

# Density-dependent succession in Caribbean seagrass communities

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## Abstract

It is important to understand the patterns of succession and competition in seagrass beds as a way of explaining recovery processes after disturbances. This project studies macroalgae-seagrass succession dynamics in the Caribbean, and tests the importance of interspecific density-dependence (competition) in predicting the successional sequence of species in a wave-disturbed ecosystem. Competition and gap disturbances seem to be the dominant factors influencing species coexistence in offshore regions whereas habitat partitioning driven by differences in depth, disturbance and wave action creates distinct zones of macroalgae and seagrass inshore. In general, density dependent processes across our study site were influenced by major physical gradients. This study has important consequences for predicting dramatic shifts in large-scale seagrass ecosystems, which act as ecological engineers and provide many ecosystem services.

## Keywords

**Succession:** Changes observed in an ecological community following a perturbation that opens up a relatively large space; **Disturbance:** Uncommon, irregular events that cause abrupt structural changes in natural communities and create opportunities for new individuals to become established; **Interspecific density dependence:** Interactions between individuals of different species that affect population demographic processes; **Seagrass beds:** Marine coastal ecosystems formed by various species of angiosperms. Seagrass beds provide an important habitat for an abundance of fish and invertebrate species, as well as many ecosystem services such as water filtration, carbon sequestration and erosion prevention; **Gaps:** Vegetation-free depressions within seagrass beds characteristic of regions experiencing moderate to severe wave action. They are typically crescent-shaped and migrate seaward.

## Introduction

Ecologists strive to explain the processes responsible for structuring natural communities in order to better predict how disturbances may alter these groupings of species, and how communities are reassembled following a perturbation. Dynamic disturbance regimes have long been recognized as important mechanisms regulating natural ecosystems (Sousa 1984) and promoting species diversity, especially by allowing subordinate competitors to colonize recently disturbed areas (Paine and Levin 1981). Although these theories have been used to explain the dynamics of seagrass ecosystems (Bell et al. 1999), recent observations suggest that more complicated

physical and biotic processes may play important roles in the maintenance of marine communities (Tewfik et al. 2007).

Caribbean seagrass beds are found to alternate between disturbed states which lack vegetation, referred to as gaps, and a variety of successional states which may include both seagrass or macroalgal vegetation (Bell et al. 1999). Constant wave action keeps the area under periodic disturbance and promotes the migration of gaps throughout the beds (Kirkman 1985). The newly exposed sediments are left to be colonized by one of the various marine species, including the grasses *Thalassia testudinum* and *Syringodium filiforme*, as well as the rhizophytic algae *Avrainvillea longicaulis* (Patriquin 1975).

One well-studied seagrass ecosystem at Bath, Barbados was initially described as being dominated by large stands of *Thalassia*, which was believed to be the competitively dominant species in the seagrass community successional hierarchy (Den Hartog 1971; Patriquin 1975). However, recent studies by Tewfik et al. (2007) at the Bath seagrass beds reported a large-scale shift in species composition from the dominant seagrass cover to monocultures of competitively subordinate macroalgae. More specifically, areas of the seagrass bed that were historically described by Patriquin (1975) as seagrass-dominated zones were found to have transitioned to monocultures of *Avrainvillea longicaulis*, creating distinct zonation within the community. Recent observations more precisely challenge the competitive dominance of *Thalassia* (Mavromatis et al. 2006). Rather than observing the expected zones of dominant seagrass in recovered gap areas and subordinate macroalgae in recently disturbed regions, Mavromatis et al. (2006) found that seagrass beds seem to be progressively replaced by large macroalgal beds wherein little to no seagrass is able to grow. However, Mavromatis et al. (2006) did not explicitly test for biotic interactions, such as competition, in the maintenance of the vegetative zones and successional sequences. Although we qualitatively observed that *Thalassia* does not grow well in the macroalgal zone or in the presence of *Avrainvillea*, it remains unknown whether habitat effects or density-dependence plays a greater role in maintaining the species assemblages observed. We can address this question by studying the dynamics of species interactions and physical parameters at the boundaries of three described vegetative zones.

