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The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay

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Long term (8 yr) continuous fertilization (via application of bird feces) of established seagrass beds in Florida Bay, FL, USA caused a change in the dominant seagrass species. Before fertilization, the seagrass beds were a *Thalassia testudinum* monoculture; after 8 yr of fertilization the seagrass *Halodule wrightii* made up 97% of the aboveground biomass. Fertilization had a positive effect on the standing crop of *T. testudinum* for the first two years of the experiment. The transition from *T. testudinum*-dominated to *H. wrightii*-dominated was dependent on the timing of colonization of the sites by *H. wrightii*; the decrease in *T. testudinum* standing crop and density at the fertilized sites occurred only after the colonization of the sites by *H. wrightii*. There were no trends in the standing crop or density of *T. testudinum* at control sites, and none of the control sites were colonized by *H. wrightii*. The effects of fertilization on these seagrass beds persisted at least 8 yr after the cessation of nutrient addition, suggesting that these systems retain and recycle acquired nutrients efficiently.

Results of these experiments suggest that *Halodule wrightii*, the normal early-successional seagrass during secondary succession in Caribbean seagrass communities, has a higher nutrient demand than *Thalassia testudinum*, the normal late successional species, and that the replacement of *H. wrightii* by *T. testudinum* during secondary succession is due to the ability of *T. testudinum* to draw nutrient availability below the requirements of *H. wrightii*.

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Species composition of plant communities is dependent on a number of factors, including prevailing resource supply rates, the length of time since the last disturbance (successional state), the historical make-up of the community, and the likelihood of colonization of the area by individual species (Harper 1977, Grime 1979, Tilman 1982, 1988). Given sufficient time for plant communities

to reach equilibrium following a disturbance, resource-based models of community structure predict that the species composition of the community will be determined by the resource supply rates to the community (Tilman 1982, 1985, 1988). A resource (sensu Tilman 1982) is any factor consumed by an organism that causes an increase in growth rate or survival. Using this defini-

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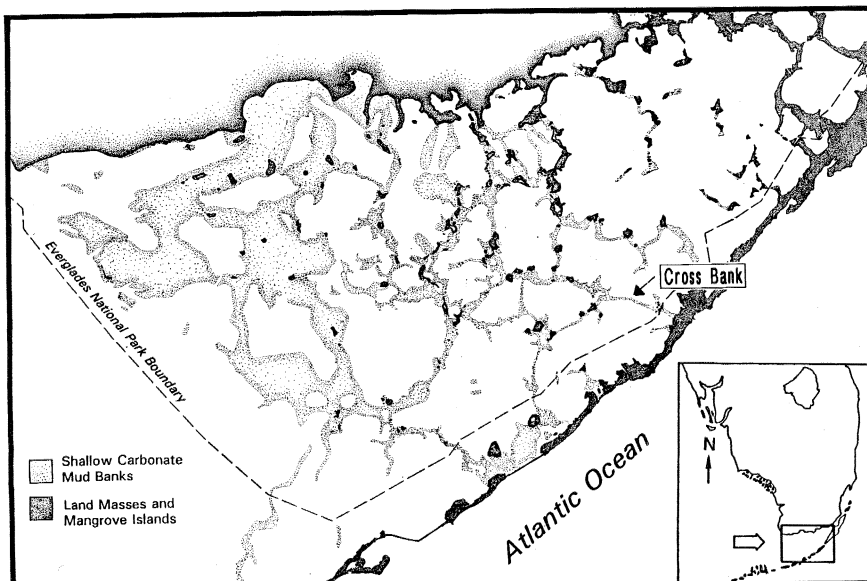


Fig. 1. Site map of Florida Bay.

tion, light, nutrients and water are resources, but factors such as temperature are not. This model explicitly considers trade-offs in the ability of plants to compete for resources in two realms: aboveground and belowground. Due to the limited energy available to a plant, allocation to gathering belowground soil nutrients and water must necessarily decrease the relative allocation to gather aboveground resources (e.g. light; for review see Chapin 1980).

The resource-ratio model predicts that availability of both soil nutrients and light exert a strong influence on the species composition of plant communities, and manipulations of the resource supply rates of either the above- or belowground resources may lead to changes in community composition. Addition of nutrients to a community composed of species with different aboveground/belowground resource acquisition strategies should favor species that have relatively less of their energy allocated to nutrient acquisition (and consequently more of their energy allocated to light gathering). Nutrient addition experiments provide a means for testing ecological theories concerning the effects of nutrient availability on community composition and successional development.

Seagrass meadows of the tropical western Atlantic provide an accessible system in which to test the resource-based model of ecological succession. The small number of seagrass species, the simplified successional sequence of these seagrass communities, and the strengths of environmental gradients in shallow marine systems, all are desirable features for testing model predictions on the roles of resource supply rates in structuring plant communities.

Seagrass communities in Florida Bay (Fig. 1) are strongly affected by the availability of nutrients. Development of seagrass meadows in northeast Florida Bay is

nutrient-limited; fertilization of the *Thalassia testudinum*-dominated seagrass meadows in northeast Florida Bay increases biomass of *T. testudinum* (Powell et al. 1989). The biomass of *T. testudinum* on a bay-wide scale is positively correlated with the concentration of dissolved inorganic phosphorus in the sediment porewater (Fourqurean et al. 1992a), and the observed increasing trend in biomass from northeast to southwest in Florida Bay is a direct result of the increase in P availability along the same transect (Fourqurean et al. 1992b).

