

SEAGRASS ZONATION: TEST OF COMPETITION AND  
DISTURBANCE AT SEAHORSE KEY, FLORIDA

Stephen A. Bloom  
Ecological Data Consultants, Inc.  
P.O. Box 760  
Archer, Florida 32618

ABSTRACT

The zonation of Halodule wrightii and Thalassia testudinum (which occur in adjacent, virtually non-overlapping monocultures in the intertidal and shallow subtidal respectively at Seahorse Key, Florida) was subjected to experimental manipulations. Transplantation was done above, within and between beds, and mean blade length (as a measure of plant health) was monitored. Upper limits appeared to be set by exposure (desiccation and/or heat) stress while the lower limit of Halodule was not set physiologically since transplants into clearings in the Thalassia bed flourished. Experimental evaluations of shading, leaf abrasion, short term allelopathy and root-root interactions were performed to isolate potential competitive mechanisms. Thalassia outcompeted Halodule via long-term root interactions. Herbivory were modeled by cropping at the border zone and was capable of decreasing the ability of Thalassia to exclude Halodule and enabling Halodule to invade. Other potential forces which could alter the outcome of the competition were discussed.

INTRODUCTION

Subtropical grassbeds along the coast of the Gulf of Mexico often exhibit zonation of the shallow, intertidal shoal grass, Halodule wrightii Aschers., and the deeper, subtidal turtle grass, Thalassia testudinum Banks ex Konig (Humm 1956; Phillips 1960, 1962; Moore 1963; Keller & Harris 1966; den Hartog 1970; Iverson & Bittaker 1986) though mixed beds are known to exist (Voss & Voss 1985; Humm 1956; Strawn 1961). Little experimental work has been done on the zonation of Halodule and Thalassia (but see Phillips 1960 as an early approach). The purpose of this research was to explore experimentally the causal mechanisms of the zonation of Halodule and Thalassia and to examine phenomena which could affect the zonation.

STUDY SITE

All experiments were performed on the south beach of Seahorse Key (83 04' West and 29 06' North), a small island 5 kilometers offshore from Cedar Key, Florida on the Gulf Coast. Stations were established at approximately 60 cm (Upper Beach), 30 cm (Middle Beach), 15 cm (Halodule bed) and -15 cm (Thalassia bed) from the mean tide level. These correspond to 2, 10, 30 and 80 meters respectively from the extreme

high spring water (EHSW) mark. The Upper Beach station was located on a stretch of clean sand. Middle Beach was placed centrally on a muddy sandflat, and the grass bed stations were located 4 meters from their leading edges. Four stations were established along one transect in 1979 and another four stations were established along a parallel transect 10 m to the west in 1980. All grassbed stations were carefully raked to remove all plants and root systems, and the level of the sediment in the experimental plots (approximately 1 meter by 3 meters with the long axis of the plot paralleling the edges of the beds) was matched to the level of the sediment in the surrounding bed.

## METHODS AND MATERIALS

The question of physiological limitations was addressed by transplanting grasses with a modified plug technique (Phillips 1976; Van Breedveld 1975). A steel sleeve (17.8 cm diameter by 30 cm long) was driven into the sediment at the transplantation site and the sediment within the sleeve was removed. A capped polyvinyl chloride (PVC) core (15.2 cm diameter by 30 cm long) with a lateral vent in the cap was placed over the grass to be transplanted, was pushed into the sediment 30 cm and the vent hole was closed. The core was extracted, carried to the sleeve and inserted. The sleeve was removed and sediment was packed around the core. The vent hole was opened and the core removed from the sediment. Care was taken to match the depth of the sleeve and the core so that the plug would be level with the surrounding sediment.

A method was required which would measure the relative health of the grasses and would not require destructive sampling of experimental plots. Techniques using the ratio of physiologically active to inactive chlorophyll, leaf stapling, photography or clip-and-recover methods were not applicable due to diatom contamination, the leaf morphology of *Halodule*, turbid water and the confounding effects of removing photosynthetic tissue, respectively. The only feasible measure of plant health was blade length (Phillips 1960). Both macrophytes have distinct morphologies which allow accurate measurements.

