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Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*

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Abstract

In this study, we experimentally investigate the interspecific interactions operating between the dominant seagrass and an abundant, native rhizophytic macroalga within a mature seagrass community. Treatments consisted of density manipulations of the dominant seagrass species, *Thalassia testudinum*, and of the most common representative of the rhizophytic algae, *Halimeda incrassata*. Evidence of interaction was measured by changes in relative short-term productivity and biomass of both algae and seagrass over a 4-month period. There was an asymmetrical effect of density manipulation: the presence of seagrass decreased the size of algal thalli by 20.4% and the macroalgal growth rate by 33.3%, but the presence of macroalgae had no significant impact on seagrass growth rate and decreased the mean size of short-shoots of *T. testudinum* by only 10.3%. These results support a competitive interaction theory for *T. testudinum* and rhizophytic macroalgae. Nutrient and light limitation were investigated as possible underlying mechanisms of the interaction. Seagrass leaf tissue C:N was significantly lower ($P = 0.06$) in algal removal treatments whereas no significant treatment effect was demonstrated for substrate-level irradiance, suggesting that competition for N was the mechanism of the interaction.

Keywords: Caulerpales; Competition; *Halimeda incrassata*; Productivity; Seagrass; *Thalassia testudinum*

1. Introduction

Rhizophytic macroalgae of the order Caulerpales make up a substantial component of the dominant macrophyte communities forming tropical seagrass meadows. These are the predominate macroalgal species capable of colonizing the unconsolidated sediments that

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seagrasses occupy. Although possible mechanisms of interaction between these macroalgae and seagrasses have been suggested in the literature (den Hartog, 1971; Patriquin, 1975; McRoy and Lloyd, 1981; Zieman, 1982; South, 1983; Multer, 1988; Williams, 1985, 1988; Ceccherelli and Cinelli, 1997), attempts at field experimentation or observational analysis concerning possible interactions are limited. Williams (1990) suggested a possible facilitative interaction in early succession, as macroalgal removal slowed recolonization of neotropical seagrass beds. She also demonstrated a decline in macroalgal densities as seagrasses became re-established, lending indirect evidence toward a development of competitive interactions later in the successional sequence. South (1983) and Multer (1988) observed the highest rhizophytic macroalgal productivities in areas of low to medium seagrass densities, lending additional indirect evidence of competition. It is possible that rooted seagrasses and rhizophytic macroalgae could be competing for either light or nutrients: they both rely on downwelling light, and they both potentially have access to nutrient sources both in the water column and sediment. In a manipulative experiment, Ceccherelli and Cinelli (1997) demonstrated that the invasive exotic macroalga *Caulerpa taxifolia* has a negative impact on the density of seagrasses in the Mediterranean, and suggested that this impact was due to competition for below-ground nutrients.

This study attempts to determine whether a competitive interaction exists between neotropical seagrasses and native rhizophytic macroalgae through experimental manipulation of species densities within a mature seagrass community. For the experimental analysis of seagrass and rhizophytic macroalgal interaction, it was necessary to select representative species from each group. We chose to use *Halimeda incrassata* Lamouroux as a representative of the rhizophytic macroalgae for a number of reasons. First, during a preliminary analysis, we found that this species recovered well after transplantation. In addition, new growth over time was easier to measure relative to other rhizophytic macroalgae. Most importantly, *H. incrassata* is the most abundant representative of the rhizophytic green algal species found within our study area and many other tropical seagrass systems (Multer, 1988; Williams, 1990; Freile and Hillis, 1997). We were also primarily interested in *Thalassia testudinum* Banks ex König, as it is the most abundant neotropical seagrass species and is usually considered the dominant primary producer in late-successional or climax seagrass communities (den Hartog, 1971).

Marked differences in morphology and life histories of *H. incrassata* and *T. testudinum* may have been produced by evolutionary trade-offs in colonization potential, longevity, and competitive ability (Tilman, 1994), which may be important when considering potential interspecific interactions. *T. testudinum* expands horizontally using rhizomes, producing root bundles and lateral buds at regular intervals. The buds become vertical short-shoots with photosynthetic foliage leaves that usually reach heights of 10–25 cm. Rhizomes are found buried 5–25 cm in the sediment. Horizontal rhizome expansion occurs via apical meristems, and branches may occur from vertical shoots (Tomlinson and Vargo, 1966). *T. testudinum* has relatively slower growth, greater longevity (Gallegos et al., 1993) and lower reproductive investment (reviewed in Moffler and Durako, 1987) than *H. incrassata*.

Rhizophytic macroalgae anchor themselves in the sediment with a rhizoid bulb. Interwoven, coenocytic filaments make up an erect thallus that is photosynthetic to varying degrees and supports a photosynthetic frond. Most of the rhizophytic macroalgae secrete a calcareous outer layer, which may comprise 20–90% of its total dry weight (Bach, 1979; Multer,

1988). The macroalgal species are considered pioneers of the successional sequence (den Hartog, 1971; Zieman, 1982), with rapid turnover rates (Wefer, 1980; Freile and Hillis, 1997), shorter longevities (Bach, 1979), and greater investments in reproduction (Clifton, 1997). *H. incrassata* has a thallus supported by a rhizoid bulb that is buried within the sediment. Branches from the thallus are made up of thin, photosynthetic, calcified segments linked together by small, non-calcified joints.