Species composition of seagrass beds of Florida Bay also is correlated with nutrient availability. Zonation of species in relation to point sources of nutrients in otherwise oligotrophic northeast Florida Bay suggests that *Halodule wrightii* occurrence is correlated with areas of higher nutrient availability than *Thalassia testudinum* (Powell et al. 1991), and after four years of continuous fertilization of once-monospecific *T. testudinum* beds, *H. wrightii* colonizes the fertilized sites (Powell et al. 1991). Across the entire bay, areas that support *H. wrightii* have higher concentrations of dissolved inorganic P in the sedimentary porewater than areas that support only *T. testudinum* (Fourqurean et al. 1992a).

Why *Halodule wrightii* should be restricted to areas of high nutrient availability is not well understood, but it has been suggested that *H. wrightii* has a higher demand for nutrients than *Thalassia testudinum* (Fourqurean et al. 1992a). In most places in Florida Bay, *T. testudinum* is the competitive dominant; Zieman et al. (1989) state that *H. wrightii* is the dominant seagrass only in areas physically unsuitable for *T. testudinum*. In the secondary successional sequence in seagrass beds of south Florida and the Caribbean, *H. wrightii* is an early successional species and *T. testudinum* is a late successional species (see Zieman 1982 for review). The mechanism of the replace-

ment of *H. wrightii* by *T. testudinum* during the successional process has been speculated to be competition for light, with *T. testudinum* eventually overtopping *H. wrightii* due to its larger size. This proposed mechanism is unsatisfactory in Florida Bay, since the *T. testudinum* canopy that replaces *H. wrightii* is often thin and sparse, with small effects on the amount of light that reaches the sediment surface (pers. obs.). Further, *H. wrightii* is more shade-tolerant than *T. testudinum* (Wiginton and McMillan 1979, Iverson and Bittaker 1986), and *H. wrightii* exists in many locations as an understory in very dense seagrass beds (pers. obs.).

This paper presents the results of experimental manipulations of the nutrient supply to shallow water seagrass beds in Florida Bay. These experiments were designed to elucidate the mechanisms underlying the apparent competition between *Thalassia testudinum* and *Halodule wrightii*. Two types of manipulations were performed: 1) continuous fertilization of previously undisturbed, *T. testudinum*-dominated seagrass beds, and 2) cessation of fertilization of *H. wrightii*-dominated seagrass beds previously created by 28 months of continuous fertilization.

Methods

Experimental design

This study was conducted on Cross Bank, a shallow (< 30 cm deep), narrow (< 50 m wide) seagrass-covered carbonate mud bank in east-central Florida Bay (Fig. 1). In July 1981, location markers were placed at 100-m intervals along the center of Cross Bank as part of a separate study on feeding behavior of wading birds (Powell 1987). The markers were constructed of 1.5 m long, 1.2 cm diam. PVC pipe with a 5 cm × 10 cm × 10 cm block of wood on top. Once in place, these markers were heavily used as roosts by royal terns (*Sterna maxima*) and double-crested cormorants (*Phalacrocorax auritus*). By November 1983, a patch of unusually dense seagrass was evident around each location marker. At that time, we began our experiment to test the hypothesis that deposition of feces by the roosting seabirds was responsible for the observed increase in seagrass density around the markers. Five of the markers, spaced at 600-m intervals, were pushed down into the sediment so that birds could no longer roost on them, and a pair of new markers were placed 5 m on either side of the old marker. One of the new markers was identical to the old marker, while the other new marker was cut to a point to prevent birds from roosting. This design provided five sites, each with three treatments: 1) a control treatment, in which the pointed stake provided the same hydrological effects as the bird roost stake (CONT); 2) a fertilization treatment, where birds could roost on the marker and defecate into the water (FERT); and 3) a treatment in which 28 months of fertilization was discontinued where the markers had been pushed into the sediment (DISC).

Data collection

The species composition, leaf biomass and short shoot (SS) density of the seagrass bed around each control and fertilization treatment stake was measured when the experiment was begun, and in late October or early November for the next 8 yr. Short shoot density data were not collected in 1988. In 1987, 1989, 1990 and 1991, these same variables were measured at the markers where fertilization had been discontinued in 1983. For each sampling, 4 quadrats (10 cm × 10 cm) were placed within 50 cm of the marker stakes. The number of short shoots of each seagrass species were counted, and the seagrass leaf biomass within the quadrats was harvested. These leaves were separated by species, washed in 10% V/V HCl to remove epiphytes, and dried to a constant weight. Leaf biomass, commonly called standing crop in seagrass literature, and short shoot (SS) density, were expressed on a m⁻² basis.

Statistical analyses

The average value for the four quadrats from each stake were used in statistical analyses. Differences in the standing crop and short shoot density of seagrasses at control (CONT) and fertilized (FERT) stakes as a function of both treatment and time were assessed using mixed-model univariate repeated measures analysis of variance (Winer 1971) with treatment (CONT vs FERT) and year as within-subjects factors. Each pair of CONT and FERT stakes constituted a subject in these analyses. Five of these ANOVAs were run: one each for differences in short shoot densities of *Thalassia testudinum* and *Halodule wrightii*, differences in standing crop of both species, and differences in total seagrass standing crop.

