

Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon*

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ABSTRACT: In typical Caribbean seagrass beds, several seagrass species co-occur and may compete for resources. The decline in *Syringodium filiforme* as *Thalassia testudinum* becomes abundant during successional development of Caribbean seagrass beds suggests that competition occurs between these seagrasses. The hypothesis that *T. testudinum* outcompetes *S. filiforme* for light and sediment nutrients was tested *in situ* within a shallow seagrass bed in St. Croix, U.S. Virgin Islands. Exploitative competition with *T. testudinum* for primarily sediment nutrients but also light limited the leaf shoot density of *S. filiforme* but had little effect on leaf growth. Removal of the *T. testudinum* leaf canopy increased light above the saturation level of photosynthesis by *S. filiforme* and leaf shoot density and belowground biomass of *S. filiforme* doubled within 9 mo compared to control areas. The *T. testudinum* canopy protected *S. filiforme* leaves from breaking. Fertilization of the sediments with nitrogen and phosphorus increased leaf shoot density and belowground biomass of *S. filiforme*, an effect enhanced by *T. testudinum* canopy removal. Belowground competition for nutrients limited the areal aboveground productivity of *S. filiforme* more than exploitation of light by *T. testudinum*. Increased shoot density of *S. filiforme* resulting from greater rhizome density, rhizome branching, and leaf pairs per node contributed more to enhanced aboveground productivity with additional light or nutrients than increases in leaf growth.

INTRODUCTION

Caribbean seagrass beds are commonly assemblages of green macroalgae of the order Caulerpaceae and the seagrass species *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*. During the successional development of Caribbean seagrass beds, *H. wrightii* and *S. filiforme* colonize bare sediments before *T. testudinum* (Den Hartog 1971, Patriquin 1975, Zieman 1976). Seagrass bed recolonization experiments on St. Croix, U.S. Virgin Islands indicate that densities of *S. filiforme* leaf shoots peak before *T. testudinum* becomes abundant and decline thereafter (Williams 1984, 1985). The decline in *S. filiforme* with increasing *T. testudinum* abundance suggests that *T. testudinum* interferes with the growth of *S. filiforme*. Interference is defined *sensu* Harper (1977) as a change in the environment created by the proximity of

individuals that 'may alter the growth rate or form' of neighboring individuals. 'Interference' does not specify mechanisms responsible for the changes, hence the major objective of my study was to elucidate those mechanisms.

One obvious change in the environment as *Thalassia testudinum* becomes increasingly dominant is the reduction of light under the canopy formed by *T. testudinum* leaves. *T. testudinum* has a much greater leaf area for interception of light than *Syringodium filiforme*. For example, a typical leaf width for *T. testudinum* is 1 cm in contrast to just over 1 mm for *S. filiforme*. Zieman et al. (1984) have shown that only 25 to 43 % of the light impinging on the canopy penetrates to the substratum in 2 seagrass beds on St. Croix. The seagrasses *Zostera marina* and *Heterozostera tasmanica* respond to reduced light by decreasing leaf shoot density (Bachman & Barilotti 1976, Dennison & Alberte 1982, Bulthuis 1983). Photosynthesis of *S. filiforme* is presumably light-limited under a *T. testudinum* canopy. Earlier studies demonstrated that photosynthesis of *S. filiforme* reaches saturation at

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light levels > 50 % of the irradiance reaching the surface of the water column (Williams & McRoy 1982).

The primary objective of my study was to determine whether the leaf canopy of *Thalassia testudinum* interferes with *Syringodium filiforme* in terms of shoot density and leaf growth. The predicted effects of removing the *T. testudinum* canopy would be increases in shoot density and rates of leaf growth of *S. filiforme*. I tested this hypothesis *in situ* at the site of previous recolonization experiments. Another objective was to determine belowground interactions between the 2 seagrasses. Sediment nutrients limit seagrass growth in some seagrass beds but the limitation has never been tested in the Caribbean (Orth 1977, Bulthuis & Woelkerling 1981, Short et al. 1985, Dennison et al. in press). I fertilized the sediments of the study seagrass bed to assess belowground competition between *T. testudinum* and *S. filiforme* for nutrients.

METHODS

The study site was a seagrass bed in 2 m of water in Tague Bay on the northeast coast of St. Croix, U.S. Virgin Islands at a site locally known as Romney Point (17° 45' N, 64° 42' W).

