EFFECTS OF SNAIL GRAZING AND ENVIRONMENTAL FACTORS ON THE EXPANSION OF MANGROVES INTO SALT MARSHES

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TABLE OF CONTENTS

.

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

A central goal of ecosystem ecology is to describe and understand the abiotic and biotic factors controlling an ecosystem. Global climate change models, with its predictions of rising sea levels, shifts in biogeochemical cycling rates, and elevated temperatures necessitates understanding these controls in order to better predict the impacts brought on by widespread climactic change. Although there have been numerous studies on terrestrial and marine systems, it is in the intermediary area, the coastal wetlands, that may be among the first to exhibit these impacts.

Because of their position between land and sea, coastal systems are not only under the influence of abiotic terrestrial controls, i.e. soil chemistry, hydrology, geology, meteorological, and atmospheric influences but also marine controls such as salinity and tidal variation (Levin et al. 2001). Biotic factors increase the complexity of the system, as floral and faunal community members can come from both terrestrial and marine sources potentially leading to strong competition for nutrients and space. Regularly occurring natural disturbance can range from flooding and drought, hurricanes, fire, burial, erosion, grazing, and exposure to toxins (McKee et al. 1999) .

Regularly flooded salt marshes, common along the Atlantic and Gulf coasts of the United States are highly productive systems (Squiers et al. 1974). Nutrient manipulation studies on several dominant marsh species have shown they are

mainly nitrogen limited (Gallagher 1975, Hopkinson et al. 1984, Howes et al. 1986, Mendelssohn 1989, Alexander et al. 2006), exhibiting little or no response to phosphorus additions (Sullivan et al. 1974, Buresh et al. 1980, McHugh et al. 2004). Substrate in salt marshes was found to have higher bulk densities than that found in fresh and brackish marshes (Hatton et al. 1983). Plant community structure in the marsh is thought to be influenced by elevation, salinity, inundation periods, and tidal amplitude (Wiegert et al. 1983, Howes et al. 1986, Hester et al. 1998, Alexander et al. 2002, McHugh et al. 2004, Roland et al. 2005). Floral assemblages are often not diverse (Howard et al. 2000) and often occur with distinct zonation (Bertness 1991) based upon individual species' ability to tolerate these stressors. In the low marsh zone of the Atlantic Coast and the interior marsh zone of the Gulf Coast smooth cordgrass, *Spartina alterniflora* Loisel. is the dominant emergent plant species (Bertness 1991).

Historically, salt marsh systems were thought to be controlled by abiotic factors, but recent studies suggest top-down control exerted by the marsh periwinkle, *Littoraria irrorata* (Say) (Gastropoda:Prosobranchia) was shown to drastically reduce live *S. alterniflora* biomass (Silliman et al. 2001). *Littoraria irrorata* is a ubiquitous marsh detritivore, found on both the Atlantic and Gulf coasts (Stiven et al. 1976, Vaughn et al. 1992) but often climbs stalks of live and dead *S. alterniflora.* Earlier work thought that *L. irrorata's* vertical movement on *S. alterniflora* was for prey avoidance, in response to tidal alteration, and/ or thermoregulation, (Vaughn et al. 1992, Hovel et al. 2001), and that *L. irrorata* did

not feed on green *S. alterniflora.* A tagging experiment also showed that *L. irrorata* has a narrow horizontal range of movement (1 m from its release point over a 4-month time period) (Vaughn et al. 1992). Laboratory trials further support *L. irrorata's* position as an omnivorous detritivore, e.g., the periwinkles were found to positively orient itself to both *S. alterniflora* extracts as well as to extracts of crushed conspecifics (Wollerman 2003). Further, Cammen et al (1980) calculated *L. irrorata* consumption rate to be only one-tenth of total net marsh production and made up mainly of detritus and marsh sediment. More recent studies however, suggested that *L. irrorata* will radulate healthy *S. alterniflora,* which enhances the growth of fungi that are a primary food source (Silliman et al. 2003b, Lee et al. 2006). While one study did not find this type of feeding to be significant in dead *S. alterniflora* at periwinkle densities of 85 individuals m^{-2} (Newell 2001), the extent of this type of feeding on green shoots has been suggested to be so great that estimates of *S. alterniflora* biomass, without the removal of *L. irrorata*, have been largely underestimated (Silliman et al. 2003a). Further it is argued that the combined effect of high densities of *L. irrorata* and drought stressed *S. alterniflora*, can cause the transformation of entire marshes to mudflats (Silliman et al. 2005).

Along the Gulf Coast of the United States temperate salt marsh meets tropical mangrove systems. During the past two decades, the absence freezing winters, has allowed the expansion of *A. germinans* (L) into areas previously dominated by *S. alterniflora* (Stevens et al. 2006, Stuart et al. 2007). Although a tropical

species, prior studies found tidal action and propagule predation limited propagule establishment (Patterson et al. 1997) rather than environmental factors such as salinity and temperature (McMillan 1971). Indeed, tolerance of salinity by *A. germinans* (Lugo et al. 1974, Lovelock et al. 2006) together with it's high photosynthetic water use efficiency (PWUE) (Lovelock et al. 2003) may have facilitated its survival in 2000 when an apparent drought-induced die-back of *S. alterniflora* occurred along the Mississippi River deltaic plain (McKee et al. 2004).

Shifts in species distribution and dominance are thought to be some of the effects of increased global temperatures. Global vegetation models have been developed in an effort to better predict the effect of wide-scale climate change on ecosystems (Bergengren et al. 2001, Iverson et al. 2001, Bonan et al. 2003, Thomas et al. 2004). These models predict poleward migration of vegetation in which increased temperature, shifts in precipitation patterns and biogeochemical nutrient cycling rates have profound effects on ecosystem assemblages and productivity across the globe. These findings are supported by experimental studies that have found shifts in dominance patterns in various ecosystems when exposed to stressors such as increased nutrient availability, changes in freshwater availability, and increased CO_2 levels (Emery et al. 2001, Alexander et al. 2002, Bertness et al. 2002, Breshears et al. 2005, Klanderud 2005, Forbes et al. 2006).