The first set of experiments addressed physiological limitations of the grasses and the potential impact of transplantation procedures. In 1979 and in 1980, 5 cores of each grass were moved to Upper Beach, and 10 cores of each grass were moved to the other three stations. In each year, all 70 cores were transplanted within one tidal cycle (August 1, 1979 and June 9, 1980). Qualitative data was gathered in both years and quantitative data was taken in 1980. In that year, between 10 to 15 plants were collected from each grass at each station and the approximately 30 blades from each grass and station were measured. Sampling periods increased from weekly, initially, to twice a month after one month.

The second group of experiments addressed potential competitive

mechanisms. Relative shade tolerance was estimated by placing 2x and 4x neutral density platforms (1 meter square) 30 cm above plots of both grasses and monitoring the grass lengths. After one week, diatom growth had converted both filters into opaque surfaces. Grass lengths were monitored for 79 days (July 24 to October 11, 1980).

Leaf abrasion of Halodule by Thalassia was estimated by planting artificial Thalassia plants (3 strips of 4 mm clear polyethylene plastic 22 cm by 0.6 cm fastened to aluminum nails with rubber bands) at the normal density of Thalassia plants in an experimental plot in the Halodule bed. The monitoring period was the same as for the shading experiment. The artificial plants were allowed to remain for one year to qualitatively assess long-term effects.

To ascertain potential short-term allelopathic (e.g., toxic) interactions and to examine long-term root-root interactions, 10 cores of Halodule in 1979 and 10 more in 1980 were transplanted into the Thalassia bed. Except for damage caused by the transplantation procedure, Thalassia plants within the experimental plot were not disturbed. Five of the cores each year were enclosed in 30 cm long plastic sleeves (17.8 cm in diameter) and the other five were implanted without sleeves. The latter group was marked with small PVC stakes. The sleeves were set flush with the sediment, extended below the Thalassia rhizomes, and would presumably protect the enclosed plants from any root allelopathic effects while still exposing the plants to potential leaf interactions. Grass in the cores transplanted in 1980 were monitored for blade length for 75 days (July 18 to October 11).

The final effort addressed herbivory. Three 1 meter square plots were established on the border between the grassbeds (with the border bisecting each plot and with Thalassia to the south and Halodule to the north). The corners and the midpoints of all four sides of the three plots were marked with PVC stakes protruding 1 cm from the sediment. Each plot was effectively reduced to 80 cm on a side for experimental manipulations, leaving a 10 cm margin around the borders of the plots as a secondary control. The southeast quadrant (Thalassia) of the west plot, the west half (Thalassia and Halodule) of the center plot and the northwest quadrant (Halodule) of the east plot were cropped weekly from April 23 to August 20, 1981. Grass was clipped with garden shears 2 to 3 cm above the substrate mimicking the grazing activities of green turtles (Bjorndal 1979). After 119 days of simulated herbivory, the plots were divided into four quadrants. Twenty-five core samples (5 rows of 5 cores, each being 10 cm in diameter) were taken from each quadrant (300 cores total). The number of emergent shoots and the ash-free dry weight (weight difference before and after combustion at 550°C for 3 hours) of each grass in each core sample was determined.

## RESULTS

The responses of Halodule and Thalassia to the transplantation treatments through time are presented in Figure 1. Covariance analyses