The discontinuation of fertilization treatment (DISC) was not included in the above analyses since there were no measures made of the seagrasses around these stakes in the years 1983–1986 or 1988. Differences between years in the standing crop and short shoot density at these stakes were assessed with repeated measures ANOVA, with years as the within-subjects factor.

Results

Some results from the first four years of this experiment have been reported elsewhere (Powell et al. 1989, 1991). Marker stakes in the FERT treatment group hosted roosting birds 84% of the time; 0.68 g of nitrogen and 0.13 g of phosphorus were deposited daily as bird feces at each of these roost markers. From 1983–1987, this nutrient input caused increases in the leaf biomass and a change in the species composition of the seagrass meadows in 5.4 m × 2.6 m elliptical patches surrounding the roost marker stakes, while no trends occurred at the control

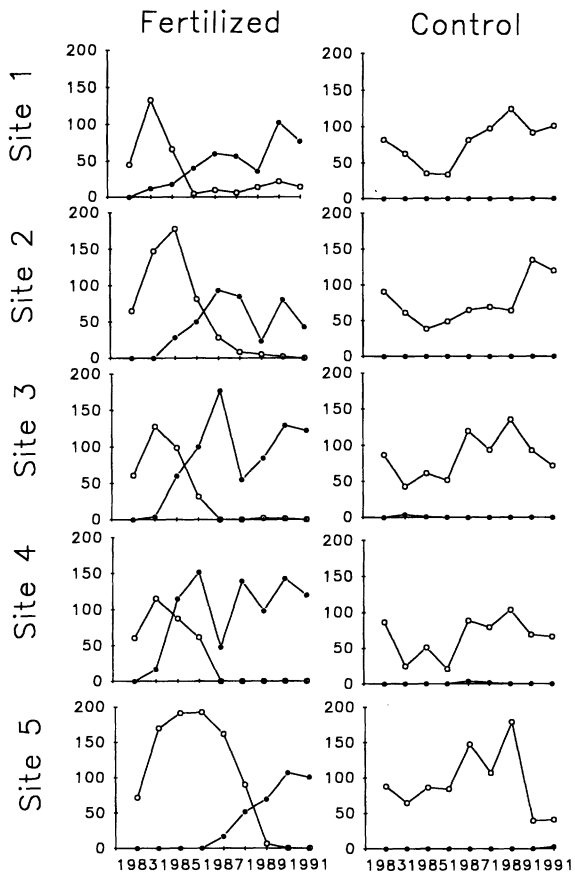


Fig. 2. Trajectories through time of the standing crop (in g(dry) m^{-2}) of *Thalassia testudinum* (open circles) and *Halodule wrightii* (filled circles) at the paired control and fertilized sites.

markers. The fertilization led to 20-fold increases in pore-water dissolved phosphate concentration, and a 6-fold increase in porewater ammonium. Water column nutrient concentrations were not different between FERT and CONT sites, owing to the flow of water past the sites.

After 8 yr of fertilization, the seagrass beds surrounding FERT stakes differed from CONT stakes. While there was no significant difference in the total standing crop of seagrass after the 8 yr, the species composition and the relative contributions of seagrass species to the total biomass of the beds was very different. Analysis of the seagrass bed composition around the DISC stakes showed that the differences in the seagrass beds caused by fertilization persisted until the end of the experiment in 1991, even in the absence of continued nutrient inputs.

Fertilized versus control treatments

The species composition of the seagrass beds changed markedly at the FERT sites when compared to the controls. At the beginning of the experiments in 1983, monospecific *Thalassia testudinum* meadows surrounded all of

the sites. Very small patches of *Halodule wrightii* grew elsewhere on Cross Bank, but none was within 10 m of our sites. In 1991, after 8 yr of fertilization, the seagrass beds at the FERT sites were dominated by *H. wrightii*, while *T. testudinum* remained the only seagrass species present at the CONT sites. In 1991, there were 860 ± 125 (± 1 SE) $SS\ m^{-2}$ of *T. testudinum* at the CONT stakes, compared with 40 ± 35 $SS\ m^{-2}$ at the FERT sites. *H. wrightii* densities were 6260 ± 319 $SS\ m^{-2}$ at FERT sites, and 90 ± 80 at the controls.

Annual trajectories of the standing crop of *Thalassia testudinum* and *Halodule wrightii* were site-specific (Fig. 2). At all of the FERT sites, *T. testudinum* standing crop increased in the first year. At the sites where *H. wrightii* became established in 1984 (sites 1, 3 and 4), *T. testudinum* standing crop decreased thereafter. At sites 2 and 5, *T. testudinum* standing crop continued to increase until *H. wrightii* became established (1985 and 1987, respectively); after *H. wrightii* became established, *T. testudinum* standing crop at these sites decreased. By 1989, *H. wrightii* was the dominant seagrass at all of the FERT sites, while there was no *H. wrightii* at any of the CONT sites. There was considerable yearly variation in the standing crop of *T. testudinum* at the CONT sites.

The total standing crop of seagrass was affected by fertilization (Fig. 3). When averaged through time, there was a significant difference in the total seagrass standing crop between CONT and FERT treatments (ANOVA, Treatment main effect, $F_{1,4} = 10.1$, $P = 0.03$), but when averaged across treatments, there were no significant differences in seagrass standing crop as a function of time (Time main effect, $F_{8,32} = 1.12$, $P = 0.38$). However, there was a significant treatment by time interaction ($F_{8,32} = 9.8$, $P < 0.001$), indicating that the pattern through time in the total seagrass standing crop differed between CONT and FERT treatments. For the first three years of fertilization, FERT sites had 2–3 fold higher seagrass standing crops than controls, but from 1987–1991, there was no difference (Fig. 3).