Based on the indirect evidence of competitive interactions between rhizophytic macroalgae and seagrasses found in the literature, we hypothesized that these species would compete for resources (nutrients and light) within mature seagrass communities. It has been argued that competitive ability is greater in late successional species than early successional species (e.g. Connell and Slatyer, 1977; Tilman, 1994). We can therefore predict that the effect of the presence of seagrasses (the late successional species) on macroalgae (the early successional species) will be greater than the effect of macroalgae on seagrass. Such asymmetries in competitive interactions are quite common (Connell, 1983; Schoener, 1983).

We tested these hypotheses by measuring growth responses of the macroalga and seagrass relative to density manipulation treatments. Seagrass average size and growth rates were expected to decline in algal addition plots relative to algal removal plots; while the average size and growth rates of the macroalga were expected to increase in seagrass removal plots relative to controls. We also measured changes in light availability and nutrient content of the seagrasses as potential indicators of the mechanism underlying any competitive interaction.

2. Study area and methods

2.1. Study area

The seagrass meadow studied was within John Pennekamp Coral Reef State Park, approximately 5 km offshore of north Key Largo in the upper Florida Keys and 3 km inshore of the main reef tract (ca. 25°10′N, 80°17′W). The water was 7 m deep. The site was selected based on high densities of *H. incrassata*, the presence of *T. testudinum*, and low densities of other species encountered. The seagrass bed was dominated by *T. testudinum*, with densities of 400–800 short-shoots (SS) m^{-2}. The average height of the seagrass canopy was 18.3 cm. Seagrass cover, as defined by the proportion of the substratum obscured by seagrass blades when viewed from directly above, was less than 50%. *H. incrassata* was by far the most abundant rhizophytic macroalgal species, with a mean density of 100 thalli m^{-2}. The average height of *H. incrassata* plants was 14.9 cm, similar to the seagrass canopy height. *Halimeda monile* was common, with an average density of 24 thalli m^{-2}. Densities of other macroalgal species were negligible.

2.2. Experimental treatments

We measured short-term changes in growth rate and biomass during three sampling events, over a 4-month period. Treatments consisted of: (1) the complete removal of *H. incrassata*; (2) the doubling of the average density of *H. incrassata*; (3) the complete removal of *T. testudinum*; and (4) control quadrats. Additions of *T. testudinum* were not attempted due

to the difficulties involved in transplanting this more structurally complex species. Manipulations were performed within 0.25 m^2 quadrats made from PVC tubing. The quadrats were laid out in a 6×6 grid, with approximately 1.5 m of separation between quadrats. Treatments were randomly assigned to quadrats in this grid, and each quadrat was sampled only once during the experiment. In control and seagrass removal quadrats, densities of *H. incrassata* were 25 thalli per 0.25 m^2 plot, the average density of this species in the surrounding seagrass beds. In algae removal plots, rhizoid bulbs and the thalli of *H. incrassata* were gently removed from the sediment and discarded. Any other non-epiphytic macroalgae found within the quadrats were also removed. For seagrass removal plots, vertical short-shoots were plucked from the horizontal rhizomes, which were left in place in order to minimize disturbance to the plot. Manual manipulation of the sediment was done in other plots to mimic the sediment disturbance caused by seagrass and algal removal. A keyhole saw was used to cut 50 cm into the substratum around the perimeter of all quadrats in order to sever seagrass rhizome connections to short-shoots outside the quadrats, eliminating any possible nutrient translocation into or out of the quadrats. For the *H. incrassata* density-doubling treatment, intact plants (rhizoid mass and thallus) of average height ($\sim$15 cm) were transplanted into each quadrat from the immediate area, producing a total density of 50 thalli per 0.25 m^2 plot.

2.3. Productivity measurement techniques

To measure the short-term production rates of the seagrasses and algae simultaneously, we used two established techniques to measure new growth over time by creating a marker that separates new growth from previously existing biomass. First, we used Zieman's (1974) leaf-punching technique to mark the existing seagrass leaves at their base with a needle. The leaves were harvested after a period of 7–9 days. Because leaf growth of seagrasses is basal, all new growth was formed under the marking scar and could easily be separated from previously existing leaf material.