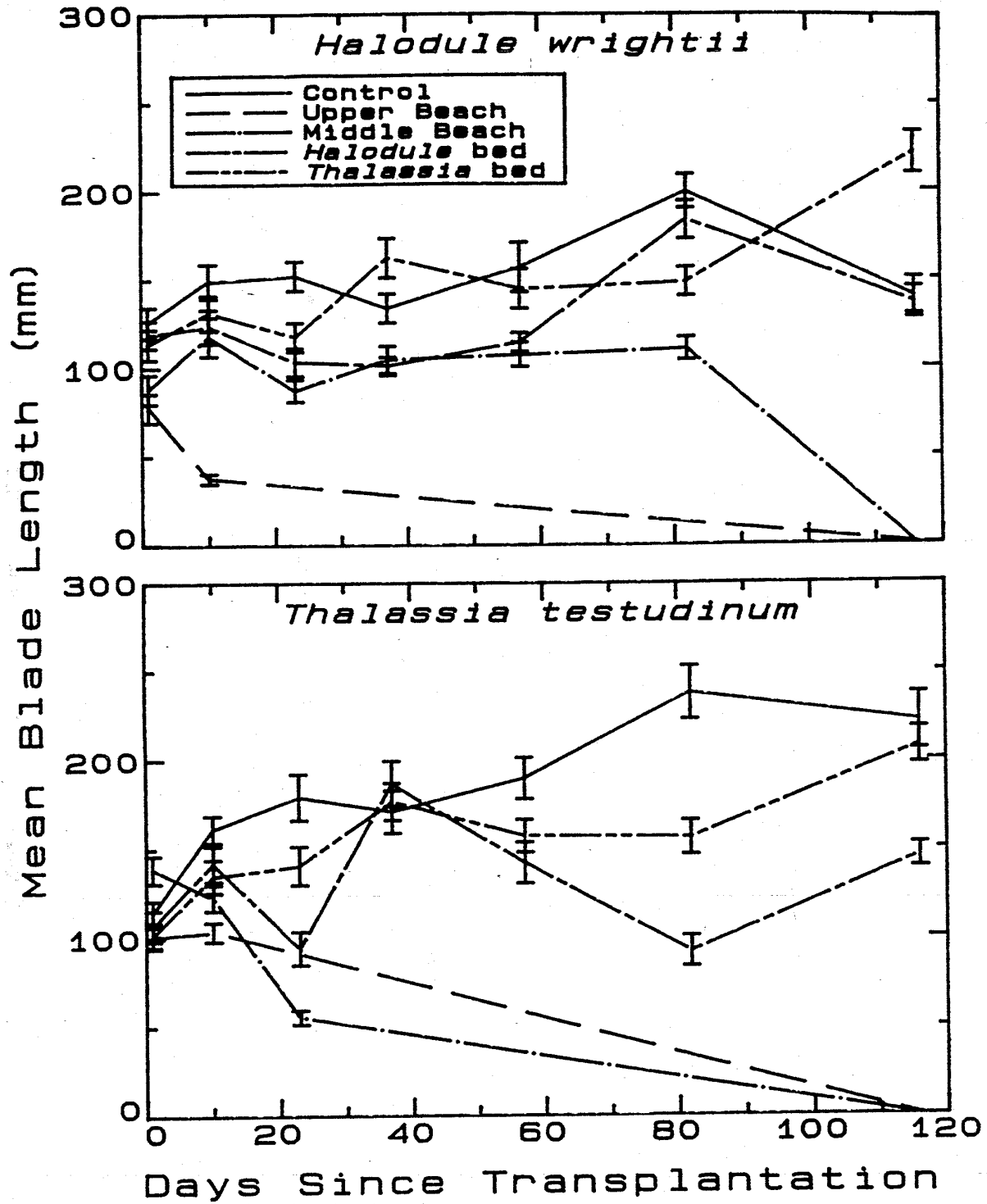


Figure 1. Response to *Halodule wrightii* (A) and *Thalassia testudinum* (B) to transplantation along a tidal gradient (Upper Beach > Middle Beach > Halodule bed > Thalassia bed in terms of tidal depth). Vertical bars represent two standard errors.

were performed between experimental and control treatments ( $\alpha = 0.05$ ). Both grasses rapidly perished at the Upper Beach station and Thalassia perished after 14 more days at the Middle Beach station. Leaves of both grasses initially turned brown and became visually indistinguishable from detrital blades except that they were still attached to the rhizomes (mean blade length then underestimates the degradation of the plants and is, therefore, a conservative measure of plant health). Halodule at Middle Beach eventually perished but it did persist for an appreciable period of time. Transplants of Thalassia into the Halodule bed persisted for the duration of quantitative measurements but the blades were discolored by brown patches and eventually the plants disappeared. All Halodule transplants into either grassbed and Thalassia transplants into its own bed appeared normal throughout the experimental period.

