

# Successional Dynamics in Seagrass Communities

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## **Abstract**

The sequence of ecological changes in which one species is replaced by another is known as succession. Den Hartog (1971) was the first to propose successional schemes for seagrass communities based on competition-colonization hierarchies, which have rarely been challenged. Wave-disturbed subtidal systems are characterized by the presence of gaps, the distinct topographic depressions devoid of vegetation defined. We present a study of a Caribbean seagrass bed exemplifying macroalgal-seagrass succession dynamics in relation to gap disturbance. We report a shift in species composition at the study site consisting of the replacement of seagrass by an extensive macroalgal cover. Succession patterns were tested in each zone by sampling macrophyte cover along transects running across gaps. Our results show that seagrass is always the first colonizer, independent of dominant cover in control plots. The reversal of competitive hierarchy described has important consequences for the understanding and management of seagrass ecosystems.

## **Introduction**

For the past several decades, marine ecology has studied life history traits of various forms of seagrass attempts to explain the relative importance of these angiosperms in coastal ecosystems. Aside from being an important stabilizer of bottom sediments (Patriquin 1973, p. 111), seagrass provides the organic substrate needed for the establishment of epibiotic fauna and a diverse assemblage of plants and animals (Aladro-Lubel & Martinez-Murillo 1999, p. 239). Since these communities develop rapidly, and are found in soft-bottomed coastal systems worldwide (Williams 1990, p. 450), it is important to understand the patterns of succession in seagrass beds as a way of explaining recovery processes after disturbances.

Ecological succession is defined as changes observed in an ecological community following a perturbation that opens up a relatively large space (Connell & Slatyer 1977, p. 1119). During successional sequences, the first species arriving in the disturbed area are called the primary colonizers. These species usually have poor competitive abilities, and rapid colonization rates on bare sediments. These species are soon displaced from the system by the secondary colonizers. Secondary colonizers are strong competitors for resources with relatively slow colonization rates.

Disturbance, succession and recovery processes have been at mainstays in ecological theory since the early 1950s in terrestrial and marine systems. Their importance for understanding and managing natural ecosystems is well recognized. In a classic example, Mediterranean forest systems rely on frequent fire disturbances to maintain their structure and function through natural successional processes (Fernández-Abascal et al 2004, 147). In seagrass ecosystems, Den Hartog (1971) was the first to propose successional schemes based on competition-colonization hierarchies, with seagrass species as the climax of a sequence involving macroalgae and seagrasses.

This study examines succession dynamics in a wave-disturbed seagrass ecosystem located on the east coast of Barbados. The dominance of the seagrass *Thalassia testudinum* in this ecosystem was originally attributed by Patriquin (1975) to wave disturbances, which disrupt the seagrass matrix and create sharp topographic depressions known as gaps. These gaps are hypothesized to contribute to the maintenance of the subordinate seagrass species

*Syringodium filiforme* and of a subordinate algal species complex, *Avrainvillea* sp. in the seagrass bed. More recently, Tewfik et al. (in review) documented a historical shift in the species distribution within the ecosystem, showing that *Avrainvillea* has formed a dominant cover in a region (40m wide and 45m offshore) previously occupied by seagrass. This species shift could potentially contradict the established model for the competitive hierarchy in seagrass communities.

The general goal of our study is to present a model for the species shift and the maintenance of extensive cover of *Avrainvillea* by examining the complex successional patterns within a wave-disturbed seagrass community. Assuming that gaps migrate and that patterns of species composition in their trail can inform us about spatial and temporal successional sequences, the following hypotheses were tested: (1) *Avrainvillea* is a dominant species and its cover varies in relation to physical gradients and (2) recovery and disturbance intensities are explained by offshore and alongshore physical gradients (hydrodynamics and biomass loss).

## Materials and Methods

The experimental part of this study was carried out at Bath, Barbados during May and June of 2004 (Fig. 2B). The seagrass site under investigation is 100m wide and 120m long (Fig. 2A). Gaps were defined as sharp topographic depressions created by wave disturbance, over 0.2m deep and not less than 3m wide. All gaps fitting these criteria found between 10-30m and 60-80m alongshore and offshore were mapped and measured. These gaps were also pegged at four different points (scarp, beginning of leeward slope, and left and right edges) in order to measure their migration rate over 30 days. Succession sequences were characterized by measuring the percentage surface cover for each species using 1m<sup>2</sup> quadrants at every meter along a 17m transect running offshore from 4m before to 12m after the scarp of each gap. Control transects were sampled at 2m from the right and left edges of each gap (Fig. 2C).

## Results and Discussion

Our study reveals three distinct zones. Zone I is composed of seagrass *Thalassia testudinum* and *Syringodium filiforme*, Zone II is mainly occupied by the macroalgae *Avrainvillea*, and offshore Zone III is a mixed assemblage of seagrasses and macroalgae. The macroalgal zone

documented here results from a historical (<30 years) shift from the original mixed assemblage documented by Patriquin (1975). The data was filtered for the interactions between seagrass species and *Avrainvillea*, present exclusively in Zones II and III.