Thus, the northward expansion of *A. germinans* may indicate a shift away from temperate salt marsh to tropical mangrove. While the extent of the sedimentation has been found to vary based upon mangrove location (riverine, basin, fringe) mangrove forests have long been attributed with sediment trapping and increasing elevation (Lugo 1980, Ewel et al. 1998). Similar to salt marsh systems, species zonation occurs due to environmental factors (Lugo et al. 1974, Chen et al. 1998, Sherman et al. 1998, Allen et al. 2003). The shift from fast growing herbaceous salt marsh systems to a slower growing woody forest dominated system would slow nutrient cycling but would support a greater variety of faunal species although species, particularly birds, dependent upon salt marshes would be forced out.

The purpose of this study was twofold: to determine what role the marsh periwinkle has in the competitive interaction between *A. germinans* and *S. alterniflora* and, to examine how environmental factors such as nutrient availability or salinity stress affects the competition between *A. germinans* and *S. alterniflora.*

METHODS

PLANT SPECIES

Spartina alterniflora Loisel.

Spartina alterniflora Loisel. is a temperate grass with a latitudinal distribution from the Atlantic and Gulf coasts of the United States and to Newfoundland. Along the Atlantic coast, *S. alterniflora* occurs in two growth forms, tall and short, while in Louisiana, such growth forms are less distinct with plant heights being intermediate to that in Atlantic marshes. Numerous studies have documented *S. alterniflora's* ability to thrive in anoxic (Koch *et al.* 1989, Bertness 1991) nitrogen limited (Hopkinson et al. 1984, Howes et al. 1986) soils which is often cited as the reason for the distinct interspecies zonation seen in Atlantic coast marshes where *S. alterniflora* dominates the low marsh (Bertness, 1991). In Louisiana, *S. alterniflora* exists in highly productive monospecific stands with reported biomass figures ranging from 161.5-1061 g m^{-2} (Kirby et al. 1976, White et al. 1978, Buresh et al. 1980, Hopkinson et al. 1980).

Avicennia germinans

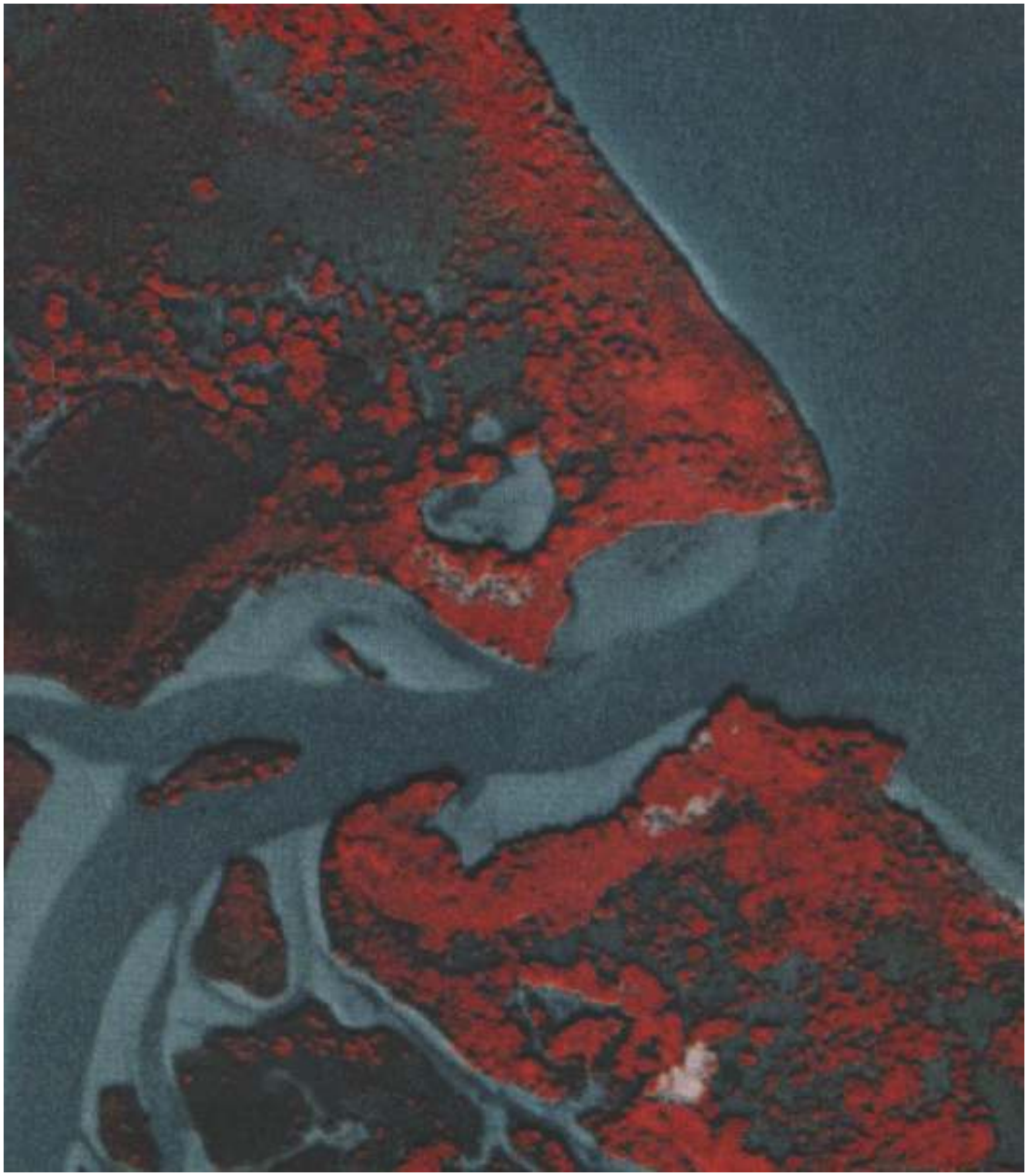
Avicennia germinans occurs in as a perennial shrub in the saline marsh zone in coastal Louisiana where salinity levels were found to range from 8-29% (Visser et al. 1998) . *A. germinans* is vulnerable to freezing temperatures which Stuart et al. (2007) found to disrupt xylem function and ultimately limiting its northern expansion, while Stevens, et al (2006) hypothesized that the failure of *A. germinans* to flower and produce propagules was due to the freezing conditions