The regressions of blade length through time for both grasses at the upper two stations were noncoincident with the control samples (mean length being 53% and 61% relative to the control for Halodule and Thalassia respectively). The regression of Halodule transplanted into the Halodule bed paralleled the control samples (mean length of 83% of the control) while the regression of Halodule transplanted into the Thalassia bed was noncoincident with the control (mean length of 97% but with a steeper positive slope). Thalassia transplants within the Thalassia bed paralleled the control (86% of mean length) while the regression for those in the Halodule bed were noncoincident (at 73% of mean length). The parallel (but lower) regressions of transplants compared to control regressions can be interpreted as being due to the initial impact of transplantation.

The results of the manipulative experiments were uniformly negative. While shading platforms did not completely block light, insolation was appreciably and equally reduced at both sites. After 79 days, there was no statistically demonstrable damage to either grass. Leaf abrasion by Thalassia was found to have no discernable effect on Halodule. The artificial plants were left in place for one year and even after that period, no perceivable damage had taken place. Transplants of Halodule which were not protected by plastic sleeves into the Thalassia bed were statistically indistinguishable from the control samples while those that were protected exhibited greater transplantation damage but no evidence of competitive interactions (all tests were covariance analyses at  $\alpha = 0.05$ ). Thus, interactions by shading, abrasion, or short-term allelopathic effects were not found to occur.

In 1979 and in 1980, 10 plugs were tested for short-term allelopathic effects and the plugs were allowed to remain undisturbed for one year (20 total, 10 with and 10 without sleeves). After that year, a distinct and statistically valid difference did exist between treatments (Fishers Exact Probability test for two independent samples with  $\alpha = 0.05$ ). Eight of 9 plugs protected by sleeves persisted (the tenth plug had been excavated by a blue crab and that plug was excluded from analysis). Of the cores without sleeves, 9 of the plugs perished. Since the location of each plug was marked, the sediment transplanted

with the grass could be examined. In all cases in which the transplanted Halodule perished, rhizomes of Thalassia interdigitated the sediment. The unprotected plug which persisted was located in a small clearing and the sediment under it was free of Thalassia rhizomes. The competitive mechanism thus appears to require root-root interdigitation.

Two sets of disturbance experiments were performed (one inadvertently and one by design). The Thalassia bed stations were established 4 meters into the Thalassia bed from the border. Sampling was done on all visits to the site in 1979 and 1980 at high tide. In August of 1981, the site was visited during a spring low tide (0.06 m below mean tide level). A tongue of Halodule was found to extend from the old border zone 2 meters towards the 1979 station and 4 meters towards the 1980 station. Apparently, foot-traffic generated by sampling in 1979 and 1980 damaged either the rhizome system and/or the blades sufficiently to allow invasion by Halodule and to cause a noticeable decrease in the density of Thalassia.

The results of the herbivory (cropping) experiment are clear (Figure 2). Cropping resulted in an increase of Halodule in the Thalassia bed and softened the sharp decline at the border between the beds. Conversely, the extent of Thalassia in the Halodule bed declined and the border between the beds sharpened for Thalassia. Statistically (Newmans-Keuls Multiple Range Test at  $\alpha = 0.05$ ), there was no difference between Halodule in control and cropped area in the Halodule bed while Halodule numbers in the cropped area were greater than the control samples in the Thalassia bed. For Thalassia, there was a significant difference (a decrease) between the control and the cropped areas in both beds. The patterns derived from analysis of biomass paralleled all of the above and are not presented here.

## DISCUSSION

Seagrass distributions have long been of interest. One prominent feature of subtropical seagrass beds is the zonation of Halodule wrightii and Thalassia testudinum. Just as in algal systems where physiological limitations were first postulated to control zonation and only later were the roles of biological interactions appreciated (Lubchenco 1980), seagrass zonation patterns have been attributed to physiological limitations (Strawn 1961). Suggestions have been made that the relationship might be competitive (Phillips 1960; den Hartog 1970). As Dayton (1973) has strongly asserted, assuming the operation of an ecological mechanism (competition, predation, etc.) solely on the basis of descriptive and correlative data can be highly misleading and experimentation is often required for verification.