A similar marking technique was used for calcareous macroalgae that utilized the incorporation of a stain, Alizarin Red S, into the calcium carbonate shell (Wefer, 1980; Multer, 1988; Freile and Hillis, 1997). The stain is incorporated into the living plants as a consequence of calcification, staining the algae pink-red. Algal growth subsequent to the dye marking adds new white $CaCO_3$ material distal to the stained carbonate skeleton. After a period of growth, the algae were then harvested and bleached with a dilute sodium hypochlorite solution. Each alga's old skeleton is stained pink or red, and all new growth is white. In the experiment, new growth was quantified by dry weight of new segments. Any possible but unquantified effect of staining on growth rate would not effect the interpretation of our results since stained plants were used to assess growth in all treatments. In a preliminary experiment, we measured the effect of transplantation on the growth rate of *H. incrassata*. Immediately after transplanting, growth rates were depressed (1.56 ± 0.87 mg per thallus per day compared to 7.32 ± 2.23 mg per thallus per day for unmanipulated plants). One week after transplanting, there was no difference between the growth rate of transplants (9.04 ± 2.84 mg per thallus per day) and unmanipulated plants (ANOVA, post-hoc test, $P > 0.05$).

We randomly collected 45 thalli of *H. incrassata* in the neighboring area for measurement of organic matter content of the calcified segments. These were cleaned by hand, rinsed,

dried and weighed for total dry weight, and subsequently ashed for 3 h at 500°C. The ash weight is equal to the dry weight of the calcium carbonate shell. Organic content of the algae was determined by subtracting the ash weight from the dry weight.

2.4. Sampling methodology

The study ran from July through November, 1997, with three sampling events: initially, after 2 months, and after 4 months. The first sampling event took place 1 day after the site establishment. During each sampling event, the same sequence of work took place. First, the macroalgae in three replicate quadrats of algal doubling, seagrass removal and control quadrats were covered with weighted, clear plastic 240 ml cups. These were injected with 20 ml of a solution of 5 g Alizarin Red S dissolved in 1 l distilled water (the stain does not dissolve well in salt water, so a minimal volume of distilled water was injected into each cup). After 24 h, the cups were removed. Next, all of the seagrass short-shoots within two 10 cm × 20 cm subquadrats were marked within the same three replicate algal doubling and control quadrats, and in three replicate algal removal quadrats. The macroalgae and seagrasses were left to grow over the following 7–9 days. During harvesting, all biomass was collected from within each quadrat in order to determine average above-ground dry weights of seagrasses and macroalgae. Algal growth and biomass measures were not taken from algal doubling plots during the initial sampling event because of the transient effect of transplanting on algal growth rate. Each quadrat was sampled only once during the experiment, since biomass and productivity measurements required destructive sampling.

In order to measure possible mechanisms of the interaction, we sacrificed five shoots of *T. testudinum* from all quadrats (excluding seagrass removal quadrats) during the sampling event for each quadrat. All leaves collected from a quadrat were pooled, ground to a fine powder and analyzed for tissue carbon:nitrogen:phosphorus as an assay for N and P availability (Fourqurean et al., 1992, 1997) using a Fisons 1500 CN analyzer for C and N and a dry oxidation, acid hydrolysis method for P content (Fourqurean et al., 1992). In addition, we used a 4π quantum light sensor to measure the percent of canopy-level irradiance reaching the substratum for each treatment. We sampled three quadrats of each treatment, and took four measures of canopy and substrate-level irradiance over 15 s intervals for each quadrat.

2.5. Statistical analyses

Treatment and event effects on seagrass leaf biomass and production rate were assessed with analysis of variance, with the treatment factor having the levels of algal removal, Algal Addition, and control; and the sampling event factor having the levels of 0, 2, and 4 months. Because algal growth and mass measures were not collected within algal addition plots within the first sampling event, we used analysis of variance to test for significant changes in masses or growth rates of *H. incrassata*; with the treatment factor having the levels of seagrass removal and control, and the sampling event factor having the levels of 0, 2, and 4 months. An additional analysis of variance was used to test for significant changes in masses or growth rates of *H. incrassata* for the second and third sampling events; with the treatment factor having the levels of seagrass removal, algal addition, and controls,

and the sampling event factor having the levels of 2 and 4 months. Seagrass leaf tissue C:N and C:P were also tested for significant treatment and event effects using ANOVA. Substrate-level irradiance was tested for significant treatment effects only using a one-way ANOVA.

3. Results

3.1. Growth rates of T. testudinum and H. incrassata

Averaging across all treatments and collection times, *T. testudinum* had a mean production of 1.47 ± 0.09 (± 1 S.D.) mg (dry weight) per short-shoot per day over the course of the study. In contrast, *H. incrassata* had a much higher rate of addition of dry weight, averaging 7.73 ± 0.36 mg (dry weight) per thallus per day. Mass increments of *H. incrassata* include both production of new organic matter and calcium carbonate shell; we found that newly-produced *H. incrassata* segments from this area to be $80.6 \pm 0.5\%$ $CaCO_3$. Based on this, the net above-ground organic production of *H. incrassata* averaged 1.50 ± 0.07 mg (organic matter) per thallus per day over the course of the study, roughly equal to that of an individual short-shoot of *T. testudinum*. Based on average densities within the study area (100 thalli m^{-2} for *H. incrassata* and 564 short-shoot m^{-2} for *T. testudinum*), the macroalga contributed approximately 150 mg (organic matter) m^{-2} per day compared to production rate of 829 mg m^{-2} per day for *T. testudinum*. The algal growth rates reported in all other figures and tables include calcium carbonate production; we did not test for treatment effects on the organic content of the algae.