from the winter prior. While freeze intolerant, *A. germinans* is known to be tolerant of high saline environments. Lovelock et al (2003) suggests that *A. germinans'* high photosynthetic water use efficiency (PWUE) was at least a contributing factor to its ability to dominate high and hypersaline environments. Comparatively, *A. germinans* leaf litter had greater nitrogen concentrations and greater dry mass loss in litter bags than that of *R. mangle* and *L. racemosa* suggesting faster rates of decomposition of *A. germinans* leaf litter (Twilley et al. 1986). *Avicennia germinans'* ability to expand into new areas may be due to its buoyant cryptoviviparous propagules that are capable of establishing roots in areas that are regularly inundated (Patterson et al, 1997; McMillan, 1971).

STUDY AREA

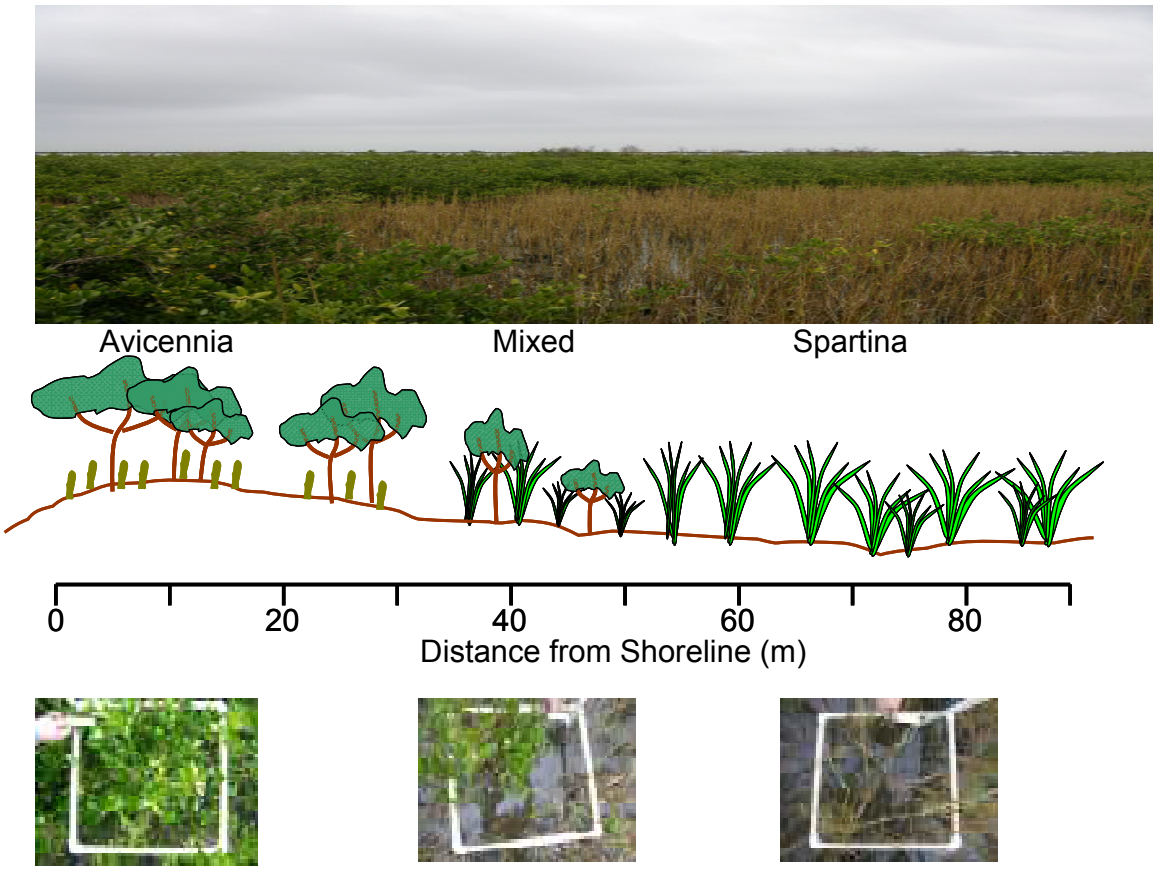
A field experiment was conducted along Bayou Lafourche near Port Fourchon, Louisiana (29º 06'20 N, 90º11'39 W) which is at the southern tip of Lafourche Parrish (Fig 1). Three vegetation zones (Fig 2) occur in relation to this waterway: the mangrove zone, closest to the water and dominated by *A. germinans* (areas in red in aerial photo-Fig 1); an inner marsh zone dominated by *S. alterniflora* (darkest area in aerial photo-Fig 1), and a narrow zone where the two species meet, hereafter referred to as the Mixed zone (gray area in aerial photo Fig 1).