Desiccation has often been identified as the factor controlling the upper limit of seagrasses (den Hartog 1970; Humm 1956; Keller & Harris 1966; Moore 1963; Phillips 1960, 1962). At Seahorse Key, desiccation (drying) and head stress are typically paired and all heat

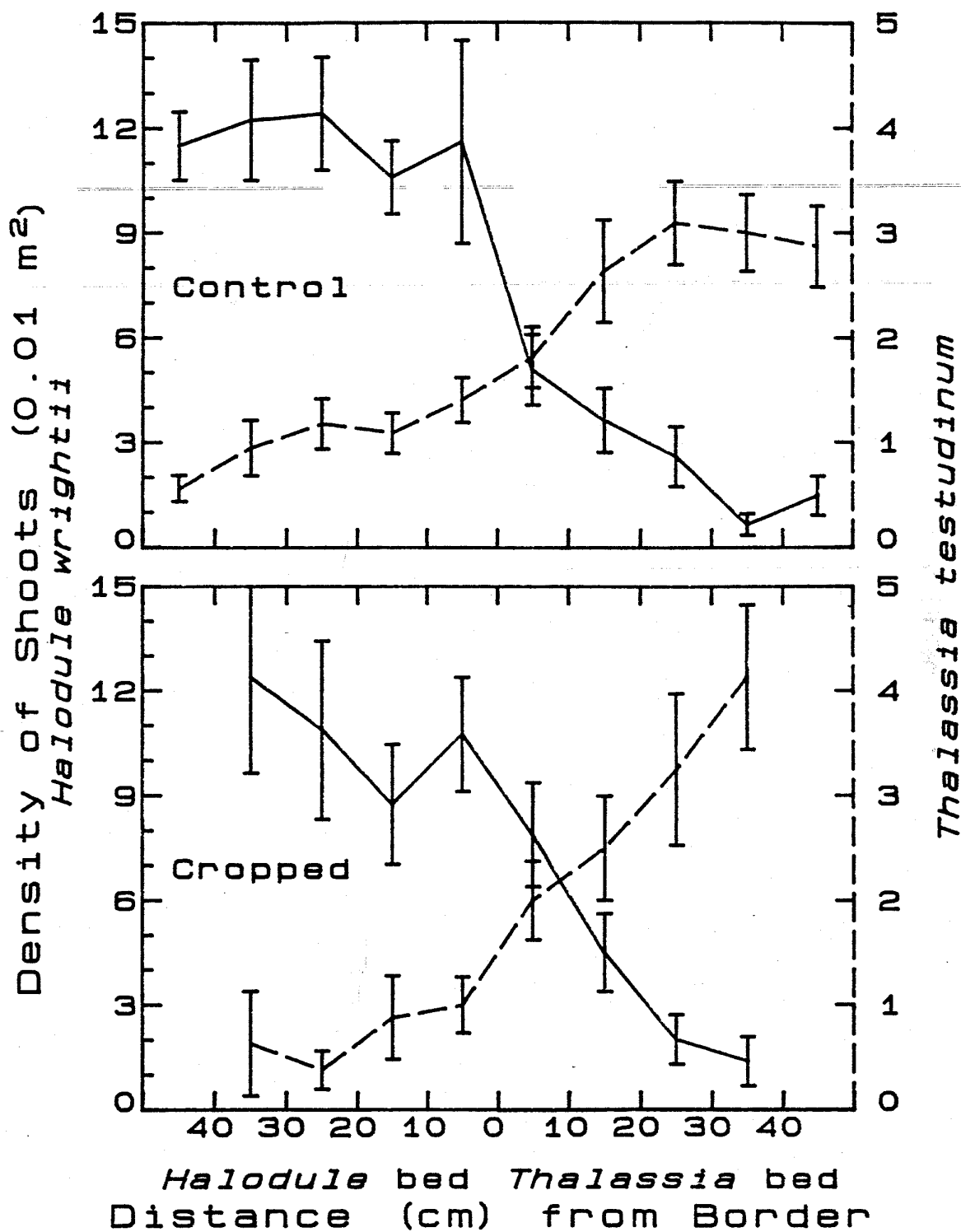


Figure 2. The pooled result of weekly cropping of *Halodule* and *Thalassia* in three experimental 1 meter square plots centered on the border between the grassbeds for a period of 119 days. Vertical bars represent two standard errors.