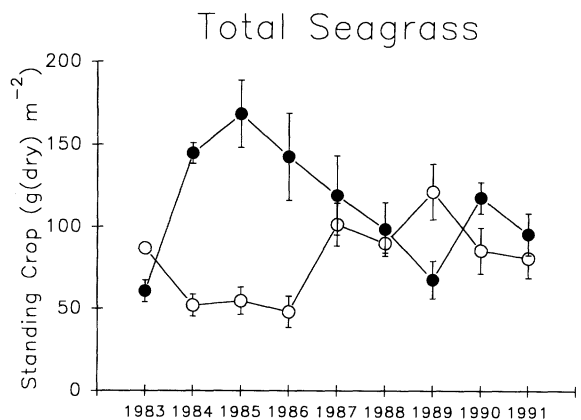


Fig. 3. Total seagrass standing crop at the fertilized (filled circles) and control (open circles) sites. Values are means ± 1 SE.

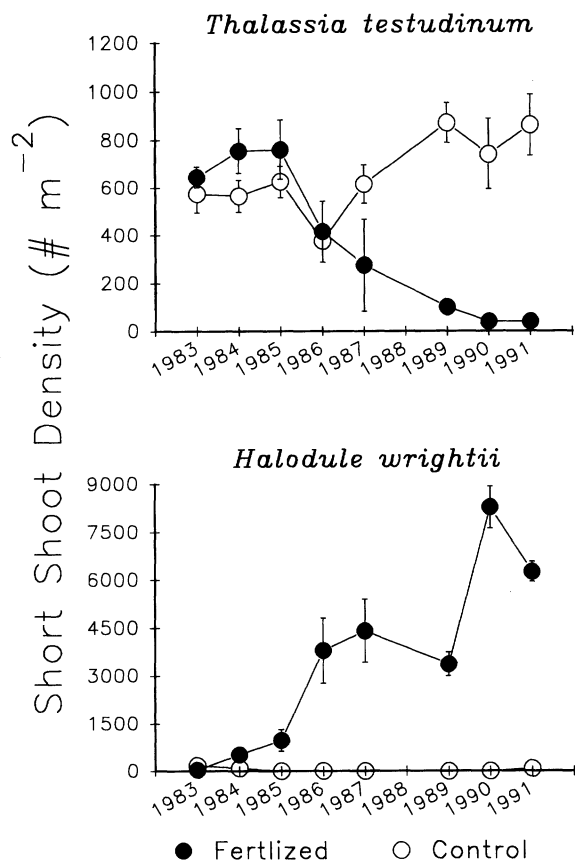


Fig. 4. Mean short shoot densities (± 1 SE) for *Thalassia testudinum* (top) and *Halodule wrightii* (bottom) at both control and fertilized sites.

The change from *Thalassia testudinum*-dominated seagrass beds to *Halodule wrightii*-dominated beds occurred gradually from 1983 to 1991 (Fig. 4). There were significant differences in the SS density of *H. wrightii* between CONT and FERT treatments throughout the experiment (ANOVA, Treatment main effect, $F_{1,4} = 85.7$, $P = 0.001$). Also, averaged across treatments, the density of *H. wrightii* changed through time (Time main effect, $F_{7,28} = 23.8$, $P < 0.001$). At FERT sites, *H. wrightii* density increased through time, while there was no change at the controls (Treatment by Time interaction, $F_{7,28} = 23.5$, $P < 0.001$). A more complicated pattern was evident in the SS density of *T. testudinum* during the experiments (Fig. 4). There was an overall effect of the treatment on *T. testudinum* density when averaged through time (ANOVA, Treatment main effect, $F_{1,4} = 21.0$, $P = 0.01$). Also, there were significant differences among years averaged across treatments (Time main effect, $F_{7,28} = 2.4$, $P = 0.05$). The density of *T. testudinum* at FERT sites exhibited a different pattern through time than the CONT sites (Treatment by Time interaction, $F_{7,28} = 11.4$, $P < 0.001$). At the FERT sites, *T. testudinum* density remained constant from 1983–1985, and then decreased rapidly from 1985–1991.

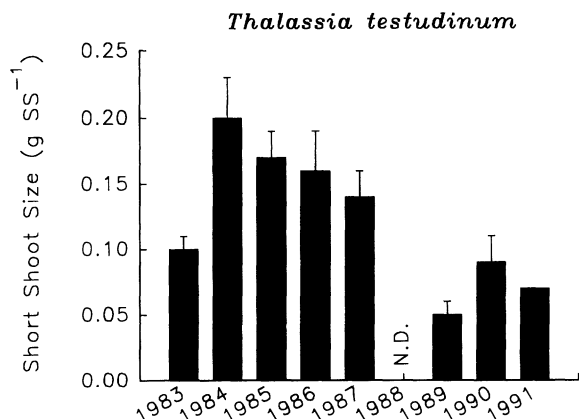


Fig. 5. Size of short shoots (g of green leaves per short shoot) of *Thalassia testudinum* at the FERT sites. N.D. indicates no data for 1988. Each value is the mean of the 5 site means, ± 1 SE, $n = 5$.