Figure 1-Aerial photo of study area



From K. McKee, NWRC

Figure 2-Zonation across waterway

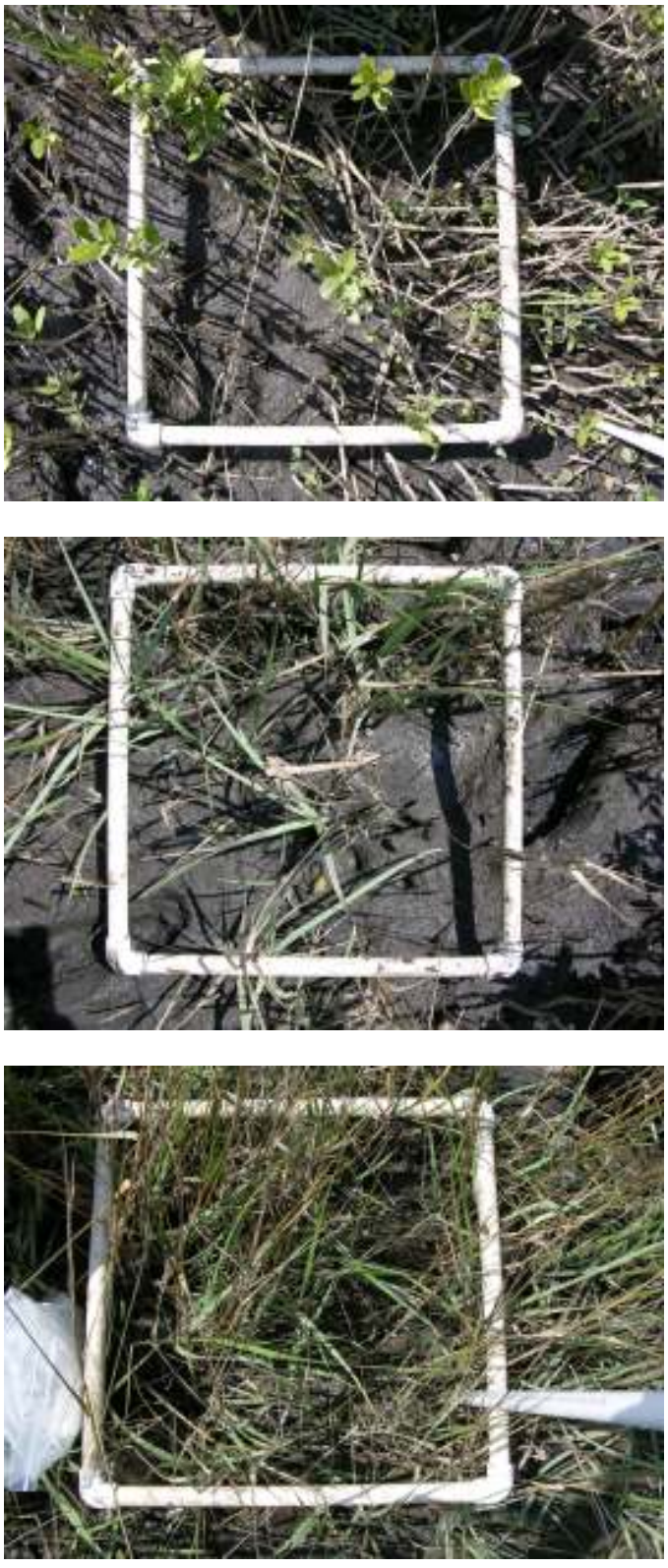


In April 2006, a detailed survey of the vegetation was conducted across the mangrove, mixed, and marsh zones (described below). A manipulative field experiment (described below) was also established in April 2006 in the *S. alterniflora*-dominated zone about 60 m from the waterway. Plant material was collected from this same salt marsh, in the vicinity of the field plots, in April 2006 for a greenhouse experiment (described below).

VEGETATION AND SNAIL SURVEY

Natural densities of snails and vegetation structure were determined across the three marsh zones: *S. alterniflora* mono-specific (S), Mixed *A. germinans* and *S. alterniflora* (M), and *A. germinans* (A) mono-specific. Within each zone, sampling stations were randomly selected from a larger pool of sites that had been pre-identified and flagged. Numbered flags were placed at locations with a juvenile *A. germinans* within a 0.25 m^2 radius. Corresponding numbers were written on sheets of paper and randomly chosen for census (5 stations per zone). Once the sample stations were identified, a 0.25 m^2 quadrat was used to delineate the sampling area (Fig 3). Within each of these quadrats, all snails located on the ground or on the vegetation were collected and bagged, according to the snail's location within the quadrant, i.e., ground, base or stalk of live, dead, stumps of S*. alterniflora*, on *A. germinans* pneumatophores, or on *A. germinans* seedlings. After removal of snails from within the quadrat, canopy height measurements and plant density were then determined to characterize the occurrence and morphology of *A. germinans* and *S. alterniflora*. Within each quadrat, overall height of live *S. alterniflora*, counts of live and dead *S. alterniflora* culms, and count of *A. germinans* present were recorded. After counting and measuring the vegetation, the shoots were clipped at ground level and bagged (Fig 4).

Figure 3-Photos of 0.25 m^2 quadrats in Avicennia (top), Mixed (center), and Spartina (bottom) zones



Taken by K.McKee April 2006

Figure 4-Photos of 0.25 m^2 clipped quadrats in Avicennia (top) and Spartina (bottom) zones

Taken by K.McKee April 2006

The samples were weighed to the nearest 0.1 g and archived. The collected snails were sorted by species, and all species were recounted in the laboratory. *Littoraria irrorata* was examined in more detail. Shell diameters, at the widest point with the apex of the shell oriented to the left, were measured using calipers. After measurements, the live snails were placed in labeled bottles and preserved in ethanol.