3.2. H. incrassata response

The removal of seagrasses had a positive impact on sizes and growth rates of *H. incrassata.* Averaged across all three sampling events, mean individual dry weights of algal thalli were higher in seagrass removal plots (1.42 ± 0.06 g per thallus) compared to control plots (1.13 ± 0.05 g per thallus; Fig. 1; Table 1). There were no significant differences in the mean mass per thallus among sampling events when seagrass removal and control plots were averaged, and there were no significant treatment by event interactions (Table 1). Restricting the analyses to the September and November sampling events when data from Algal Addition plots were available resulted in the same pattern: there was a significant treatment effect (Table 1), with event-averaged means of 1.59 ± 0.08, 1.32 ± 0.06 and 1.10 ± 0.05 g per thallus for seagrass removals, algal additions, and controls, respectively. There were no differences in the mean mass per thallus between sampling events, nor were there significant interactions between treatment and event (Table 1).

Seagrass removal also led to an increase in the growth rate of *H. incrassata*. There was a significant treatment main effect in the ANOVA (Table 1): thallus-specific mean growth rates for seagrass removal plots was 10.5 ± 2.0 mg per day per thallus, compared to 7.0 ± 0.7 mg per day per thallus in control plots (Fig. 2). Growth rate decreased throughout the study period, with significantly higher growth in July (12.3 ± 1.1 mg per day per thallus averaging

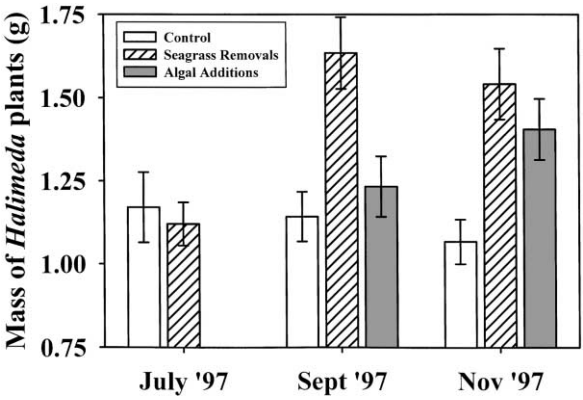

Fig. 1. Mass of thalli of *H. incrassata* (g (dry weight) per thallus) as a function of sampling event (July, September and November, 1997) and treatment (control, seagrass removal and algal addition). Bars are means, error bars represent 1 standard error, $n = 3$.

across treatments) than in September and November (6.5 ± 0.4 and 7.4 ± 0.7 mg per day per thallus, respectively). There was also a significant treatment effect when algal addition data were included in the analysis (Table 1). Growth rates in the seagrass removal plots (9.0 ± 0.6 mg per day per thallus) were higher than in algal addition or control plots, but there was no consistent pattern in the relative growth rates of algal addition and control plots (5.4 ± 0.4 and 4.9 ± 0.4 mg per day per thallus, respectively). September growth rates were significantly lower than November growth rates, averaging 5.4 ± 0.3 and 7.4 ± 0.5 mg per day per thallus, respectively (event main effect, Table 1).

Table 1
The effects of manipulation of seagrass and algal density on thallus size and growth rate of *H. incrassata*[a]

Source of variance	2 Treatments × 3 events				3 Treatments × 2 events			
	Mean squares	d.f.	*F*	*P*	Mean squares	d.f.	*F*	*P*
Mass of *H. incrassata* plants								
Treatment	**0.42**	**1**	**7.49**	**0.02**	**0.35**	**2**	**4.79**	**0.03**
Sampling event	0.09	2	1.63	0.24	0.00	1	0.00	0.99
Treatment × event	0.14	2	2.54	0.12	0.03	2	0.45	0.65
Error	0.06	12			0.07	12		
Growth rate of *H. incrassata*								
Treatment	**53.5**	**1**	**4.80**	**0.05**	**30.4**	**2**	**10.37**	**0.002**
Sampling event	**59.2**	**2**	**5.31**	**0.02**	**17.9**	**1**	**6.10**	**0.03**
Treatment × event	3.8	2	0.34	0.72	7.7	2	2.63	0.11
Error	11.1	12			2.9	12		

[a] Treatments were controls, seagrass removals and algal additions, sampling events were July, September and November 1997. Because Algal Addition plots were not measured in July, two ANOVAs are presented for each dependent variable (thallus size and growth rate): one comparing means of controls and seagrass removals across all three sampling events, and one comparing means of all three treatments across the September and November sampling event. Significant effects are highlighted with bold type.