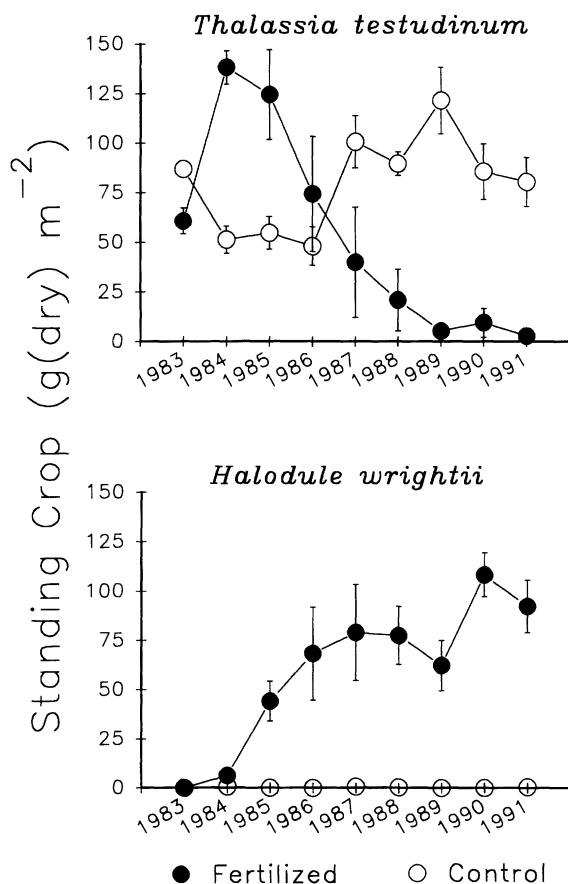


Fig. 6. Mean standing crop (± 1 SE) for *Thalassia testudinum* (top) and *Halodule wrightii* (bottom) at both control and fertilized sites.

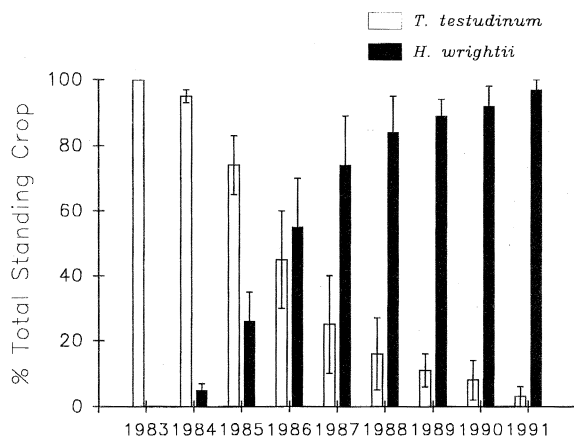


Fig. 7. Average proportion (± 1 SE) of the seagrasses *Thalassia testudinum* and *Halodule wrightii* at the fertilized sites.

There was no apparent pattern in the density of *T. testudinum* at the CONT sites.

Changes in SS density do not completely describe the change in the species composition of these seagrass beds since short shoots of *Thalassia testudinum* are much more massive than those of *Halodule wrightii*. Averaged over all of our measurements, *T. testudinum* shoots averaged 0.133 ± 0.009 g of dry leaves per shoot, compared to 0.013 ± 0.003 for *H. wrightii*. At the FERT sites, the size of *T. testudinum* shoots was strongly effected by nutrient additions (Fig. 5). After one year of fertilization, the average mass of *T. testudinum* shoots doubled. As *H. wrightii* became established at the FERT sites and began replacing *T. testudinum*, the size of the remaining short shoots decreased.

The standing crop of *Halodule wrightii* was strongly affected by the addition of nutrients in the form of bird feces to the FERT sites (Fig. 6). Averaged across all the years of the experiment, there were significant differences between FERT and CONT treatments (ANOVA, Treatment main effect, $F_{1,4} = 28.6$, $P < 0.01$): in all instances except for the beginning of the experiment, *H. wrightii* standing crop was higher at the FERT sites than

at the controls. Standing crop of *H. wrightii* increased through time when averaged across treatments (Time main effect, $F_{8,32} = 7.0$, $P < 0.001$), and the trend in standing crop through time was different for the FERT sites than the controls (Treatment by Time interaction, $F_{8,32} = 6.8$, $P < 0.001$).

As with the SS density data (Fig. 4), the pattern in the standing crop of *Thalassia testudinum* through the experiment was more complicated than for *Halodule wrightii* (Fig. 6). Averaged across all years of the experiment, there was a significant difference in the standing crop of *T. testudinum* between FERT and CONT sites (ANOVA, Treatment main effect, $F_{1,4} = 8.2$, $P = 0.05$), and averaging both treatments, the change in standing crop of *T. testudinum* was significant (Time main effect, $F_{8,32} = 2.5$, $P = 0.03$). The patterns in standing crop through time were very different between CONT and FERT treatments, however (Treatment by Time interaction, $F_{8,32} = 21.9$, $P < 0.001$). At FERT sites, standing crop of *T. testudinum* almost tripled between 1983 and 1984, and then declined steadily between 1984 and 1991. There was no such discernable pattern at the CONT sites.