At the scale of individual gaps, we were able to analyze a temporal successional sequence from spatial transects sampled across migrating gaps (Fig. 3). In contrast with previous studies, we showed that seagrass species are the first colonizers after disturbance, irrespective of the surrounding dominant cover. *Avrainvillea* progressively replaces the strong competitor seagrass species. Furthermore, *Avrainvillea* recovery is slower in the mixed zone compared to the macroalgal zone. These results suggest that disturbance dynamics, rather than an equilibrium succession endpoint, prevent the full recovery of *Avrainvillea*, and maintain the mixed assemblage observed in the offshore zone.

## Conclusion

Our results failed to support den Hartog's (1971) successional sequence, which established macroalgae as the first subordinate colonizers and seagrasses as the climax species (Fig. 1A). The reversal of competitive hierarchy shown here (Fig. 1B) will have important consequences for the understanding and management of seagrass ecosystems. Future research should examine the underlying processes explaining the large-scale historical shifts from seagrass to macroalgal assemblages, in light of our results establishing *Avrainvillea* as the potential endpoint of succession.

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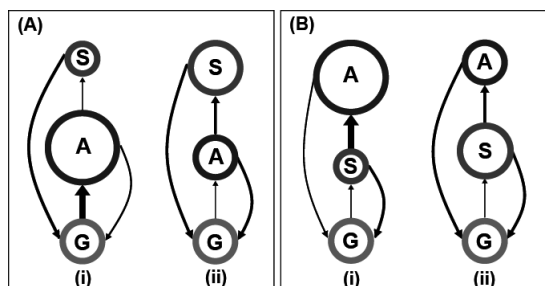


Figure 1. Schematic representation of the two conflicting hypotheses, where G: gap, A: *Avrainvillea* and S: seagrass. The size of the circle symbolizes the abundance of each species during succession and the size of the arrows the strength of the transition from one state to the other.

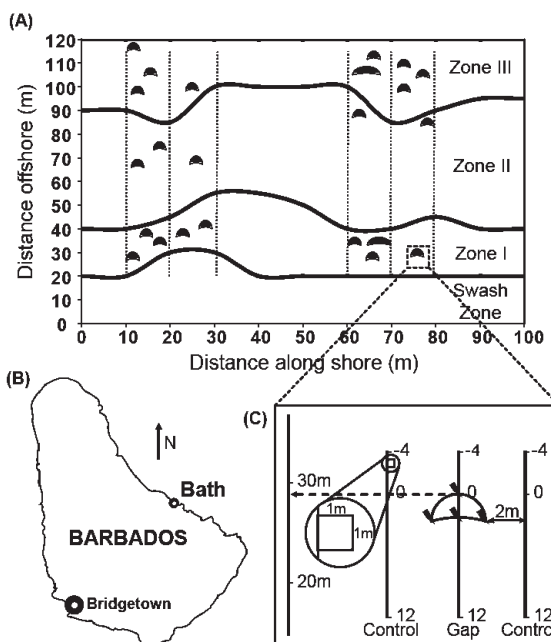


Figure 2. Sampling design. (A) Study site map with all the gaps and transects, (B) Map of Barbados, (C) Close up of a pegged gap describing the vegetation sampling design: 2 control, 1 gap transect and a 1m<sup>2</sup> quadrant are depicted. Extreme left line depicts the transect used to map the gap on the site.

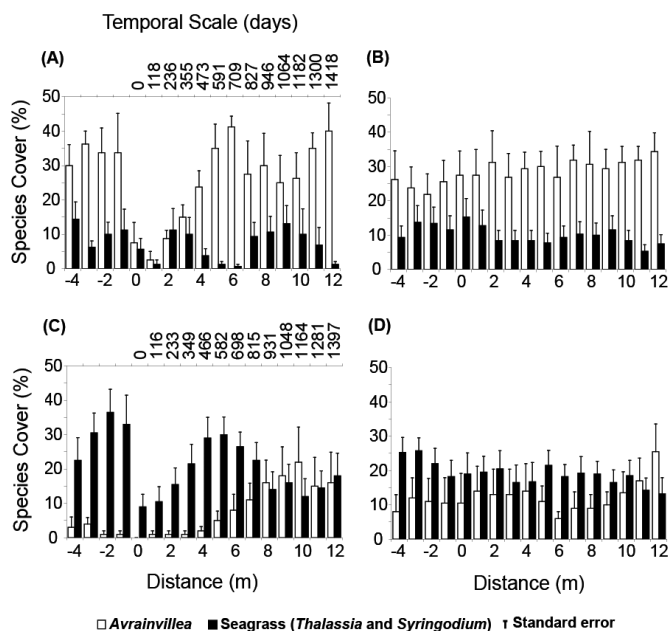


Figure 3. Gap (A & C) and control (B & D) profiles for Zone II (Macroalgae) and Zone III (Mixed) respectively. The gap profile depicts both the spatial and temporal successional sequences and shows how the species abundance changes over time after gap creation (distance = 0m). Comparisons of species abundance can be made with the control profiles that are devoid of disturbances.