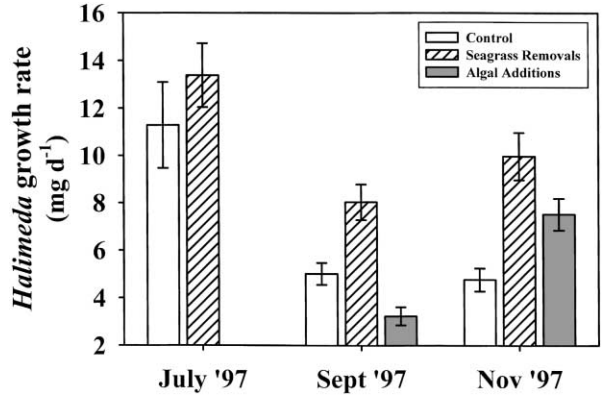

Fig. 2. Growth rate of *H. incrassata* (mg (dry weight) per thallus per day) as a function of sampling event (July, September and November, 1997) and treatment (control, seagrass removal and algal addition). Bars are means, error bars represent 1 standard error, $n = 3$.

3.3. *T. testudinum* response

The presence of *H. incrassata* significantly influenced the size of *T. testudinum* short-shoots (Fig. 3, Table 2), but not their growth rates. Averaging across sampling events, *T. testudinum* short-shoots were largest in algal removal plots (64 ± 14 mg (dry wt) per short-shoot), intermediate in control plots (58 ± 17 mg (dry wt) per short-shoot), and smallest in algal addition plots (49 ± 10 mg (dry wt) per short-shoot). There was also a significant variation in short-shoot size over time: short-shoots were smaller on average in November than July and September (event main effect, Table 2). There were no signif-

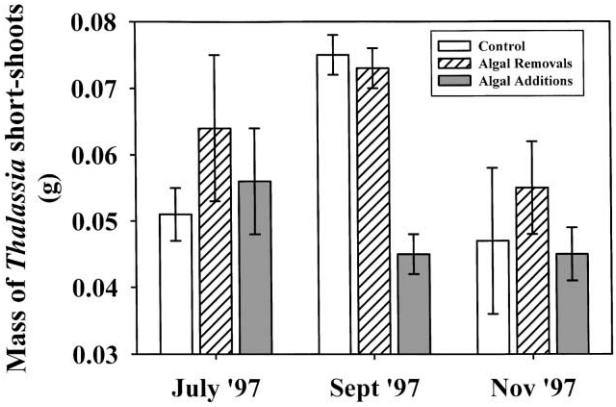

Fig. 3. Mass of short-shoots of *T. testudinum* (g (dry weight) per short-shoot) as a function of sampling event (July, September and November, 1997) and treatment (control, algal removal and algal addition). Bars are means, error bars represent 1 standard error, $n = 3$.

Table 2
ANOVA results for the effects of manipulation of algal density on mass of *T. testudinum* short-shoots and growth rate treatment[a]

Source of variance	Mean squares	d.f.	*F*	*P*
Mass of *T. testudinum* short-shoots				
Treatment	**0.001**	**2**	**3.97**	**0.04**
Sampling event	**0.001**	**2**	**3.71**	**0.05**
Treatment × event	0.000	4	2.05	0.13
Error	0.000	18		
Growth rate of *T. testudinum*				
Treatment	0.12	2	1.12	0.35
Sampling event	**1.35**	**2**	**12.49**	**<0.001**
Treatment × event	0.07	4	0.62	0.66
Error	0.11	18		

[a] Treatments were control, algal removal and algal addition; and sampling events were July, September and November 1997. Significant effects are highlighted with bold type.

icant effects of manipulation of algal densities on growth rates of *T. testudinum* (Fig. 4, Table 2). Short-shoots grew at a rate between 1 and 2 mg (dry wt) per short-shoot per day, or 0.3–0.6 cm^2 per short-shoot per day, without regard to the algal density. Growth rates differed between sampling events; the rates declined from summertime highs in July to lower autumnal rates in September and November (event main effect, Table 2).

3.4. Possible mechanisms of interaction

We could detect no differences in the amount of light reaching the sediment surface as a function of treatment (ANOVA, $F = 1.34$, $P = 0.28$). Mean substrate-level irradiance

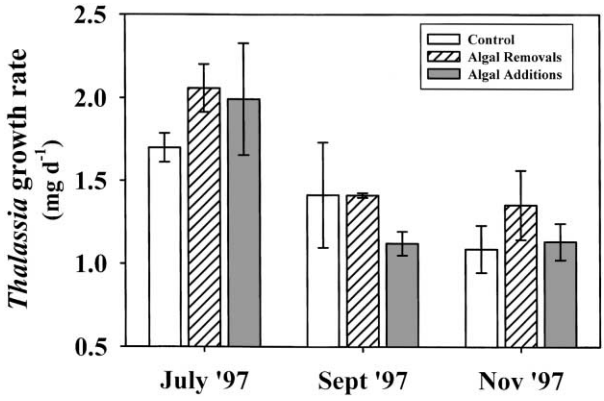

Fig. 4. Growth rate of *T. testudinum* (mg (dry weight) per short-shoot per day) as a function of sampling event (July, September and November, 1997) and treatment (control, algal removal and algal addition). Bars are means, error bars represent 1 standard error, $n = 3$.