The general goal of our study is to test the importance of interspecific density-dependent processes (competition) in explaining successional sequences in wave-disturbed seagrass ecosystems. We will more precisely test the hypotheses that (1) both habitat differences and direct species interactions produce the patterns of species assemblage observed and (2)

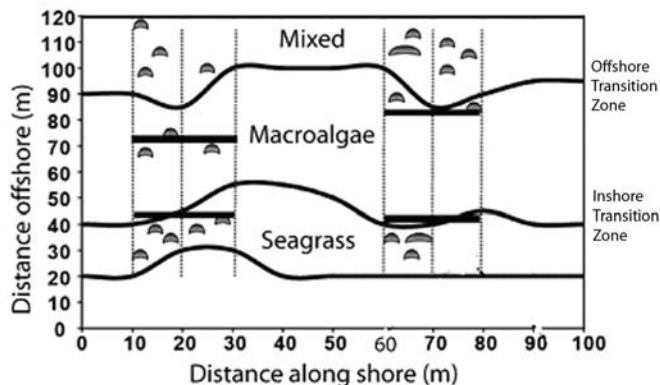
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that the relative contributions of these two components differ in the two transition zones. From these hypotheses, we predict that the presence of interspecific competitors of *Thalassia* in the seagrass bed inhibit the growth and proliferation of *Thalassia* in areas where species interactions are the strongest. Furthermore, these density dependent processes should be influenced by major physical gradients such as the intensity of water motion and habitat partitioning across our study site. This study will have important consequences for predicting dramatic shifts in large-scale seagrass ecosystems, which act as ecological engineers and provide many ecosystem services.

## Methods and Materials

### Study site

This study was based on observations and experiments on the seagrass community in Bath, Barbados (N 13° 11', W 59° 28') during May and June 2004. The study site covered an area of the seagrass bed 100m wide by 120m long. Three distinct vegetative zones were described in Mavromatis et al. (2006) and named based on the dominant cover of the region. The seagrass zone exists 20 to 40m offshore, and is followed by the macroalgal zone. The macroalgal zone extends from approximately 40 to 90m offshore, making it the largest continuous area of all zones. Finally, the mixed zone extends to 120m offshore (Figure 1).

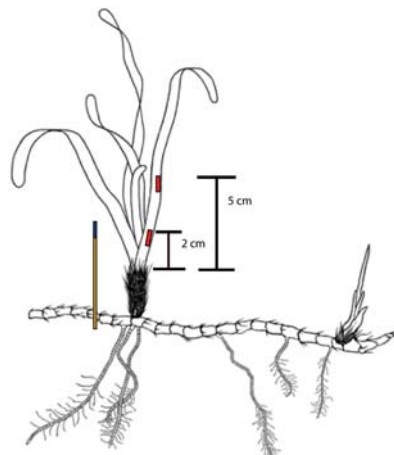


**Figure 1.** Diagram of the study area depicting 3 vegetation zones, 4 horizontal growth transects, 6 vertical physical gradient transects, and gaps (denoted by grey crescents). Figure modified from Mavromatis et al. 2006.

In order to address our hypothesis that both biotic and abiotic processes affect species assemblages in seagrass beds, we measured a series of physical characteristics of the study site including sediment type, water depth, erosion levels, and disturbance frequency (gap number) to see whether there were strong differences in these parameters between the three vegetation zones that might account for the patterns observed. Since we also wanted to see whether interactions between macroalgae and seagrass species influence the zonation of the study area, we measured blade growth and elongation of *Thalassia* in 25cm<sup>2</sup> quadrates along transects running lengthwise across the two transition regions between the vegetation zones (approximately 45m and 85m for the inshore and offshore transition zones respectively, 10 quadrates in each transition zone). In quadrates where *Thalassia* abundances were greater than 30% cover, one of three possible treatments was used: seagrass species only were present (n=6), seagrass and macroalgae species were present (n=7), or macroalgae species were experimentally removed

leaving only seagrass in the quadrate (n=7). *Thalassia* blades in each quadrate (n= 12) were randomly selected, marked and measured after 3-6 days of growth (Figure 2).