FIELD EXCLOSURE EXPERIMENT

An experiment was conducted to determine the effects of snail grazing on *S. alterniflora* and interactions with soil nitrogen on relative growth of *A. germinans*. The experiment was located at the interior edge of the Mixed zone where the dominant vegetation was *S. alterniflora* and a few *A. germinans* seedlings occurred, i.e., the zone of active expansion of mangrove into salt marsh. The experimental design was a randomized block with a factorial treatment arrangement. Twenty-four plots were established with each plot centered on an *A. germinans* seedling that had established naturally. The targeted seedlings (Fig 5) were all of approximately the same size and were part of the cohort that had been produced the previous fall (10-17 cm, 2-6 leaves, cotyledons attached). Plots were established in four blocks, each with 6 plots. Once the plots were located and the boundaries (1 m^2) marked, each plot was randomly assigned to one of 6 treatment combinations as follows. There were 4 caged and 2 uncaged plots (Table 1 for notation). The caged plots were subjected to each of two snail

treatments (+/- snails) and two nitrogen treatments (+/- N as urea). Nitrogen treatments also were applied to the two uncaged control plots within each block. The uncaged controls were used to assess caging effects only.

Table 1-Notation of treatments

Notation	Caged/Uncaged	Snail Density (Ambient/Removal)	Fertilization (Y/N)
CA	Caged	Ambient	No
CAN	Caged	Ambient	Yes
CO	Caged	Removal	No
CON	Caged	Removal	Yes
UA	Uncaged	Ambient	No
UAN	Uncaged	Ambient	Yes

Reference to treatments in Results will follow this notation

Figure 5-Photo of targeted Avicennia seedling (to right of flag)

Taken by K.McKee April 2006

The 1 m^2 exclosures were erected using PVC piping, hardware cloth (1 mm mesh), and galvanized steel wire. PVC pipes (1 m tall) were placed at the four corners of the plot and the hardware cloth was attached to the pipes with zip ties (Fig 6). In order to prevent the snails from burrowing under the cloth, a portion of the hardware cloth was buried below the soil surface. Galvanized steel mesh (10 cm wide strip) was attached to prevent the snails from traversing the top of the exclosure. For the uncaged plots, PVC pipes marked the corners, but were otherwise undisturbed (Fig 7).

Figure 6-Photos of exclosure construction (top) and completed exclosure (bottom)

Taken by K.McKee April 2006

Figure 7-Uncaged Plots With PVC marker pipes

Taken by K.McKee April 2006

Interiors of all caged and uncaged plots were accessed from a portable platform (2.2 m aluminum bleacher seat) laid across the plot about 50 cm off the ground to prevent disturbance of the vegetation and snails in and around the plots. Prior to treatment application, snail densities and vegetation structure were assessed in April 2006 (Fig 8). Within each plot, a circular quadrat (0.1 m^2) was centered on the target *A. germinans* seedling, and the height; number of nodes, leaves, presence/absence of cotelydon were measured and recorded. Other *A. germinans* present within the 0.1 m^2 quadrat were removed, although this was only necessary in a few cases. Density, height, and condition (live/dead/frayed) of *S. alterniflora* within the 0.1 m^2 were also determined.

Figure 8-Circular 0.10m^2 quadrat and initial data collection prior to exclosure construction

Taken by K.McKee April 2006

After initial plant and animal measurements treatments were initiated in April 2006. Fertilization treatments were applied by inserting urea fertilizer belowground with a total 49.7 g of nitrogen m^{-2} using nine equal applications distributed across the plot to ensure that the fertilizer treatment would remain in the exclosure and not inadvertently fertilize the surrounding areas. Holes 2 cm in diameter were cored in the soil, the fertilizer was poured in (at low tide), and the top of the hole was then plugged with sediment (Fig 9). Unfertilized plots were similarly disturbed by removing and replacing nine soil cores. Fertilizer was applied initially in April 2006 and repeated in June and October 2006.

Figure 9-Application Of Urea Using Piston Corer

Taken by W. Vervaeke April 2006

The snail treatment (+/- snails) was applied to all caged plots as follows. The snail removal treatment was accomplished by removing all visible *L. irrorata* from within the exclosure in April 2006; two persons conducted a meticulous search for all adult and juvenile snails. The +snail treatment plots were not manipulated, i.e., the snail density was comparable to the average densities in the marsh. On each subsequent trip, any snails that were observed in the snail removal treatment were counted and removed.

GREENHOUSE EXPERIMENT

To test the effects of salinity levels on the competition between *S. alterniflora* and *A. germinans* as well as its effects on snail grazing, a greenhouse mesocosm experiment was conducted. The main objective of this experiment was to assess how salinity influences the interaction between *A. germinans* and *S. alterniflora* directly and indirectly by influencing the grazing by *L. irrorata*. The experiment

was a completely randomized design with a factorial treatment arrangement: 2 salinity levels (25 and 50 ppt) and 2 snail treatments (low and high density) and replicated 12 times for a total of 48 mesocosms.

Mesocosms were prepared in three stages: plant material was collected from the field site (April 2006), mesocosms were constructed and initial acclimation conducted in Louisiana at the National Wetlands Research Center (NWRC) (April to June 2006), mesocosms were then transported to Texas Christian University (TCU) for conduct of the experiment (July 2006 to February 2007). *A. germinans* seedlings with 2-6 leaves were collected from the Mixed zone at the field site. Seedlings were carefully excavated along with the surrounding soil so that roots were not damaged; any seedlings that showed signs of visible damage to shoot or roots were not used. Intact plugs (26 cm x 40 cm) of *S. alterniflora* (containing 2-3 culms) were also excavated nearby. Three plugs of *S. alterniflora* and one *A. germinans* seedling were planted in 3 gallon, 0.1 m diameter pots in an unamended mineral soil which was comprised of river sediment classified as “top soil” from a Lafayette, LA local retailer (Dominigue’s Sand and Gravel, 3198 Moss Street, Lafayette, LA). A total of 48 mesocosms were prepared and acclimated in a greenhouse at NWRC. Mesocosms were initially flooded with a 15 ppt saline solution for 10 weeks (using Instant Ocean synthetic sea salts, Aquarium Systems Inc-Marineland Systems, Mentor, OH 44060). The mesocosms were then drained and transported to TCU where they were reestablished in a polycarbonate greenhouse whose roof was covered by shade cloths from July to October 2006.