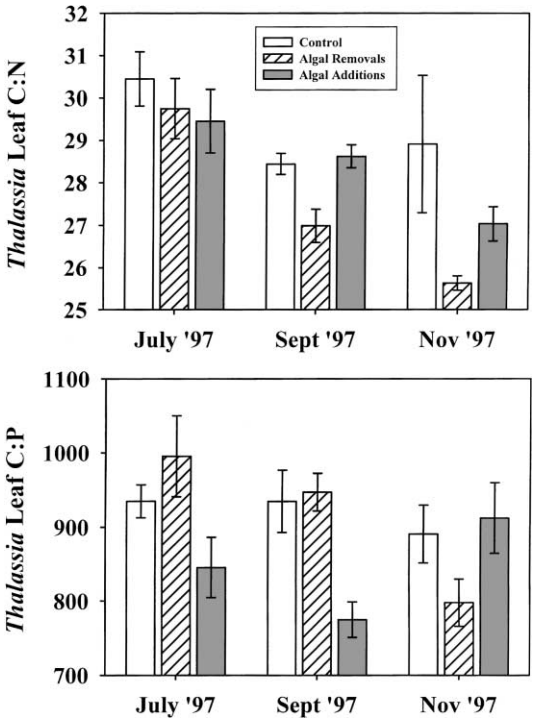

Fig. 5. Nutrient content of leaves of *T. testudinum* as a function of sampling event (July, September and November, 1997) and treatment (control, algal removal and algal addition). Bars are means, error bars represent 1 standard error, $n = 3$. Top: C:N (mol:mol) of green leaves. Bottom: C:P (mol:mol) of green leaves.

Table 3
ANOVA results for the effects of treatment (control, algal removal and algal addition) and sampling event (July, September and November) on nitrogen and phosphorus content of leaves of the seagrass *T. testudinum*[a]

Source of variance	Mean squares	d.f.	*F*	*P*
C:N ratio				
Treatment	**7.48**	**2**	**3.26**	**0.06**
Sampling event	**17.24**	**2**	**7.52**	**0.004**
Treatment × event	1.96	4	0.86	0.51
Error	2.29	18		
C:P Ratio				
Treatment	15942	2	2.48	0.11
Sampling event	8057	2	1.25	0.31
Treatment × event	**19993**	**4**	**3.10**	**0.04**
Error	6446	18		

[a] Significant effects are highlighted with bold type.

for algal removals, algal additions, seagrass removals, and controls was 93.1 ± 4.7%, 94.6 ± 5.5%, 99.7 ± 2.1%, and 83.7 ± 8.7% of the canopy-level irradiance, respectively. There was very little change in extinction of light with the plant canopy, because our study area naturally has a quite sparse seagrass–algal community (cover less than 50%). Our density manipulations did not apparently effect the light availability for the seagrasses and macroalgae.

In contrast, our manipulations did effect the nutrient content of the seagrass (Fig. 5). Averaged across all sampling events, leaf tissue C:N was significantly lower in algal removal plots (Table 3). Mean leaf tissue C:N ratios for algal removals, algal additions, and controls were 27.5±0.5, 28.4±0.3, and 29.2±0.5, respectively (Fig. 5). C:N significantly decreased from July to November (event main effect, $F = 7.52$, $P < 0.01$, Table 3); July, September, and November ratios averaged 29.9 ± 0.3, 28.0 ± 0.9, and 27.2 ± 0.5, respectively. There was no significant treatment or event effect on C:P of seagrass leaves (Fig. 5, Table 3).

4. Discussion

We interpret our results as indicating that seagrasses and rhizophytic macroalgae compete for nutrients in south Florida. Removal of seagrass competitors caused greater growth rates and an increase in the size of individual thalli of *H. incrassata*. Similarly, removal of *H. incrassata* led to an increase in the size of short-shoots of the seagrass *T. testudinum*, although there was no statistically significant increase in seagrass growth rate in response to algal removal. We ruled out competition for light as the mechanism of this interaction, because treatments did not significantly change the amount of light available to the plants. Algal removal did lead to an increase in the N content (decrease in C:N), but not a change in P content, of seagrass leaves, suggesting release from competition for N was responsible for the observed treatment effects. Our results also suggest, at least at the nutrient availability and light climate at our study site, that the presence of seagrass had a more pronounced effect on macroalgae than the presence of macroalgae had on seagrass.