The net result of fertilizing the *Thalassia testudinum*-dominated seagrass community normally prevalent on Cross Bank was a change from a *T. testudinum*-dominated meadow to one almost completely composed of *Halodule wrightii* (Fig. 7). In 1983, 100% of the total seagrass standing crop at the FERT sites was *T. testudinum*. After only one year of fertilization, *H. wrightii* began growing at these sites, and by 1986, the standing crop of *H. wrightii* exceeded *T. testudinum*. In 1991, *H. wrightii* made up 97% of the total seagrass standing crop. In contrast, *H. wrightii* never comprised more than 2% of the standing crop at the control sites, and in 1991, 99% of the total seagrass standing crop at the controls was *T. testudinum*.

Discontinued fertilization

ANOVA indicated no statistically significant changes in seagrass standing crop and short shoot density between years 1987, 1989, 1990 and 1991 at the DISC sites (Table

Table 1. Characteristics of the seagrass beds from sites at which fertilization was discontinued in 1983. Values are means ± 1 SE. ANOVA results are for repeated measures ANOVA testing for differences between years.

Year	Standing crop (g(dry) m ⁻²)			Short shoot density (m ⁻²)	
	<i>Thalassia testudinum</i>	<i>Halodule wrightii</i>	Total seagrass	<i>Thalassia testudinum</i>	<i>Halodule wrightii</i>
1987	31.9 \pm 16.2	61.2 \pm 14.7	93.2 \pm 21.3	156 \pm 77	5287 \pm 1432
1989	73.6 \pm 16.1	47.8 \pm 5.4	121.4 \pm 14.2	380 \pm 99	3310 \pm 377
1990	71.9 \pm 18.3	51.3 \pm 18.3	123.2 \pm 8.1	440 \pm 128	4795 \pm 1483
1991	56.1 \pm 17.1	34.8 \pm 16.4	90.8 \pm 7.9	460 \pm 124	3115 \pm 998
ANOVA					
$F_{2,3}$	1.6	1.3	16.0	0.5	4.0
P	0.4	0.5	0.06	0.7	0.2

1). The total seagrass standing crop at these sites was about equally divided among *Thalassia testudinum* (34% – 58% of total) and *Halodule wrightii* (40% – 66%). These proportions are similar to what was present at the FERT sites between 1985 and 1986 (Fig. 6). Assuming that the 28 months of fertilization from July 1981 to November 1983 had the same effect on the surrounding seagrass beds as the fertilization from November 1983 to October 1986, the seagrass beds at the DISC sites did not change appreciably between 1983 and 1991.

Discussion

The development of seagrass beds in south Florida and the Caribbean is often nutrient, and specifically phosphorus, limited (Short et al. 1985, 1990, Williams 1987, 1990, Powell et al. 1989, 1991, Fourqurean et al. 1992a, b). Not only is seagrass biomass controlled by nutrient availability, but there are documented differences in the nutrient availability in seagrass beds dominated by *Thalassia testudinum* and *Halodule wrightii* in Florida Bay (Fourqurean et al. 1992a). *H. wrightii* beds have higher concentrations of dissolved inorganic phosphorus in the sediment porewater than *T. testudinum* beds. This observed correlation does not prove that *H. wrightii* beds are restricted to areas of high P concentration, since the elevated P concentrations may be a consequence of the presence of *H. wrightii*. The experiments described herein, however, demonstrate that *H. wrightii* colonizes *T. testudinum*-dominated seagrass beds and out-competes *T. testudinum* when nutrient availability is increased in Florida Bay.

The dominance of *Thalassia testudinum* in the nutrient-limited seagrass beds of Florida Bay can be explained by the relative nutrient demands of *T. testudinum* and *Halodule wrightii*. Using the relative growth rates and the nutrient contents of the two species to estimate relative nutrient demands, Fourqurean et al. (1992a) have shown that *H. wrightii* has a four-fold higher demand for phosphorus, the limiting nutrient, than *T. testudinum*. Another method for assessing the relative nutrient demands is estimating the equilibrium resource requirement, or R^* , for each species (Tilman 1982). R^* can be approximated by the concentration of a resource in the environment when population sizes reach equilibrium. Assuming that populations reach equilibrium with respect to nutrient supply when additional nutrient supply does not cause an increase in population size, R^* for sediment nutrients in Florida Bay seagrass beds can be estimated by the “saturating” porewater concentrations of nutrients for each seagrass species. In the case of sedimentary P supply, the limiting nutrient for seagrass growth in Florida Bay, R^* for *T. testudinum* and *H. wrightii* are approximately 0.2 μM and 0.9 μM P, respectively (Fourqurean et al. 1992a). Since R^* for *T. testudinum* is substantially lower than R^* for *H. wrightii*, *T. testudinum* should have a lower de-

mand for P than *H. wrightii*; this agrees with the estimates based on the specific growth rates of the species (Fourqurean et al. 1992a). Therefore, *T. testudinum* should be able to out-compete *H. wrightii* for nutrients in a nutrient-limited environment, which explains why *T. testudinum* dominates the nutrient-limited seagrass beds of Florida Bay. Similarly, Williams (1987, 1990) found that *T. testudinum* could out-compete *Syringodium filiforme* for nutrients in seagrass beds in St Croix, U.S.V.I.