Submarine photosynthetically active radiation (PAR) was measured with a LI-COR 1935B 4 π sensor and a LI-COR 188B integrating quantum meter. At least 10 integrations of 10 s were taken from 1030 to 1200 h Atlantic Standard Time at each depth in October 1984 and December 1985.

Experimental manipulations of the seagrass bed are summarized in Table 1. In September 1984 I began clipping all *Thalassia testudinum* leaves at or just below the substratum every 7 to 10 d in eight 40 × 40 cm plots. Four 40 × 40 cm plots in the surrounding seagrass bed were unclipped controls ('controls'). Plots were selected haphazardly but treatments were assigned randomly to plots. In November 1984 in 4 of the original 8 clipped plots, I added clear plastic strips

that mimicked the size and density of *T. testudinum* leaves in the surrounding bed to create a light-transmitting canopy (hereafter referred to as 'clipped & plastic'). The plastic was tied to thin metal rods longer than the plot width and with 12 cm of each end bent at a right angle. The ends were gently pushed into the sediments outside the plot borders so that the rod rested just above the substratum. Care was taken to avoid bending *S. filiforme* leaves during placement. The plastic 'leaves' were replaced and *T. testudinum* was clipped every 7 to 10 d.

In January 1985, 8 new 40 × 40 cm plots were established. Solid time-released fertilizer stakes (International Spike, Inc., Lexington, Kentucky, USA) were driven into the sediments of 4 newly clipped plots (hereafter referred to as 'clipped fertilized') and 4 new unclipped plots ('unclipped fertilized'). *T. testudinum* leaves were removed in the fertilized clipped plots every 7 to 10 d. The fertilizer supplied a total of 35 g N and 8 g P per ¼ m². An equivalent mass of the same fertilizer stimulated seagrass growth into cleared areas in previous experiments at this site (Williams unpubl. data). Half this amount of fertilizer was added again 11 mo later (see 'Results' for rationale).

Leaf shoot densities (hereafter referred to as shoot densities or densities) of *Syringodium filiforme* were counted in ¼ m² quadrats placed haphazardly in each of the 4 plots corresponding to a different manipulation (i.e. control, clipped, clipped & plastic, clipped fertilized, unclipped fertilized). Quadrats were removed after counts were made. Two-way analysis of variance (ANOVA) was used to compare changes in densities of *S. filiforme* among experimental treatments and over time (Sokal & Rohlf 1969). The assumptions of ANOVA were tested using Tukey's test for nonadditivity. If this test was significant, a data transformation was performed followed by another test of assumptions. Student-Newman-Keuls tests were used for multiple comparisons among means following significant ANOVA's. A 5 % probability level (p) was used unless otherwise stated. Fertilized control and clipped fertilized treatments were not compared to the clipped

Table 1. Experimental plan. Four plots per treatment. *Thalassia testudinum* canopy removal occurred every 7 to 10 d

Plot	Initiation date	Treatment
Control	Sep 1984	None
Clipped	Sep 1984	Remove canopy
Plastic		
Initially clipped	Sep 1984	Remove canopy
Plastic added	Nov 1984	Add plastic, continue canopy removal
Clipped fertilized	Jan 1985	Remove canopy Add N + P to sediments
Unclipped fertilized	Jan 1985	Add N + P to sediments

and clipped & plastic treatments because of the 4 mo lag between initiation of the 2 experiments.

In 2 separate control and 2 separate fertilized plots, concentrations of ammonium and reactive phosphate were measured in sediment porewaters collected in diffusion chambers similar to those of Winfrey & Zeikus (1977). Chambers were filled with 0.3 μm glass fiber-filtered seawater which had been degassed with N_2 . A 0.2 μm Nuclepore polycarbonate membrane was placed over sampling ports in the chamber and secured by a thin plexiglas faceplate. Immediately after fertilization, one chamber per plot was inserted in the sediments to a depth of up to 33 cm. Two wk later the chambers were removed and kept cool and dark during immediate transport to the laboratory. Porewater processing followed methods in Williams et al. (1985).