effects are subsumed within the term "desiccation" in this paper. However, see McMillan (1984) for systems in which the two effects can be separated. Halodule, relative to Thalassia, is characterized by a high volume-to-surface ratio due to narrower blades (0.5-1.5 mm versus 4-12 mm respectively) (den Hartog 1970) and a greater ability to form moisture-retaining mats due to a greater density of emergent shoots and the ability of those shoots to lie closer to the substrate (Phillips 1960). Thus, the morphologies of the grasses lend credence to the concept that Halodule is more desiccation-resistant and is able to penetrate further into the intertidal than Thalassia. The responses and the rapidity of those responses of Halodule and Thalassia to transplantation into water shallower than their respective grassbeds fully support the contention that the upper limit of the grasses is set by desiccation stress. Thalassia was more rapidly eliminated at either Upper Beach or Middle Beach than was Halodule and was demonstrably harmed when existing in clearings in the Halodule bed, but was able to overcome transplantation damage when placed in its own bed. Halodule was able to tolerate conditions at Middle Beach longer than Thalassia and was able to overcome transplantation damage in both grassbeds.

Based on quantitative transplantation data, the appearance of the grasses, and the distributional features of the beds (the leading edges trace depth contours), desiccation stress sets the upper limits of both beds. The presence of the Halodule bed with its moisture-retaining ability, however, does allow the Thalassia to intrude somewhat into the Halodule bed (Figure 2).

While this study did not address the factor(s) which control the penetration of Thalassia into deeper water (although light intensity and its correlate, water turbidity, have often been identified as causal) (den Hartog 1970; Phillips 1960), it has unequivocally demonstrated that Halodule can persist and thrive in clearings in the Thalassia bed at greater depths than the border zone of the zonation (Figure 1 & 2). Physiological limitations do not limit Halodule from extending its range from its observed limit at Seahorse Key to deeper waters. Causal sediment characteristics are highly unlikely given the invasion of Halodule into the Thalassia bed along paths to the Thalassia bed stations or within the herbivory experiments. If physiological limitations and sediment distributions can be eliminated, biological interactions must be considered.

Of the two major biological interactions which are known to control organismal distributions, predation and competition, predation does not appear to be of importance at Seahorse Key. There are relatively few herbivores which directly consume seagrass (Moore 1963; Randall 1965; den Hartog 1970; Ogden 1976) although herbivores are known to affect seagrass distributions (Camp et al. 1973) and the vigor of cropped plants (Phillips 1960). Of the major herbivores, reef fishes do not occur at Seahorse Key, turtles and manatees are rare, and while sea urchins are common in adjacent channels, they have not been observed in the grassbeds south of Seahorse Key. Furthermore, there has not been any evidence of cropping, i.e. clipped blades (Greenway



1976), grazed areas (Camp et al. 1973; Randall 1965), bitemarks (Greenway 1976) or evidence of differential epiphyte grazing (Howard & Short 1986). Since herbivory does not appear to be occurring to any noticeable extent, competition is implicated.

Competitive mechanisms between plants fall into several categories: (1) competition for light (Dayton 1975); (2) physical interactions via abrasion or whiplash (Dayton 1975); (3) allelopathic effects (Krebs 1972); and (4) root-root interactions including nutrient competition and root crowding (Richlefs 1976). Shading has been identified as a potential intraspecific competitive mechanism (McRoy & McMillian 1977) and thus could be an interspecific mechanism. Since Thalassia has a broader blade and, due to the structure of the emergent shoot, stands higher than Halodule, Thalassia has the potential of out-competing Halodule for light. The results of the shading experiment indicated that the potential is not realized. Given the reality of shifting currents and high turbidity, it is highly unlikely that Thalassia could outshade Halodule.

Leaf interactions by abrasion were quantitatively assessed for 79 days and qualitatively assessed for over a year. In neither instance was any evidence generated to support leaf abrasion as an effective competitive mechanism.

Short-term allelopathic effects could be due to soluble, dispersing compounds or to contact-toxins, and Halodule is known to exude significant amounts of fixed organic carbon into the sediment (Moriarty et al. 1986). The presence of soluble compounds was tested by exposing one cohort of Halodule to Thalassia root-systems and protecting another cohort from contact. The results were unambiguous. Halodule experienced no deleterious effect due to exposure to Thalassia over the experimental period. This result was not unexpected since mixed beds and some interdigitation at the border zone do exist. If there were soluble compounds, a bare zone would be predicted.