Seagrass and algal growth rates we measured were consistent with those reported in the literature (Wefer, 1980; Zieman et al., 1989; Williams, 1990; Gallegos et al., 1993, 1994). A seasonal effect on plant growth rates was evident in the data (Figs. 2 and 4). Algal growth rates were significantly higher in July than in the following months. Seagrass production rates were significantly higher in July as well. The single macroalga *H. incrassata* contributed a significant portion of the benthic primary production in the area; in the study area *H. incrassata* produced about 20% of the leaf production of *T. testudinum*. *H. incrassata* is but one of many species of macroalgae, rhizophytic and otherwise, that contribute primary production in this region; it is likely that in total the macroalgae approach the seagrasses in importance to primary production in south Florida. While the organic production of *H. incrassata* is significant, it is important to recognize that 80% of the dry weight produced is inorganic carbonate. Using the mean production value per thallus, multiplying by carbonate content and thallus density yields an estimate of carbonate production of ca. 225 g m^{-2} per year. Carbonate production by *Halimeda* has been estimated to range between 23 g m^{-2} per year on a backreef carbonate mound in the Florida Keys (Bosence et al., 1985) to 1 kg m^{-2} per year in the Marquesas Keys, ca. 200 km SW of our study site (Hudson, 1985).

The differing life history strategies of rhizophytic macroalgae and *T. testudinum* result in differing roles in the successional development of neotropical seagrass beds. Following a disturbance that removes a *T. testudinum*-dominated seagrass bed, rhizophytic macroalgae are usually the first colonizers (den Hartog, 1971; Patriquin, 1975). After *T. testudinum* colonization of a disturbed area, the abundance of rhizophytic macroalgae decreases (Williams, 1990). We have provided direct evidence that *T. testudinum* and one species of rhizophytic macroalgae do compete. It is likely that competition is the mechanism responsible for the decrease in the density of rhizophytic macroalgae during secondary successional sequences in neotropical seagrass beds. As noted by Williams (1990), however, complete competitive displacement of macroalgae by *T. testudinum* does not always occur; either small-scale disturbances or differing resource requirement ratios may lead to the stable coexistence of macroalgae within seagrass beds.

The presence of seagrass decreased the size of algal thalli by 20.4% and the macroalgal growth rate by 33.3% (Figs. 1 and 2), but the presence of macroalgae had no statistically significant impact on seagrass growth rate and decreased the mean size of short-shoots of *T. testudinum* by only 10.3% (Figs. 3 and 4). Such an asymmetry in relative effects was expected, because it was assumed that *T. testudinum*, the late successional species, was the competitive dominant over *H. incrassata*, the early successional species, at least under the resource availability conditions at our study site. Under different conditions, it is quite likely that the hierarchy of dominance could reverse. In contrast to our finding of competitive dominance of *T. testudinum* over *H. incrassata* under ambient nutrient conditions, the introduced alga *C. taxifolia* is the competitive dominant over the native seagrass *Cymodocea nodosa* under nutrient-enriched conditions in the Mediterranean (Ceccherlli and Cinelli, 1997). It is possible that an increase in nutrient availability in our system would also reverse the competitive hierarchy, so that the faster-growing *H. incrassata* would outcompete the slower-growing *T. testudinum* in a manner similar to the competitive displacement of *T. testudinum* by the early succesional seagrass species *Halodule wrightii* under conditions of nutrient enrichment (Fourqurean et al., 1995).

Three possible mechanisms may explain the observed significant increase in the size of short-shoots of *T. testudinum* in the algal removal treatment with no significant increase in the growth rate. The most likely explanation is that the size of the short-shoots is the result of a long-term integration of the growth rate and leaf loss rate, while the growth rates were measured for relatively short periods (7–9 days). Small differences in growth rate among treatments could be undetectable with our statistical power, but may have led to differences in the size of the short-shoots after 2 months. Alternatively, algal removal could have decreased the loss rate of seagrass leaves, perhaps by changing the rate of herbivory on the leaves, which we did not measure. Finally, it is also possible that our growth rate measurements missed the period of peak growth that led to different sizes. The asymmetrical nature of the competitive interaction — algae affected seagrass less than seagrass affected algae — is evident in the non-significant differences in seagrass growth rates among treatments. Were the effect of algae on seagrasses greater, we would have expected that seagrass growth rate and short-shoot size would be lower in algal additions, intermediate in controls, and highest in algal removals.

It was curious that we did not measure any effect of algal density manipulations on algal size (Fig. 1) or growth rate (Fig. 2). If intraspecific competition were important in the *H.*

incrassata population, we would expect that both average size and growth rate in the algal doubling treatment would be less than the control treatment, but this was not the case. This may mean that the resource availability to *H. incrassata* was not drawn below a critical level (*sensu* Tilman, 1982) by additional thalli, hence there was effectively no intraspecific competition at the densities created with the algal doubling treatment. Further, algal density doubling did not lower the growth rate or average size of seagrass below the levels of the controls (Figs. 3 and 4), further suggesting that added thalli did little to alter resource availability. It is possible that the thalli transplanted to algal Addition plots did not act as functional equivalents to non-transplanted thalli, perhaps because of disturbance to the rhizoid bulb that could have prevented it from functioning as a nutrient gathering structure. However, since the transplanted thalli survived for the 4 months of the experiment and had growth rates identical to non-transplanted thalli (see Section 2.3), any artifact caused by the transplanting appears to have been small.