Growth of *Syringodium filiforme* leaves was measured by marking a leaf near its base with a strip of aluminum tape 1.5 mm wide. At least 35 leaves were marked in each plot in each treatment. Temporary wire quadrats served as reference levels for taping and measuring. Leaf elongation was measured after 7 d. Some leaves were not relocated and leaves and tags may have been lost, reducing the final sample size. Length increments were converted to dry weight using a regression between leaf length and dry weight after calcareous epiphytes were removed using 5 % HCl (sample size $n = 100$; $r^2 = 0.89$). The sample included leaves of all sizes and ages. Small (less than 1 mm) changes in leaf diameter are associated with *S. filiforme* leaves in this seagrass bed and such changes are positively associated with leaf age and frequently length. The regression thus calculates the dry weight of leaves of an average diameter. Because leaves from all 4 replicates of each treatment were pooled for a mean growth rate, the variance among samples within treatment replicates was lost (i.e. 'sacrificial pseudoreplication': Hulbert 1984). For this reason I did not use inferential statistics to test for differences in growth among treatments.

In February 1986, above and belowground biomass samples were collected from 0 to 30 cm sediment depth using a PVC corer (21 cm diameter). The depth interval included over 90 % of the seagrass belowground biomass. A core was randomly selected and taken from each of 3 of the clipped, clipped fertilized, unclipped fertilized and control plots. Lengthy sample processing time restricted sample size. Sediment was washed from the samples and seagrass species were separated. Rhizome (long shoot) meristems, leaf shoots and rhizome branches (including those arising from branching of rhizome apices and from vegetative branching of short shoots, i.e. branch rhizomes or proliferation shoots) were counted, based on Tomlinson (1974). Total rhizome length was measured. Rhizome

number was defined as the number of rhizome segments longer than 5 cm, which may overestimate the actual number due to inadvertent breakage of rhizomes during sample processing. Rhizome number gives a relative measure of the numbers of individual long shoots in each core because presumably inadvertent breakage of rhizomes was equal among cores. All rhizome diameters and internode lengths were measured and averaged for each species in each core. Leaf biomass was separated from root and rhizome biomass at the base of the leaf sheath which was included in leaf biomass. All biomass was rinsed in freshwater, dried at 90 °C and weighed.

Aboveground areal productivity of *Syringodium filiforme* was estimated because it is a parameter commonly used to compare seagrass growth (McRoy & McMillan 1977, Zieman & Wetzel 1980) and it combines measures of leaf growth and shoot density. Mean leaf growth rates and the range in density counts from December 1985 were used. Leaf growth rates were multiplied by 2 leaves per shoot and converted to dry weight using the empirically-derived regression.

All data were converted to a m^2 basis for ease of comparison with other seagrass studies.

RESULTS

Canopy removal

Light reaching the top of the *Thalassia testudinum* canopy was approximately 70 % of irradiance at the top of the water column. Light levels at the base of the canopy were reduced to 33 % of surface values (Fig. 1).

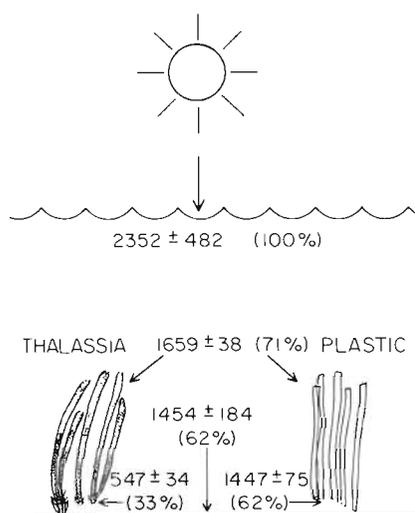


Fig. 1. Light transmittance through a canopy of *Thalassia testudinum* leaves, transparent leaves, and no canopy. Mean $\mu\text{Ein m}^{-2} \text{s}^{-1} \pm 1$ standard deviation

Irradiance at midday within the canopy was therefore below the 50 % level necessary to saturate photosynthesis of *Syringodium filiforme* (Williams & McRoy 1982). Removal of the *T. testudinum* canopy increased the light passing through a canopy of *S. filiforme* leaves and rhizophytic algae to >50 %.

Density of *Syringodium filiforme* increased significantly in the plastic plots 9 mo after plastic was added (2-way ANOVA, $p < 0.01$; Fig. 2). Thereafter, all treatments were significantly different from controls.

Syringodium filiforme leaf growth did not appear to increase with increased light following canopy removal (Table 2). Within 1 wk after canopy removal, *S. filiforme* leaves were shorter than under the *Thalassia testudinum* canopy (Fig. 3). The plastic canopy did not noticeably affect the growth rate of *S. filiforme* leaves but leaves were longer under it (Fig. 3). The plastic canopy transmitted light well (Fig. 1). *S. filiforme* leaves rarely grew above the top of the plastic or the *T. testudinum* canopy in the control areas (Fig. 3). *S. filiforme* density was eventually highest under the plastic canopy (Fig. 2). These data suggest that the *T. testudinum* canopy plays a role in protecting *S. filiforme* leaves from breakage caused by water motion or the background level of grazing activity present, which may enable increased leaf shoot density.