Average daily growth rates were calculated for marked blades, and we examined growth rate differences between treatments in the inshore transition zone. Square-root transformations were performed on the growth rate data to improve the normality of residuals. We used a 2-way factorial ANOVA to test for differences between the 2 factors (treatment and transition zone) and Bonferroni-corrected LSD comparisons were used to test for differences between the means.



**Figure 2.** Diagram of blade identification and growth measurement procedure. Coloured toothpicks were inserted into the sediment and used to identify *Thalassia* blades. Leaves were stapled at 2cm and 5cm above the rhizome base, and after 3-6 days, measurements were taken from rhizome base to each staple to obtain measurements of blade growth and elongation.

## Results

### Abiotic patterns

Water movement intensity (erosion) was measured overnight using plaster of Paris cylinders (Guichard and Bourget 1998). A one-way ANOVA found that the offshore transition area experiences significantly higher levels of wave action and disturbance than the inshore region (n= 18,  $p < 0.0003$ ) (Figure 3a).

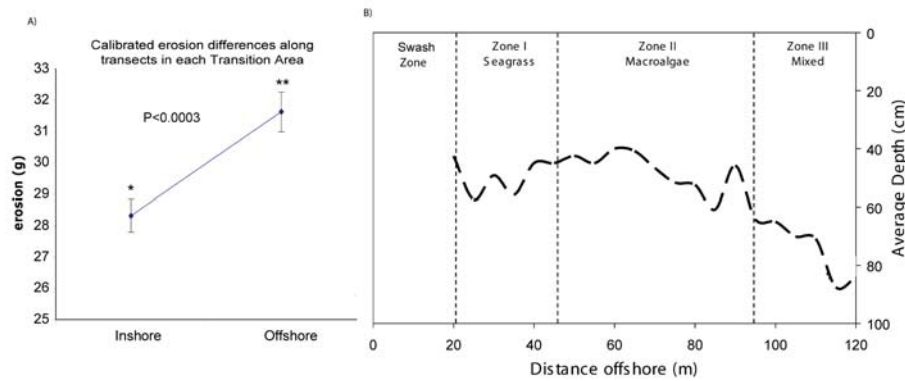
Nine measures of water depth associated with each growth transect were analyzed for differences between inshore and offshore transition areas (2 transects per area, n=18). A one-way ANOVA indicated no significant difference in depth at the level of our transects ( $p > 0.05$ ). However, water depth was variable across the study site (Figure 3b).

Twenty-three gaps (vegetation-free depressions measuring  $\geq 3$ m wide,  $\geq 2$ m long and  $\geq 1$ m deep) were mapped across the study site (Figure 1): 9 were found in the seagrass zone, 5 in the macroalgae zone and 8 in the mixed zone. Gaps in the seagrass zone occupy an area of approximately 31m<sup>2</sup> representing a total surface area of 3.9%. Gaps in the large macroalgae zone cover only 19.2m<sup>2</sup> or less than 1% of the area. The mixed zone has the highest surface area disturbed by gaps at 56.7m<sup>2</sup>, which represents 4.7% of the surface.

### Biotic processes

There is a significant effect of treatment on the growth of *Thalassia* ( $p < 0.001$ ) as well as a significant interaction term between transition zone and treatment ( $p < 0.008$ ). Bonferroni-corrected LSD comparisons found that inshore areas with no *Avrainvillea* were significantly different from all other means

( $p < 0.001$ ), but no other treatment level was found to be significantly different from the others ( $p > 0.0738$ ) (Figure 4).