Long-term effects did exist. Plugs of Halodule exposed to Thalassia root-systems for one year disappeared while those which were protected persisted. In all cases where Halodule vanished, Thalassia root systems interdigitated the sediment of the Halodule plug. This effect could be due to a number of mechanisms which are not distinguishable by the experimentation used here, but all involve slow root-growth of Thalassia and the close proximity of the root-systems of the two grasses.

The distinct zonation observable at Seahorse Key appears to be a result of Thalassia being unable to penetrate into the intertidal due to physiological limitations (desiccation resistance) and the inability of Halodule, which can survive in the intertidal, to penetrate into the subtidal due to being outcompeted by Thalassia. Mixed beds, however, are known to exist (see Introduction for references) and a discussion of zonation would be incomplete without consideration of the mechanisms such as tidal gradients and disturbance, which can obscure the zonation

pattern.

One potential generator of mixed beds is the slope of the substrate. Given the desiccation-ameliorating effects of the Halodule bed, there should be an extension of Thalassia into the Halodule bed effectively creating a zone-of-confusion along the border extending over a few centimeters of tidal height and a mixed bed over some horizontal distance. If the slope would double, the horizontal extent would be halved, or if the slope became twice as shallow, the horizontal extent would double. At Seahorse Key, a raised bank approximately 15 m wide parallels and borders the main channel. The broad flat bank occurs at the same tidal height as the grassbed border zone and is covered by a mixture of both grasses.

Disturbance can also cause mixed beds or tongues of Halodule extending into the Thalassia bed by decreasing the competitive ability of Thalassia and thereby allowing Halodule to invade and coexist in the Thalassia bed. Sources of such disturbance include physical disruption due to propeller damage or waders, defoliation due to storms or environmental fluctuations, or reduction in photosynthetic tissue by herbivory. Zieman (1976) has discussed the effects of propeller damage on grassbeds. At Seahorse Key at the border zone, new scars are devoid of vegetation, scars of moderate age often have Halodule extending up the scar into the Thalassia bed, and old, deep scars occasionally have Thalassia extending into the Halodule bed along the bottom of the trough made by the propeller. Similarly, the observation that weekly wading along the transects across the grassbeds allowed tongues of Halodule to extend from the border zone to the Thalassia bed stations indicates that low-level but repeated physical disruption can affect the ability of Thalassia to exclude Halodule.

Storm damage can also result in mixed beds. The degree of damage is obviously a function of the propensity of the blades to separate from the rhizomes, and the storm intensity. Thalassia blades are easily broken from the rhizome (Tomlinson 1972) and this grass can be expected to be more severely impacted by the storms than Halodule. While the extent of storm damage has ranged from slight (Oppenheimer 1963) to reports of whole plants being ripped from the bottom (Moore 1963; Reid 1954), the normal impact of storms is defoliation (den Hartog 1970). Reid (1954) described the hurricane of 1950 in the Cedar Key area as having winds greater than 100 mph, being accompanied by 24 inches of rain (causing a salinity drop from 23.5 to 9.7 ‰ for 4 days), and being responsible for substantial seagrass disruption. A survey of seagrass distributions was carried out in the same area after only a few months (Strawn 1961) and documented that Halodule extended through the Thalassia bed. The same area was examined qualitatively in 1980 and zonation of the grasses was visible. Strawn's (1961) observations could be due to defoliation of the grassbeds in 1950 due to the hurricane, followed by a rapid colonization of the disrupted zone by Halodule (which has a faster growth rate and greater dispersal abilities than Thalassia (den Hartog 1970)). After the Halodule became established throughout the Thalassia bed, only gradually and over a

period of years would Thalassia outcompete Halodule. Large scale mixed beds on tidal gradients where zonation would normally be expected may well be due to historical events such as storm damage or, conceivably, extreme salinity fluctuations which act to depress Thalassia sufficiently to allow the invasion of Halodule. Given the slow recovery rates of Thalassia (Zieman 1976), years may pass until the zonation is reestablished.