Fertilization

Dissolution of the fertilizer during the first 2 wk following application raised porewater ammonium concentrations by 2 orders of magnitude and phos-

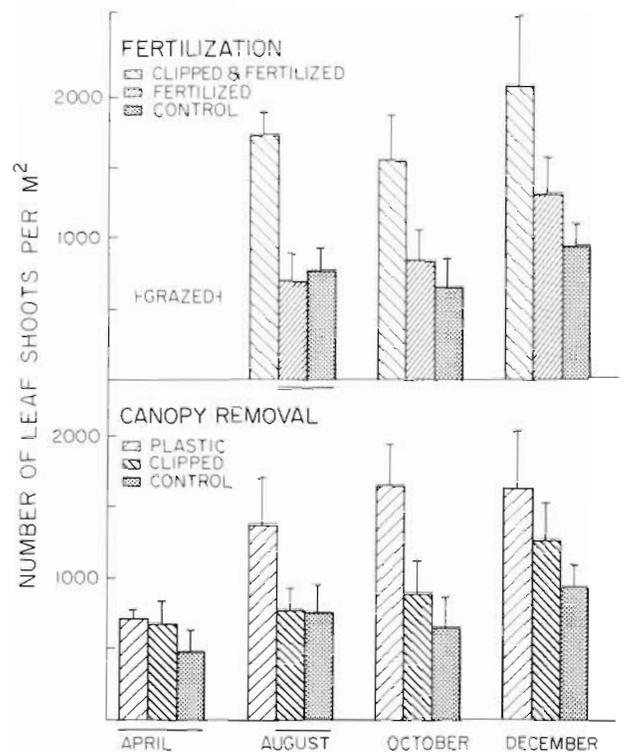


Fig. 2. *Syringodium filiforme*. Leaf shoot density during 1985 after removal of the *Thalassia testudinum* leaf canopy (lower half of graph) in Sep 1984 and fertilization of sediments (upper half of graph) in Jan 1985. 'Clipped' refers to removal of the *T. testudinum* canopy, 'plastic' to replacement of the *T. testudinum* canopy with clear plastic strips, 'control' to the natural seagrass bed (unclipped, unfertilized). Mean values from four $\frac{1}{4}$ m² plots + 1 standard deviation (vertical error bar). Lines under vertical bars indicate groups of means not significantly different at $p < 0.05$.

Table 2. *Syringodium filiforme*. Leaf elongation rates (mm leaf⁻¹ d⁻¹). Values are $\bar{x} \pm 1$ standard deviation (sample size). Dash: no data. Control: leaves within a *Thalassia testudinum* canopy

Date	Type of plot				
	Clipped	Clipped & plastic	Control	Unclipped fertilized	Clipped & fertilized
10 Sep 84	5.3 ± 4.0 (37)	—	6.3 ± 4.0 (41)	—	—
14 Sep 84	4.9 ± 2.1 (45)	—	7.5 ± 3.8 (40)	—	—
21 Sep 84	4.2 ± 2.1 (32)	—	5.0 ± 2.5 (36)	—	—
28 Sep 84	5.0 ± 1.7 (34)	—	5.7 ± 2.7 (33)	—	—
5 Oct 84	4.8 ± 2.2 (35)	—	5.5 ± 2.6 (37)	—	—
12 Oct 84	4.7 ± 2.2 (22)	—	5.9 ± 2.9 (35)	—	—
19 Oct 84	4.8 ± 2.2 (28)	—	5.4 ± 2.7 (36)	—	—
26 Oct 84	4.6 ± 2.0 (26)	—	5.8 ± 2.6 (25)	—	—
10 Nov 84	4.1 ± 1.4 (10)	—	5.1 ± 2.1 (21)	—	—
24 Jan 85	3.2 ± 1.3 (28)	3.8 ± 1.5 (27)	3.9 ± 1.7 (23)	4.4 ± 2.9 (14)	5.0 ± 2.4 (26)
31 Jan 85	3.4 ± 1.6 (26)	3.3 ± 1.2 (33)	4.0 ± 1.9 (38)	5.9 ± 2.4 (5)	—
17 Jun 85	4.0 ± 1.3 (31)	4.2 ± 1.8 (34)	4.0 ± 1.4 (24)	4.9 ± 1.9 (15)	5.2 ± 1.6 (24)
3 Jul 85	5.2 ± 1.8 (32)	4.3 ± 1.6 (19)	4.7 ± 2.3 (25)	6.0 ± 1.9 (21)	5.8 ± 1.6 (23)
27 Dec 85	8.4 ± 1.4 (32)	7.0 ± 2.1 (30)	8.5 ± 1.7 (34)	10.6 ± 1.9 (14)	9.8 ± 1.0 (11)