Daily summer temperatures were 32-37 C and were moderated by use of thermostat controlled fans and a timed misting system.

After final acclimation, the mesocosms were then randomly assigned to salinity and snail treatments. Salinity treatments were set at 25 or 50 ppt by gradually raising salinity by 5 ppt wk^{-1} to the target level. Once the pots had reached the target salinity and acclimated 1 week, galvanized steel cages were attached to the pots that were to receive the snail treatment (Fig 10). A perch (upended plastic drink cup) was installed in each pot to provide a standardized place for snail addition and to ensure a location for snails to escape from the water in the pots.

Figure 10-Greenhouse pots caged (left) and uncaged (right)

Taken by S. Eady August 2006

Approximately 1000 *L. irrorata* snails were collected from the field site in July 2006 and transported in a cooler to TCU where they were acclimated for 4 wks in two open rectangular plastic tubs with the bottoms filled with 25 ppt water and stalks of *S. alterniflora*. Hardware cloth, like that used in the caging experiment was fastened to top of the tubs to prevent escape. Water was routinely drained and refilled. Prior to application, snails were measured to document size. To each snail addition mesocosm, 25 snails, all of approximately 15 mm in diameter, were placed on the perches within the cages in on 12 August, 2006. The latter approach was implemented after a preliminary trial showed high mortality of snails added without perches. Also, once the snails were added, the densities were not readjusted and were allowed to equilibrate at that supported in each salinity level:

average of 10 snails at 25 ppt and 5 snails at 50 ppt. The other half of the pots received no snails. Pots were periodically flushed and the salinity readjusted as needed by addition of tap water. Any algal growth occurring in the pots was periodically removed.

Relative growth rates of *S. alterniflora* and *A. germinans* were determined in each pot; measurements were made at 3 week intervals. Within each pot, three shoots of *S. alterniflora* were tagged and their changes in height were measured to estimate rates of shoot elongation over time. For *A. germinans* seedlings, the height, number of nodes, and number of leaves were measured. Additionally, the terminal leaves of the *A. germinans* seedling were tagged and rate of expansion measured through subsequent weeks.

STATISTICAL ANALYSES

All statistical analysis was done using JMP IN 5.1.0 Statistical Discovery (SAS Institute, Cary, NC 2003). Analytical procedures used for each study is described below. Most graphs were created using Microsoft Excel 2002 (Microsoft Corporation, 1985-2001) but equations for lines and R^2 values were done in JMP.

Marsh Density Study

To determine whether biomass and periwinkle densities differed across the three zones, the “Fit Model” function was used with the marsh zone defined as the effect and the test metrics, i.e. total biomass, as the y-variable. With the model

"Personality" defined as Standard Least Squares and the model "Emphasis" defined as Effect Leverage. To test the relationship between periwinkle density and biomass, the "Fit X by Y" function was used with the marsh zones in the "By" factor and the "Fit line" function used to determine the correlation coefficient. Significance for all tests was determined at less than or equal to 0.05.

Field Exclosure Experiment

For all figures, all weights and densities reported are mean numbers. Data was converted from 0.25 m^2 to $1m^2$ where appropriate. Simple ANOVA was used to compare means (specific procedures follow). To test effect of interaction between periwinkle and fertilization, a 2x2 cross classified analysis of variance with two levels of periwinkles (ambient and removal) and two levels of fertilization (control and fertilization) was run on the caged plots only (specific procedures follow).

ANOVA was run using "Fit X by Y" function with treatment type used as the x factor. For significant ($p<0.05$) results Tukey's HSD post hoc analysis was used. Because of the multiple measures, growth rates were determined by fitting line through repeated measures and determining the slope of that line. In order to empirically depict field observations when *S. alterniflora* height analysis was found not be significant, mean *S. alterniflora* height was multiplied by the mean number of live *S. alterniflora* stems giving a proxy biomass figure. Predicted biomass was also calculated using biomass model developed in marsh density study.

To test the interaction of snails*fertilizer, the “Fit Model” function was used with the “Full Factorial” macro selected. Snails, Fertilizer, and Snails*Fertilizer were used as Model Effects. Significance was determined at the $p<0.05$ level. Data was converted from 0.10 m^2 to $1m^2$ where appropriate.

Greenhouse Experiment

One way ANOVA was run to test effects of salinity, with salinity levels as the x factor. Relative growth rates of *A. germinans* and *S. alterniflora* were calculated by taking the natural log of the change in height and dividing by the total number of week (28). Because of high periwinkle mortality across salinity treatments, analysis of data includes only those pots that did not have periwinkles present.