**Figure 3.** Large-scale environmental gradients. (A) Erosion levels between transition zones as measured by differences in plaster cylinder weight (B) Calibrated depth differences across the study site.

## Discussion

### *Species interactions in seagrass ecosystems*

Studies in community ecology often focus on the fundamental questions of what processes enable species to persist and what processes contribute to extinction. Here, we present a study on a dynamic marine ecosystem currently experiencing global declines for various reasons, many of which are unknown (Duarte 2002). Preliminary observations led us to believe that *Thalassia* was experiencing negative density-dependent effects of competition from the macroalgae species *Avrainvillea*, which has recently been established as a late colonizer in this system and is slowly replacing the seagrass at the level of our study site (Mavromatis et al. 2006). However, the effects of direct biotic interactions between these species were not consistent throughout the study site.

Although *Thalassia* grows better without macroalgae in the inshore transition area, removing the algae experimentally does not significantly increase the growth of seagrass. As a result, biotic processes cannot fully explain the patterns of species assemblage observed in this region; physical parameters must also contribute to the dynamics. The inshore transition zone appears to experience a species sorting effect such that habitat without algae maximizes the growth of *Thalassia*. Although competition may still be a factor influencing the presence of seagrass, habitat segregation between the species may better explain the distinct zonation observed between the seagrass and macroalgae zones since removal of algae marginally increases *Thalassia* growth.

The dynamics change in the offshore transition area. None of the three treatments showed significant differences, suggesting that habitat has less influence on species presence and persistence than biotic interactions such as competition. These results suggest that competitive interactions rather than habitat segregation may enable the persistence of seagrass and macroalgae in mixed assemblages in the offshore zone.

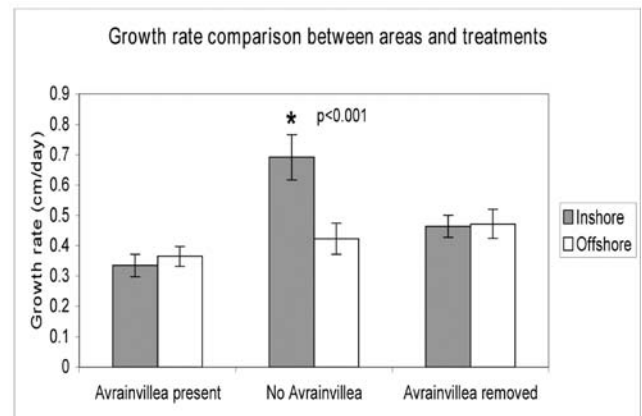
### *Mechanisms for coexistence in spatial landscapes*

Levels of disturbance in a system influence species composition by forcing life-history trade-offs and creating conditions that may enable coexistence (Tilman 1994). It has often been suggested that intermediate levels of disturbance

are responsible for the maintenance of diversity in ecological communities (Sousa 1979), and a wide body of literature exists discussing this hypothesis and its implications. However, debate continues about the role of spatial heterogeneity and whether spatially patchy disturbances or simply ecological differences between species are sufficient to promote coexistence (Chesson 1991; Roxburgh et al. 2004).

There is a clear difference in competitive ranks between seagrass and macroalgae established at Bath, Barbados (Mavromatis et al. 2006), although one that is different from previous literature (Davis and Fourqurean 2001). The vegetative zonation observed at the level of our seagrass bed is also associated with gradients of physical parameters including depth, erosion, and disturbance. Depth differences cannot explain the discrepancies in growth patterns observed in our transects. However, water depth is an important physical parameter that may promote habitat segregation. Seagrass is known to suffer desiccation stress rapidly (Birch & Birch, 1984) whereas *Avrainvillea longicaulis* prefers shallow, open sand areas that may be exposed to the air during low tide (Littler & Littler, 1999). This habitat preference may contribute to the extensive macroalgal zone occupying a relatively shallower part of the bed, since seagrass is at a disadvantage in these habitats.