* Catastrophic grazing occurred

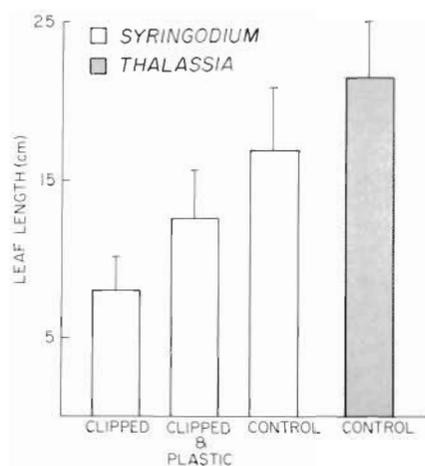


Fig. 3. *Syringodium filiforme* and *Thalassia testudinum* ($n = 30$). Mean leaf lengths + 1 standard deviation (vertical error bar). 'Clipped' refers to removal of the *T. testudinum* leaf canopy, 'clipped & plastic' to replacement of the *T. testudinum* canopy with clear plastic strips, 'control' to the unclipped canopy

phorus concentrations 1 order of magnitude above the concentrations in the control seagrass bed (Table 3). Concentrations should have been highest just after fertilization but have remained above control levels for a minimum of 6 mo, based on results from my unpublished studies. After 2 mo, the tops of the fertilizer spikes were still visible just below the sediment surface but had decreased in bulk.

Fertilization of the sediments had dramatic effects on the seagrass bed and resident foraging animals. A week after application of the fertilizer, virtually all seagrass leaves in both clipped fertilized and unclipped fertilized plots were grazed to the substratum primarily by juvenile scarid parrotfishes. Leaves were

broken possibly by the activities of goatfishes and black-eared wrasses. Fertilization resulted in a bloom of seagrass epiphytes, primarily filamentous red and some green algae but also larger species such as *Hypnea* sp. and *Dictyota* sp. The catastrophic grazing effect was apparently related to the algal bloom or other indirect effect of the fertilizer rather than a direct one, e.g. a chemical cue leaching from the fertilizer, because no enhanced grazing occurred when I placed fertilizer spikes on stakes elevated 30 cm above the canopy. These stakes decreased in size over 4 wk, indicating solubilization of the fertilizer. Recovery of seagrass leaf biomass was apparent 6 wk after fertilization but was not complete until 10 wk had elapsed.

Fertilization increased *Syringodium filiforme* leaf growth indicating nutrient limitation in the natural seagrass bed (Table 2). Nutrient limitation may provide a partial explanation for the lack of any noticeable increase in growth in the unfertilized areas after canopy removal. Fertilizer was added to the clipped fertilized and unclipped fertilized plots in December 1985 because I judged that the initial difference between leaf growth of fertilized versus unfertilized *S. filiforme* was decreasing, indicating depletion of fertilizer. I added only half the original amount to avoid catastrophic grazing. Catastrophic grazing did occur but was less severe.

A 2-way ANOVA indicated that changes in the density of *Syringodium filiforme* were significant over time ($p < 0.025$) and among unclipped fertilized, clipped fertilized, and control areas ($p < 0.01$) (Fig. 2). The density of *S. filiforme* doubled 4 mo after initial fertilization. Densities in fertilized areas increased faster and reached greater numbers when the *Thalassia testudinum* canopy was removed.