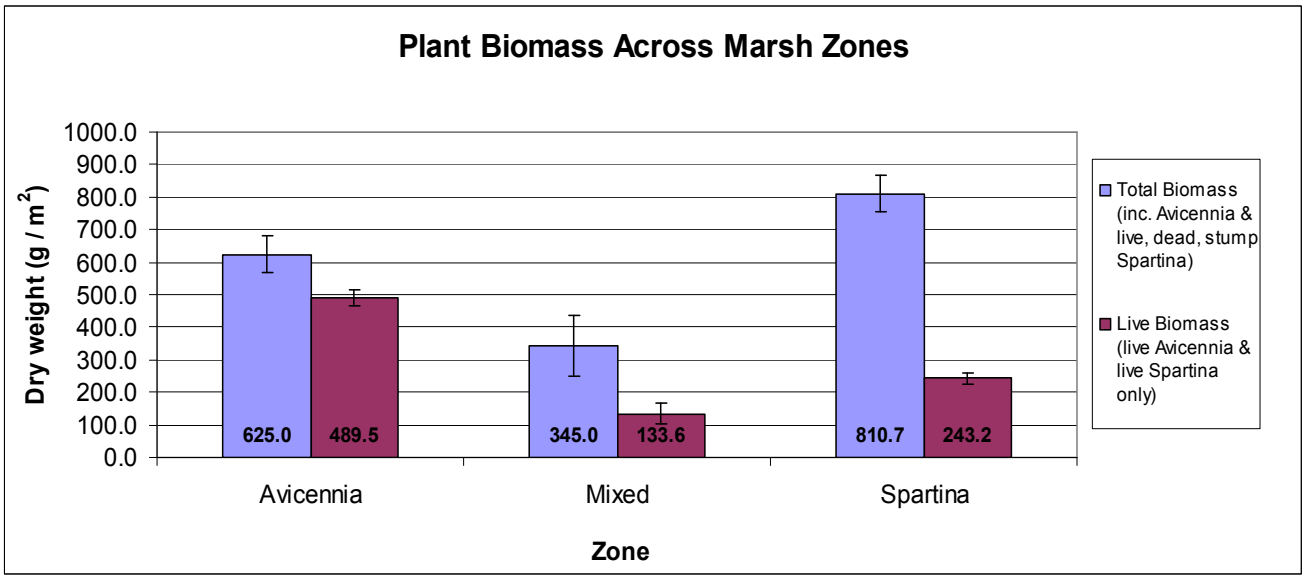
RESULTS

VEGETATION AND SNAIL STUDY

Biomass

In April 2006, total biomass varied significantly among zones ($F=10.9253$, $p<0.05$) as did live biomass ($F=51.4942$, $p<0.001$). The *S. alterniflora* dominant zone (figure 11) contained 30% more total biomass than that in the *A. germinans* zone and 135% more than the Mixed zone.

Figure 11-Total biomass and live biomass across marsh zones



Across all zones, dead *S. alterniflora* biomass was significantly different than live *S. alterniflora* biomass ($F=42.6663$, $p<0.001$). This was especially true in the *S. alterniflora* zone where a majority of the total biomass (70%) was made up of dead *S. alterniflora* versus 28% live *S. alterniflora.* Dead *S. alterniflora* was also found to be a main component (60%) of the total biomass in the Mixed zone.

Mature *A. germinans* was not present in any zone other than the *A. germinans* zone while *A. germinans* seedlings were found in both the Mixed and *S. alterniflora* zone.

Periwinkle density

Mean periwinkle density was significantly different across the marsh (Table 2) with the highest density occurring in the Mixed zone. In the *S. alterniflora* zone, 67% of the periwinkles collected were found at either the base or on the stalk of dead *S. alterniflora.* Similarly, in the Mixed zone, 49% of the periwinkles collected were found on dead *S. alterniflora.* Mean periwinkle density on live *S. alterniflora* was not found to be significantly different across the three zones. There was a significant difference in mean periwinkle density on the ground with a greater percentage (41.6%) of the periwinkles in the *A. germinans* zone found on the ground than in the Mixed and *S. alterniflora* zones (26.4% and 25.9% respectively).