The final source of disturbance which could obscure the zonation pattern is herbivory. While relatively few organisms directly consume seagrass (see above for references), herbivores can exert a disproportionate influence on plant distributions (Vance 1979; Duggins 1980) and are known to affect seagrass beds (Camp et al. 1973; Randall 1965). The procedure of weekly clipping the seagrass a few centimeters above the substrate mimics the feeding activities of green turtles (Bjorndahl 1979). Turtles repeatedly mow a given area and consume the regenerating blades. While the maximum population densities of turtles in the grassbeds of the Florida Gulf Coast are unclear (Carr & Ingle 1959), turtles may have had a major impact on the organization of seagrass beds (Randall 1965), and their form of herbivory is far less deleterious to the grass than the disruptive activities of birds (McMahan 1968) or manatees (Rathbun pers. comm.), which rip rhizomes from the substrate, or of sea urchins which can obliterate beds if they occur in dense aggregations (Camp et al. 1973). This form of herbivory was chosen to minimize damage to the grasses while simulating herbivory, and the results are clear. Whether measured by number of emergent shoots or total plant biomass, cropping of Thalassia reduced the penetration of Thalassia into the Halodule bed and permits the invasion of Halodule into the Thalassia bed. Since Thalassia plants on the border or plants which occur in the Halodule bed are stressed due to exposure, additional stress due to cropping could overwhelm the plants and result in their decline or disappearance. Plants not removed by the cropping must divert energy from root growth and competitive interactions into the regeneration of photosynthetic tissue and must contend with less energy production during the regeneration phase. Halodule with its faster growth rate should be able to tolerate moderate cropping and invade the Thalassia bed when Thalassia is no longer able effectively to exclude Halodule.

The phenomenon of zonation due to competition being broken or obscured by selective predation on the superior competitor is well established and well documented (see Dayton 1975 for an extended list of examples, and Mann 1973 and Vadas 1968 for marine plant examples). The effect of herbivory on seagrass zonation follows the same pattern but does not require selective predation. If the superior competitor, in this case Thalassia, is differentially harmed by herbivory due to a slower recovery rate, equal predation can occur on both grasses with the net effect of decreasing the competitive ability of Thalassia. Mixed beds could thus be maintained by herbivores which simply feed on the mixture of grasses without selecting one or the other.

The suggestion exists that Halodule acts as a classical pioneer or

early successional species and conditions the sediment (Phillips 1974) which then allows Thalassia to invade (Van Breedveld 1975). It is also possible, however, that seagrass succession is an example of tolerance succession rather than facilitation succession (see Connell & Slatyer 1977). Halodule may simply appear as an initial colonizer due to its high dispersal ability and rapid growth rate. If Halodule were present or absent, Thalassia might well follow the same schedule of invasion and grassbed establishment. Transplantation experiments can separate these possibilities.

In summary, the obvious zonation of Halodule and Thalassia in intertidal and shallow subtidal habitats is due to Thalassia being limited by desiccation/heat-stress to the subtidal or deep intertidal. Halodule, being more desiccation resistant, can extend farther into the intertidal and forms a monoculture there. Under conditions of little or no disruptive stress, Thalassia is able to outcompete Halodule via long-term root-interactions and to restrict Halodule to the intertidal. The steeper the slope, the more pronounced is the border zone between the grasses. If small-scale disruptions (propellers or waders), large-scale disruptions (storms or extreme environmental fluctuations) or herbivory occur, mixed beds may result and may persist for years. If such disturbances occur more frequently than the recovery period, mixed beds may persist indefinitely.

#### ACKNOWLEDGEMENTS

I thank Dr. F. J. Mauro and the Seahorse Key Marine Laboratory of the University of Florida for providing necessary facilities, and Drs. J. S. Davis and J. M. Lawrence for helpful suggestions. I especially wish to thank my field and laboratory team, and my wife, Kimmy Bloom. Partial funding of this research was made available by the Division of Sponsored Research of the University of Florida.

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This publication should be cited as:

Webb, F. J., editor. 1987 Proceedings of the Fourteenth Annual Conference on Wetlands Restoration and Creation. Hillsborough Community College, Tampa, Florida.