Table 3. Concentration of ammonium and reactive phosphorus dissolved in sediment porewaters of control and unclipped fertilized plots. Values are means from 2 plots \pm 1 standard deviation. Dash: no data due to broken membranes over sampling ports of diffusion chambers

Sediment depth (cm)	Ammonium (μM)		Phosphorus (μM)	
	Control	Unclipped fertilized	Control	Unclipped fertilized
+1-1	3.22 \pm 3.22	74 \pm 96	0 \pm 0	0.45 \pm 0.53
-2-4	5.80 \pm 1.96	1214	0 \pm 0	2.79
-5-7	4.86 \pm 0.96	1710 \pm 1820	0.04 \pm 0.05	4.76
-8-10	26.0 \pm 28.7	3800	0.14 \pm 0.19	6.12
-11-13	19.7	2840 \pm 1330	-	64 \pm 85
-14-16	-	2971	-	120
-17-19	-	1770 \pm 993	-	67 \pm 93
-20-22	-	1230	-	0.41
-23-25	-	2140	-	1.36
-26-28	38	2200	0.20	1.50
-29-31	58	2110	0.27	0.95

Biomass allocation

Although variance was high within samples from a treatment, changes in seagrass morphology and biomass were obvious upon visual inspection of the cores. The following description of these changes helps to explain how the increases in *Syringodium filiforme* density were effected following clipping of *Thalassia testudinum* or fertilization.

Seagrasses have several morphological alternatives for increasing leaf shoot density. The increased shoot density of *Syringodium filiforme* following removal of the *Thalassia testudinum* canopy or fertilization resulted from: (1) an increased number of individual rhizomes per unit area; (2) increased branching of individual rhizomes; and (3) an increased number of multiple leaf pairs per node (nodes typically have a single leaf pair) (Table 4). These increases indicate stimulation of lateral (short shoot) meristems. Internode lengths remained largely unchanged from the control plants, indicating that the rhizome growth rate may have increased.

Canopy removal or fertilization resulted in increased

above and belowground biomass of *Syringodium filiforme*. Aboveground biomass increased proportionately more than belowground biomass. The increase in leaf shoot density compensated for the loss of biomass through breakage of leaves in the clipped plots; leaf biomass in clipped plots was greater than in control plots.

Thalassia testudinum morphology and biomass changed following leaf removal but not fertilization (Table 4). Weekly removal of leaves caused a significant reduction in belowground biomass and many shells of senescent rhizomes were found in the cores.

Syringodium filiforme aboveground productivity: effects of competition with *Thalassia testudinum*

Areal aboveground productivity is an integrative measure of 2 components of plant fitness: leaf growth and shoot density. Areal aboveground productivity data indicate that: (1) belowground competition with *Thalassia testudinum* for nutrients was more important than light; and (2) the effect of competition on *Syrin-*

Table 4. *Syringodium filiforme* and *Thalassia testudinum*. Effects of canopy removal and fertilization on seagrass morphology and biomass allocation. Values represent mean \pm standard deviation per m², n = 3. Cores taken Feb 1986

Type of plot	<i>Syringodium filiforme</i>				<i>Thalassia testudinum</i>			
	Clipped	Control	Unclipped fertilizer	Clipped & fertilizer	Clipped	Control	Unclipped fertilizer	Clipped & fertilizer
Total rhizome length (cm)	5469 \pm 886	2768 \pm 2371	4377 \pm 741	5022 \pm 1064	5083 \pm 3402	11873 \pm 1328	11725 \pm 1328	5081 \pm 1414
Rhizome number	463 \pm 49	251 \pm 188	405 \pm 0	521 \pm 153	414 \pm 148	967 \pm 157	1002 \pm 509	385 \pm 73
Rhizome branches	193 \pm 88	19 \pm 33	174 \pm 76	48 \pm 83	10 \pm 17	39 \pm 44	97 \pm 35	39 \pm 67
Mean internode length (mm)	15.1 \pm 0.5	16.0 \pm 0.7	15.4 \pm 1.9	17.2 \pm 2.3	39.4 \pm 3.0	43.0 \pm 3.8	44.9 \pm 1.9	47.0 \pm 0.5
Mean rhizome diameter (mm)	2.6 \pm 0.3	2.7 \pm 0.1	2.4 \pm 0.1	2.4 \pm 0.1	4.7 \pm 0.7	4.5 \pm 0.4	4.2 \pm 0.1	4.4 \pm 0.1
Rhizome meristems	193 \pm 44	19 \pm 17	173 \pm 100	222 \pm 133	87 \pm 126	299 \pm 89	270 \pm 159	87 \pm 29
Leaf shoots	2495 \pm 73	1021 \pm 2371	2071 \pm 590	2312 \pm 827	462 \pm 356	1667 \pm 535	1137 \pm 392	482 \pm 136
Multiple shoots*	183 \pm 83	68 \pm 35	154 \pm 88	116 \pm 76	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
Leaves (g dry)	34.2 \pm 7.8	24.5 \pm 24.2	50.1 \pm 19.3	25.9 \pm 3.8	14.6 \pm 15.7	207 \pm 52	134 \pm 53	11.9 \pm 7.2
Rhizomes & roots (g dry)	99.1 \pm 27.0	57.7 \pm 46.2	62.1 \pm 5.7	61.1 \pm 4.6	412 \pm 335	1092 \pm 209	774 \pm 395	269 \pm 41
Aboveground/below-ground (g dry)	0.37 \pm 0.19	0.30 \pm 0.16	0.81 \pm 0.28	0.45 \pm 0.08	0.06 \pm 0.07	0.19 \pm 0.03	0.19 \pm 0.08	0.05 \pm 0.03