It is more difficult to explain the dominance of *Halodule wrightii* over *Thalassia testudinum* under nutrient-enriched conditions than to explain the dominance of *T. testudinum* over *H. wrightii* under nutrient-limited conditions. Once the nutrient limitation of *H. wrightii* was released at the fertilized sites, *H. wrightii* was able to colonize the fertilized areas. The decrease in *T. testudinum* at the fertilized sites was directly related to the increase in *H. wrightii* (Fig. 2). There are at least three possible reasons for the decline of *T. testudinum* at the fertilized sites, including: 1) nutrient enrichment could directly inhibit the growth of *T. testudinum* and not of *H. wrightii*; 2) *H. wrightii* could have an allelopathic effect on *T. testudinum*, or 3) *H. wrightii* could, in the absence of nutrient limitation, out-compete *T. testudinum* for some other resource (e.g. light).

It does not seem likely that nutrient enrichment directly suppressed *Thalassia testudinum*. In Florida Bay, the standing crop of *T. testudinum* is positively related to P availability (Fourqurean et al. 1992a, b), and in the first two years of this experiment *T. testudinum* was substantially enhanced at the fertilized sites compared to the controls (Figs 4–6). *T. testudinum* did not decrease at any of the fertilized sites until after *Halodule wrightii* became well established (Fig. 2). Nutrient enrichment has been cited as a factor in the decreased standing crop, productivity and persistence of some seagrass beds, however. Nutrient availability has been correlated with epiphyte loads on seagrass leaves (e.g. Sand-Jensen 1977, Silberman et al. 1986, Tomasko and Lapointe 1991), and shading of seagrasses by epiphytes has been implicated as one of the most deleterious effects of eutrophication of seagrass habitats (e.g. Bulthuis and Woelkerling 1983, Cambridge and McComb 1984). Since leaf turn-over is faster for *H. wrightii* than *T. testudinum* (unpubl.), it is conceivable that fouling of the longer-lived *T. testudinum* leaves could cause the loss of *T. testudinum* from areas of nutrient enrichment, but this mechanism was probably not operative in these experiments. While the epiphyte loads of the seagrasses at fertilized and control sites were not quantified, there were no visual differences in macrophytic or microscopic epiphyte loads at control or fertilized sites.

The initial response of *T. testudinum* to increased nutrient supply was an increase in the leaf biomass per short shoot (Fig. 5). Increased leafiness is a well-known plant response to shading, and there is some evidence that *T. testudinum* may respond to decreased light availability by increasing shoot size (Dawes and Tomasko 1988). In our

experiment, however, *T. testudinum* shoot size decreased after 1984, as light availability continued to decrease concomitantly with increases in *H. wrightii* biomass. This suggests that the initial increase in *T. testudinum* shoot size was a response to increased nutrient availability, not decreased light availability.

Allelopathic effects have been documented as important controls over interspecies interactions in some terrestrial environments (see Rice 1974). It is unlikely that *Halodule wrightii* has any allelopathic effect on *Thalassia testudinum*, since there are many locations where *H. wrightii* exists as an understory in predominantly *T. testudinum* seagrass beds (pers. obs.).

The most likely cause of the dominance of *Halodule wrightii* over *Thalassia testudinum* at the fertilized sites is direct competition for light between the two species. Under the fertilized treatment, *H. wrightii* developed a long and dense canopy, with numerous "aerial runners", or apical rhizomes extending 20–30 cm into the water column. From distributional evidence (Phillips 1960, Wiginton and McMillan 1979, Iverson and Bittaker 1986) it is apparent that *T. testudinum* has a higher light requirement than *H. wrightii*. The dense canopy of *H. wrightii* at the fertilized sites probably interrupted sufficient light so that *T. testudinum* could no longer maintain a positive carbon balance, leading to the extirpation of *T. testudinum* at those stations.

The resource-ratio theory of plant community structure (Tilman 1982, 1988) predicts that experimentally manipulated plots that receive the same supply of limiting resources should become similar in species composition, or converge on similar communities, through time. The convergence of plant communities receiving the same resource supplies is dependent on the historical composition of the communities, however (Inouye and Tilman 1988). Similarly, the outcome of the manipulations should depend on the availability of propagules of species favored by the manipulation. In the fertilization experiments presented here, *Halodule wrightii* was clearly favored by fertilization. Fertilized sites eventually converged on similar, *H. wrightii*-dominated seagrass beds, but the trajectories of the individual sites was dependent on the colonization of the sites by *H. wrightii* (Fig. 2). In the absence of *H. wrightii*, *Thalassia testudinum* biomass stayed elevated over control areas, but following the eventual colonization of the sites by *H. wrightii*, *T. testudinum* declined. The stochastic event of *H. wrightii* colonization therefore controlled the response of Florida Bay seagrass beds to manipulations in resource supply rates.

The changes caused by fertilization of seagrass beds in Florida Bay persisted for at least 8 yr after the fertilization was discontinued (Table 1). The primary source of nutrients for seagrass growth in unfertilized seagrass beds is the remineralization of organic matter in the sediments (Patriquin 1972, Capone and Taylor 1980, Short 1987). The lack of change at the sites where fertilization was discontinued suggests that seagrass beds are very efficient at retaining and recycling nutrients acquired during

fertilization. The loss of nutrients from the system over 8 yr was not great enough to draw the availability below the threshold value for *Halodule wrightii* survival. Since seagrass beds do lose some nutrients due to diffusion from the sediments and leaf loss, it is inevitable that this will eventually happen, however.