The study area was a seagrass meadow of medium seagrass and algal densities. We expect the effects of resource competition to weaken in areas of lower densities, where levels of stress may be more important than resource availability (Grime, 1979). Interspecific interactions likely have lesser effects in areas of higher seagrass or macroalgal densities as well, where *intraspecific* competition may take on more importance (Rose and Dawes, 1999).

We considered two possible mechanisms of the competitive interaction: nutrient and light limitation. Leaf tissue C:N was significantly lower in algal removal plots at $P = 0.061$, indicating an increase in nitrogen availability to the seagrass when algae were removed. There was no effect on the C:P, however, indicating that N has a more important role than P in controlling seagrass biomass at our study area. There was no increase in C:N of seagrass leaves associated with algal additions. Light was not demonstrated to significantly increase in seagrass removal plots; however, there was low power in the statistical analysis because of the few replicates (3) per treatment. Light availability and leaf tissue C:N vary seasonally, and are interrelated. Light availability was not measured over time within this study, but from the seasonal growth response in both species we assume that light availability decreased over the course of the study. Leaf tissue C:N tends to peak in the summer months as high productivity results in nutrient depletion (Fourqurean et al., 1997), corresponding with its covariance with light availability. As light availability increases, leaf tissue nitrogen concentrations decrease as the nitrogen becomes more limiting (Abal et al., 1994; Rose and Dawes, 1999). In agreement with these findings, C:N decreased significantly over the course of the study.

Nutrient uptake and translocation in both seagrasses and rhizophytic macroalgae is not yet fully understood, particularly in reference to the relative importance of sediment versus water column sources. Although early work (Patriquin, 1972; Williams, 1990) suggested that *T. testudinum* utilized only sediment nutrient sources, recent work has shown that up to 50% of the N uptake may come from the water column (Lee and Dunton, 1999). Most marine algae take up nutrients entirely from the water column and have no root-like structures within the sediment, rather they utilize small holdfasts to hard substrates or drift freely. However, Williams (1984) found that the rhizophytic algal species *H. incrassata*, *H. monile*, and *Penicillus capitatus* were capable of translocating porewater nutrients from rhizoids into the thallus. Relative resource requirements of individual seagrass shoots and

macroalgae have not yet been documented. Our results indicate that there is competition for nutrients, specifically nitrogen, between macroalgae and seagrasses. This would indicate that both are relying on nutrient resources from the same pool.

A negative impact of one species on another's ecological fitness may also occur without a direct competitive interaction. One species may affect the resource acquisition capacity of another, or affect some system-level "bottom-up" or "top-down" control that acts independently of growth resources (apparent competition, see Connell, 1990). In a system where top-down control mechanisms can be important in dictating community composition, changes in herbivory rates relative to the presence or absence of a species could appear as a competitive interaction. For example, in seagrass removal plots, herbivorous fishes may feed less on macroalgae because of limited protective cover of seagrass blades. This could result in increased growth or biomass of algal samples in seagrass removal treatments, and could then be mis-labeled "competition". Grazing on calcified macroalgae like *H. incrassata* is thought to be low, however, because calcification makes them largely unpalatable to herbivorous fishes and they are also known to produce secondary metabolites as chemical defense (Paul and Hay, 1986). Conversely, grazing can be an important loss of biomass for seagrasses (Valentine and Heck, 1999). Because the present study did not investigate the effects of species removals on herbivory rates, we cannot dismiss the potential importance of such top–down effects.

Our simple experimental design precludes a more detailed analysis of the relative effects of intraspecific and interspecific competition in this system. In our algal addition experiments, we have applied an additive design (*sensu* Snaydon, 1991). Such a design is useful for examining interspecific competition, but leaves unexplored questions of the relative magnitude of intra- and interspecific interactions (Sackville Hamilton, 1994). Because of our abbreviated design, we have not attempted to measure relative competitive intensity (see Freckleton and Watkinson, 1997) in our study. Rather, we have simply interpreted the fact that the magnitude of the change in macroalgal size and growth rate caused by seagrass removal was greater than the magnitude of the change in seagrass size and growth rate caused by algal density manipulations to suggest that *T. testudinum* is a superior competitor in the environment of our experiments.

In this paper, we have provided direct experimental evidence of a competitive interaction between the dominant macrophyte in stable seagrass beds in the Caribbean, the seagrass *T. testudinum*, and a common species of rhizophytic algae, *H. incrassata*. This interaction may explain the observed decrease in the relative abundance of rhizophytic macroalga in the recovery of seagrass beds from disturbance. Further, our proxy indicator of nutrient availability, the nutrient content of seagrass leaves, suggested that the mechanisms of this interaction was competition between the seagrass and the macroalga for nitrogen. This result suggests that the seagrass and the macroalga are both reliant on the same nutrient pools to meet their nutrient demands.

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