* Double or triple leaf pairs/node

Table 5. *Syringodium filiforme*. Comparison of effects of *Thalassia testudinum* canopy removal versus fertilization of sediments on aboveground productivity, 1985. Values are means or range

Parameter	+ Canopy	- Canopy	+ Canopy	- Canopy
	- Fertilizer	- Fertilizer	- Fertilizer	+ Fertilizer
Leaf shoot productivity (mg dry wt d ⁻¹)	1.4	1.3	1.6	1.7
Shoot density (# m ⁻¹)	816–1184	929–1552	1072–1648	1728–2768
Productivity (g dry wt m ⁻² d ⁻¹)	1.14–1.66	1.21–2.02	1.72–2.64	2.94–4.71

godium filiforme was mediated primarily through changes in shoot density rather than leaf growth (Table 5). Fertilization plus canopy removal resulted in a nearly 3-fold increase in *S. filiforme* aboveground productivity.

DISCUSSION

The majority of examples of competition among marine plants occur in the rocky intertidal environment (Lubchenko & Menge 1978, Sousa et al. 1981, Dayton et al. 1984, Dethier 1984, Paine 1984, Turner 1985). Competition among plants in the rocky intertidal is typically categorized as 'interference' competition *sensu* Miller (1967), where a dominant plant limits access by another to a resource: frequently space. The specific mechanisms responsible for pre-emption of space remain largely undetermined. A few studies on laboratory cultures of mixed species of macroalgae growing under various light-temperature gradients have provided information on the 'exploitation' component of competition (Miller 1967), i.e. resulting from collective access to a resource (Russell & Fielding 1974, Enright 1979). Results of laboratory studies, while aiding selection of hypothetical mechanisms, do not necessarily predict competitive outcomes in the field where other factors such as herbivory and physical forces combine with potential competitive relationships to structure a particular plant community.

Competition among seagrasses or seagrasses and macroalgae has been mostly inferred (Patriquin 1972, Young & Kirkman 1975, Harrison 1979, Birch & Birch 1984, Pulich 1985). However, Turner (1985) experimentally demonstrated that the surfgrass *Phyllospadix scouleri* pre-empts space from various algae in the rocky intertidal, a form of interference competition. My study indicates that the decline in *Syringodium filiforme* shoot density as *Thalassia testudinum* becomes dominant during temporal development of a Caribbean seagrass bed is a result of exploitative competition primarily for sediment nutrients but also light.

The result of removing the *Thalassia testudinum* canopy is an increase in irradiance above the saturation level of *Syringodium filiforme* photosynthesis, based on the photosynthesis-irradiance curves of Williams & McRoy (1982). Indirect evidence for increased photosynthesis following canopy removal is derived from the increases observed in *S. filiforme* biomass in the clipped plots rather than changes in leaf growth. A pattern for resource allocation in *S. filiforme* is evident from fertilization experiment results (Tables 2 & 4). Increases in either light or nutrients results in increased biomass with more devoted to the aboveground component.

In nature, environmental factors that are not essential for growth can mediate the results of competition between organisms for limited resources. The *Thalassia testudinum* canopy reduces light to levels limiting to *Syringodium filiforme* photosynthesis but protects *S. filiforme* leaves from breaking. Short, broken leaves were associated with decreased shoot density, perhaps reflecting a cost in terms of reduced photosynthetic area or increased respiration after wounding. I could not separate the effects of increased water motion or exposure to herbivory on rates of leaf breakage following removal of the *T. testudinum* canopy.

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