Succession can be viewed as the change in species composition through time caused by changing resource availabilities due to the impacts of organisms on the environment (Pickett 1976, Tilman 1987), and the ability of an organism to utilize resources may in large part determine its role in succession. In the original formulation of the resource-ratio hypothesis, Tilman (1985, 1988) hypothesized that early successional species should have lower R^* values for nutrients and be more competitive for nutrients than late successional species. This observation was directly at odds with many observations, however: one of the generalized patterns in changes in plant physiological ecology during succession is a change from high to low resource demands (Bazzaz 1979). In later work, Tilman and Wedin (1991a, b) re-evaluated this facet of resource ratio theory and found that, contrary to earlier predictions, early successional grasses have higher R^* values than late successional grasses. Tilman now considers early successional species to have an edge over later successional species due to their rapid colonizing rates (Gleeson and Tilman 1990, Tilman and Wedin 1991a), which agrees with many other assessments of early successional dynamics (e.g. Platt 1975, Connell and Slayter 1977, Bazzaz 1979). Early succession in Florida Bay seagrass beds also fits this model. *Halodule wrightii*, the normal early successional species, has a lower competitive ability for sediment nutrients than *Thalassia testudinum*, the later successional species, but a potentially much faster colonization rate than *T. testudinum*. *H. wrightii* has a much higher vegetative reproduction rate than *T. testudinum* (Tomlinson 1974, Fonseca et al. 1987), and sexual reproduction is potentially more important in the spread of *H. wrightii* than *T. testudinum* (Williams 1990). *H. wrightii* has a higher flowering rate than *T. testudinum* (Williams 1990). *H. wrightii* seeds form a seed bank in sediments of seagrass beds (McMillan 1981, 1983), and the seedling success of *T. testudinum* is very low (Williams and Adey 1983).

The replacement of *Thalassia testudinum* by *Halodule wrightii* at the fertilized sites was in contrast to the normal successional sequence in seagrass beds in south Florida and the Caribbean. Under non-enriched conditions, *H. wrightii* is commonly the early successional, colonizing species and *T. testudinum* is the late-successional, "climax" species (den Hartog 1971). Fertilization of other plant communities can also lead to the establishment of communities resembling early successional states. For example, in an old-field fertilization experiment Carson and Barrett (1988) found that nutrient enrichment of late-successional fields led to the establishment of plant communities dominated by summer annuals with high

photosynthetic rates and high relative growth rates. The resultant communities resembled earlier stages of secondary succession. Similarly, McLendon and Redente (1991) noted that fertilization of a sagebrush steppe community allowed early-successional annuals to persist as community dominants, and they concluded that the dominance of a site by annuals during the early stages of secondary succession is related to high nutrient availability. Succession in plant communities is dependent on the temporal pattern in the availability of nutrients. Increased nutrient availability may alter the trajectory of succession by allowing plant species adapted to high nutrient environments to displace established species (Grime 1979). In areas of high nutrient availability in Florida Bay, *H. wrightii* will be the dominant late successional species, while *T. testudinum* will be the dominant late-successional species in areas of low nutrient availability.

We propose that the change in species dominance from *Thalassia testudinum* to *Halodule wrightii* was caused directly by a change in the supply rates of light and soil nutrients. This shifted the outcome of competition between the two seagrass species. We have interpreted these results to be consistent with the resource ratio hypothesis (Tilman 1982, 1985, 1987, 1988), which asserts that competition is the main determinant of vegetation dominance in both nutrient-rich and nutrient-poor environments. In contrast, the triangular model of plant strategies (Grime 1974, 1977, 1979) holds that the relative importance of competition decreases in nutrient-poor environments, where the ability of plant species to weather stress becomes the primary determinant of vegetation. Experiments have shown that some aspects of competition do indeed decrease in intensity with an increase in stress (Campbell and Grime 1992), and a simulation model of succession based on the triangular model has been shown to produce results consistent with successional theory (Colasanti and Grime 1993). An alternative interpretation of the results of these experiments, consistent with the triangular model, ascribes the dominance of *T. testudinum* over *H. wrightii* in oligotrophic Florida Bay to a consequence of the low nutrient demand of *T. testudinum* caused by slow growth and efficient retention of retained nutrients compared to *H. wrightii*. In other words, *T. testudinum* is more tolerant of the stress of low nutrient availability than *H. wrightii*. The triangular model works well if we consider only one kind of stress, in this case nutrient limitation; but becomes cumbersome once light stress is also considered, because light stress and nutrient stress do not act in concert in aquatic environments. Often, light availability and nutrient availability are inversely correlated. For nutrients, *T. testudinum* is clearly the better competitor; but it is also clear that *H. wrightii* is a better competitor for light. In this case, the tradeoffs made between accumulation of light and accumulation of nutrients, as described by the resource ratio hypothesis, determines the behavior of *T. testudinum* and *H. wrightii* in Florida Bay.

Interpretation of the results of this experiment was

dependent on the duration of the fertilization of the seagrass beds. Increased nutrient availability caused a doubling of the *Thalassia testudinum* leaf biomass over controls for the first two years of this experiment; and were it to have ended at that time we would have concluded that increased nutrient supply to Florida Bay seagrasses would cause an increase in the biomass of the late successional seagrass *T. testudinum*. The true outcome of such a change in nutrient supply rates was dependent on the colonization of these fertilized, and therefore newly suitable, areas by the early successional seagrass *Halodule wrightii*. This time-dependent result underscores the importance of designing field experiments of the proper duration to capture the dynamics of the system being studied.

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