Wave action differs significantly both between growth



**Figure 4.** Treatment comparisons between all transects and treatments. Inshore transition zone areas with *Avrainvillea* naturally absent are significantly different (a) from all other means (b).

transects and zones, with the macroalgae and mixed zones experiencing higher levels of water current than the inshore seagrass zone. Since *Avrainvillea longicaulis* is thought to prefer areas of relatively low current and wave energy (Littler & Littler, 1999), this physical gradient may be a driving factor in producing the patterns observed in the offshore area. Studies have shown that the degree of wave current and action is reported to be one of the main factors determining species composition and the extent of seagrass meadows in comparable sites (Kirkman 1985). High levels of wave action may increase the competitive ability of the seagrass relative to macroalgae, and allow for resource partitioning between these



species in the mixed zone, which Tilman (1994) suggests is a required component for stable coexistence. Although it is unclear whether the seagrass zone is experiencing gradual encroachment by the macroalgae or is temporally stable, the significant differences in physical parameters found across the study zones play an important role in driving the maintenance of diversity. Small-scale disturbances may therefore have a large role in the structuring of seagrass beds since they increase the interactions between biotic and abiotic processes.

#### *Disturbance patterns and species interactions*

Competition for space and resources represents a significant challenge in nature. This struggle is especially true for sessile organisms, which are in perpetually close association with both their neighbours and local habitat (Tilman 1994). Space is a limiting resource preventing the proliferation of species in many environments, and disturbance acts as a natural force that renews this resource and allows new individuals to grow (Paine and Levin 1981). Gap phenomena have long been recognized as important processes renewing space and allowing colonization in plant communities (Watt 1947). Even though the macroalgae zone occupies the largest continuous area, it contained the fewest number of gaps and the least amount of disturbed area. The seagrass zone, containing the most gaps in the smallest area, has a much greater percentage of its overall area disturbed. As suggested by Mavromatis et al. (2006), *Thalassia* is more often found in recently disturbed areas since it is able to colonize newly opened space relatively faster than macroalgae. Differences in disturbance regimes between the macroalgal and seagrass zones may therefore contribute to the habitat segregation observed. Disturbances may play a different role in the mixed zone. Gaps may contribute to the coexistence of seagrass and algae by promoting the rapid turnover of species and preventing the competitive exclusion of *Thalassia*. In essence, biotic and abiotic processes work in conjunction with one another to enable the persistence of a diverse marine community.

#### **Conclusion**

Seagrass beds represent ecologically significant ecosystems that provide a number of vital services to marine coastal communities (Duarte 2002). Unfortunately, many seagrass beds are undergoing rapid changes in their structure and ability to persist as intact systems as a result of both direct and indirect anthropogenic disturbances (Duarte 2002). Even in the thirty years since Patriquin's studies (1972; 1975) at Bath, Barbados, remarkable changes in species assemblages, successional sequences and physical gradients have occurred that are causing a once extensive bed to be overrun with macroalgae. From this study, we were able to elucidate the relative contributions of abiotic and biotic processes in relation to the physical environment. Competition and disturbances seem to be the dominant factors influencing species coexistence in the mixed zone, whereas habitat partitioning driven by differences in depth, disturbance and wave action creates distinct zones of macroalgae and seagrass in inshore regions. Future research should focus on establishing the role of seagrass acting as ecological engineers, the scaling of seagrass recovery from disturbances, and the resistance of beds to physical phenomena such as sedimentation and eutrophication that were not tested during our experimen-

tion. Elucidating the important processes regulating the distribution of seagrass species will be useful in informing managerial decisions regarding the preservation of these endangered systems within larger tropical intertidal communities.

#### **Acknowledgements**

We would like to thank the Bellairs Research Institute of McGill University in Barbados for use of laboratory and field equipment used during data collection. We would also like to thank D. Pérez and the students of the 2004 Applied Tropical Ecology course for field assistance. Finally, we would like to thank A. Tewfik, F. Petrovic, G. Smith, and D. Roche for their comments during the discussion of the project.

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