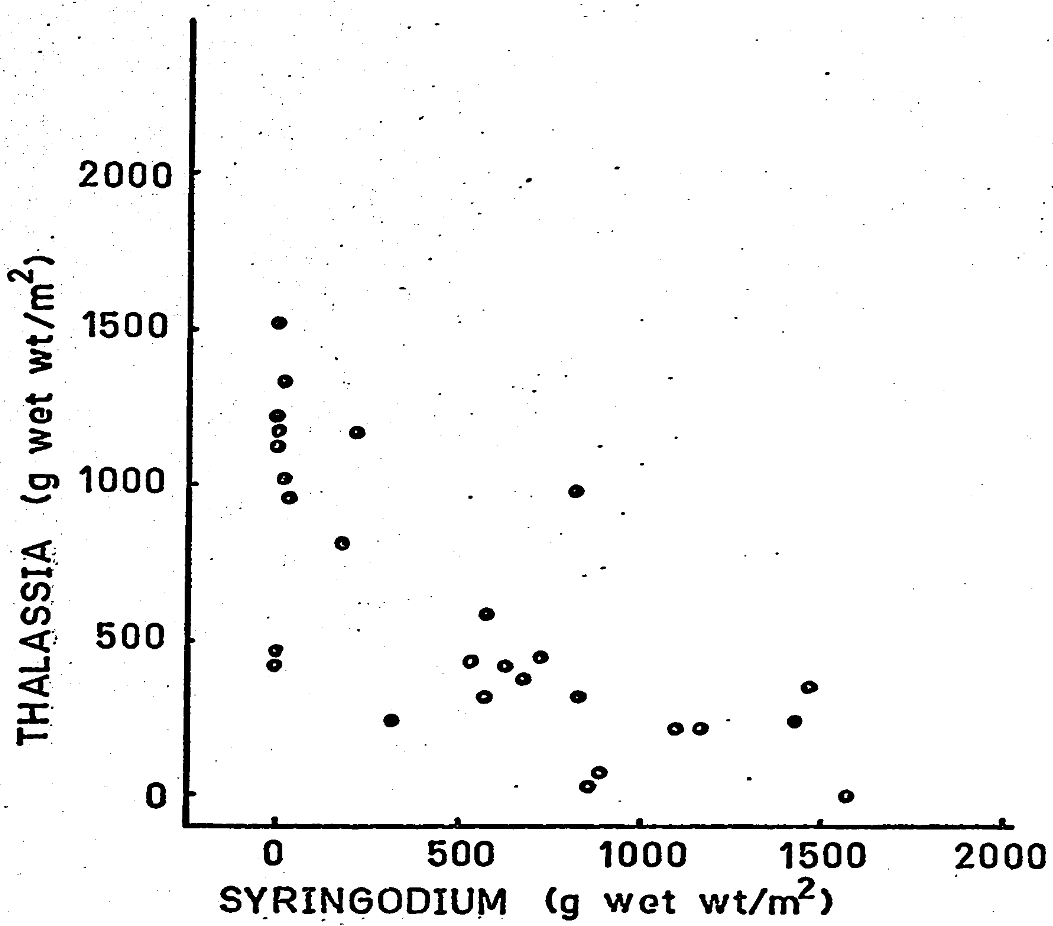

Fig. 20. Relation of standing crop of Thalassia to standing crop of Syringodium at St. Lawrence.

only one-half the P_m, 14.1 g/m^2 per day, of the Bermuda stand.