Figures 12-Mean shoot biomass by type in each marsh zone

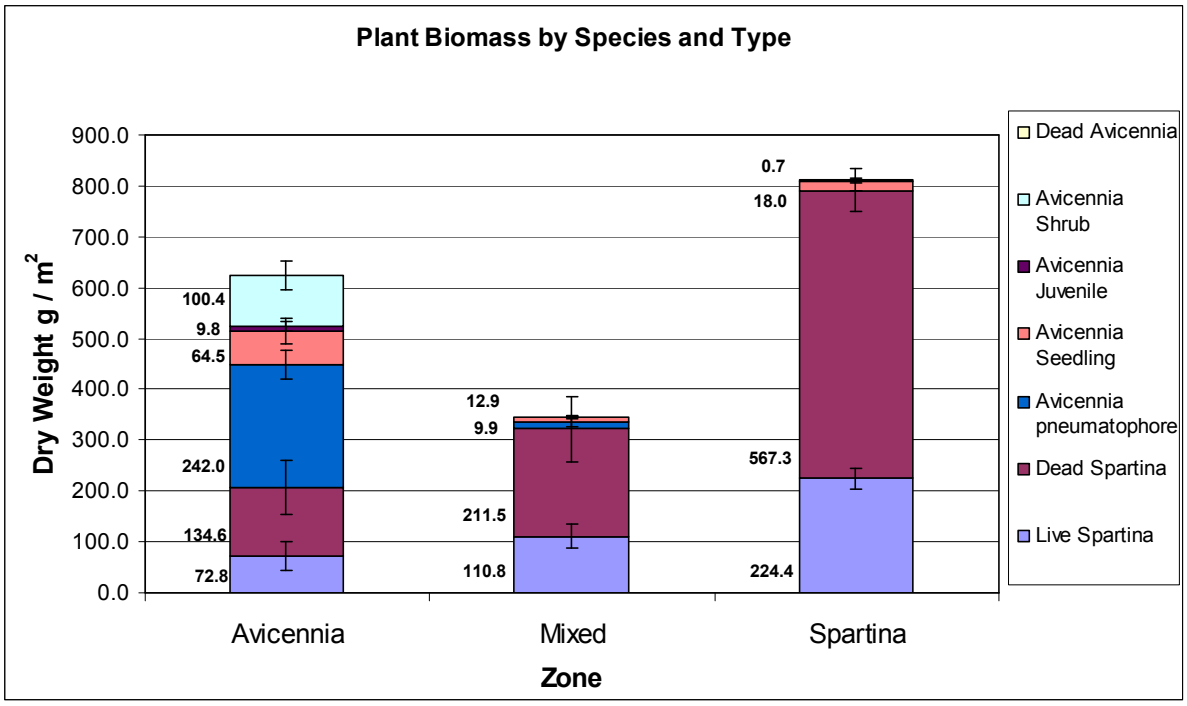


Figure 13-Mean snail density by location found in each marsh zone

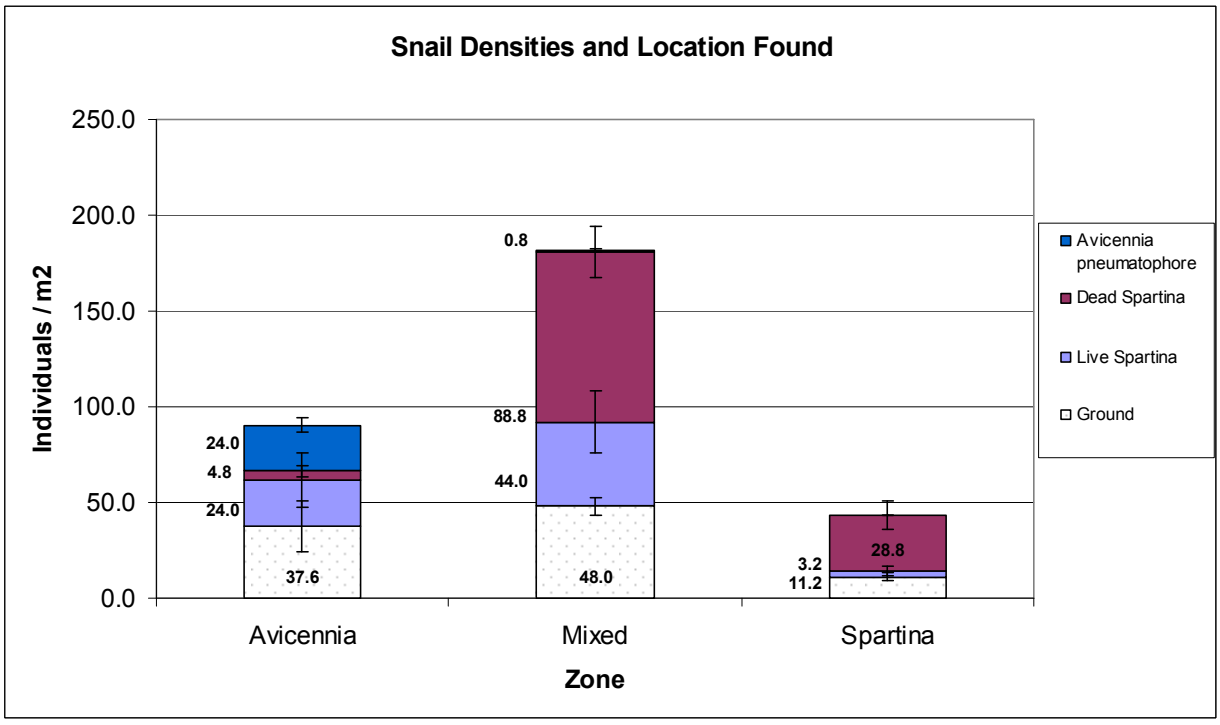


Table 2- Average shoot densities, heights, and snail densities

Plant Structure	Zone			ANOVA F-value
	Avicennia	*Mixed*	*Spartina*	
Spartina				
Overall Height (cm)	34.3	16.0	26.2	13.2704[a]
Stem Count				
Live	16.0	15.8	32.6	6.5628[b]
Dead	26.2	35.6	57.8	6.6522[b]
Avicennia				
Stem Count				
Shrub	9.2	0	0	48.6437[a]
Juvenile	3.8	0	0.2	1.2383
Seedling	25.0	4.6	7.4	3.1298
Pneumatophore	74.0	2.0	0	59.9109[a]
Dead	0.4	0.2	0.2	0.1667
Periwinkles				
Overall density	22.6	45.4	10.8	13.8401[a]
Live Spartina	6.0	11.0	0.8	2.6599
Dead Spartina	1.2	22.2	7.2	24.0082[a]
Ground	9.4	12.0	2.8	5.231[b]
Avi. Pneumatophore	6.0	0.2	0	33.5[a]

[a]p<0.01, [b]p<0.05

Average counts / 0.25m^2

Correlations among Plant and Snail Variable

In the Mixed zone, both total (irrespective of location collected) mean periwinkle density and mean periwinkle density collected on live *S. alterniflora* were found to be positively correlated to overall *S. alterniflora* height (Table 3). Also in the Mixed zone, periwinkles collected on the ground were positively correlated to the number of dead *S. alterniflora* shoots (Table 3). In the *S. alterniflora* zone, overall *S. alterniflora* height was negatively correlated to the number of

periwinkles collected on the ground (Table 3) and the density of live *S. alterniflora* shoots was found to be negatively correlated to the number of periwinkles collected on live *S. alterniflora* shoots (Table 3).

Table 3-Significant correlations between periwinkle densities and plant factors

Zone	Plant Factor (y)	Snail Factor (x)	R^2	Equation
Mix	Spartina-Overall Height (cm)	Total Snail Density	0.961446[a]	y=43.324324+0.5593761x
Mix	Spartina-Overall Height (cm)	Live Spartina	0.939141[a]	y=57.637665+1.007485x
Mix	Dead Spartina Shoot Density	Ground	0.863587[b]	y=6.9846154+2.3846154x
Spartina	Spartina-Overall Height (cm)	Ground	0.960813[a]	y=91.576471-3.5558824x
Spartina	Live Spartina Shoot Density	Live Spartina	0.772727[b]	y=35-3x

[a]p<0.01, [b]p<0.05

Biomass by proxy

A significant positive linear correlation (R^2=0.91259, p<0.0001) was found when comparing (*S. alterniflora o*verall height x live *S. alterniflora* shoot count) and live *S. alterniflora* biomass (Fig 14). This relationship yields a formula by which live biomass can be predicted when only height and density is known. This formula was then tested using data from this study as well as 2 previously published studies (Table 3). Predicted biomass was strongly correlated (R^2= 0.89847, p<0.001) to observed biomass.

Fig 14-Emperically derived model to predict live S. alterniflora biomass

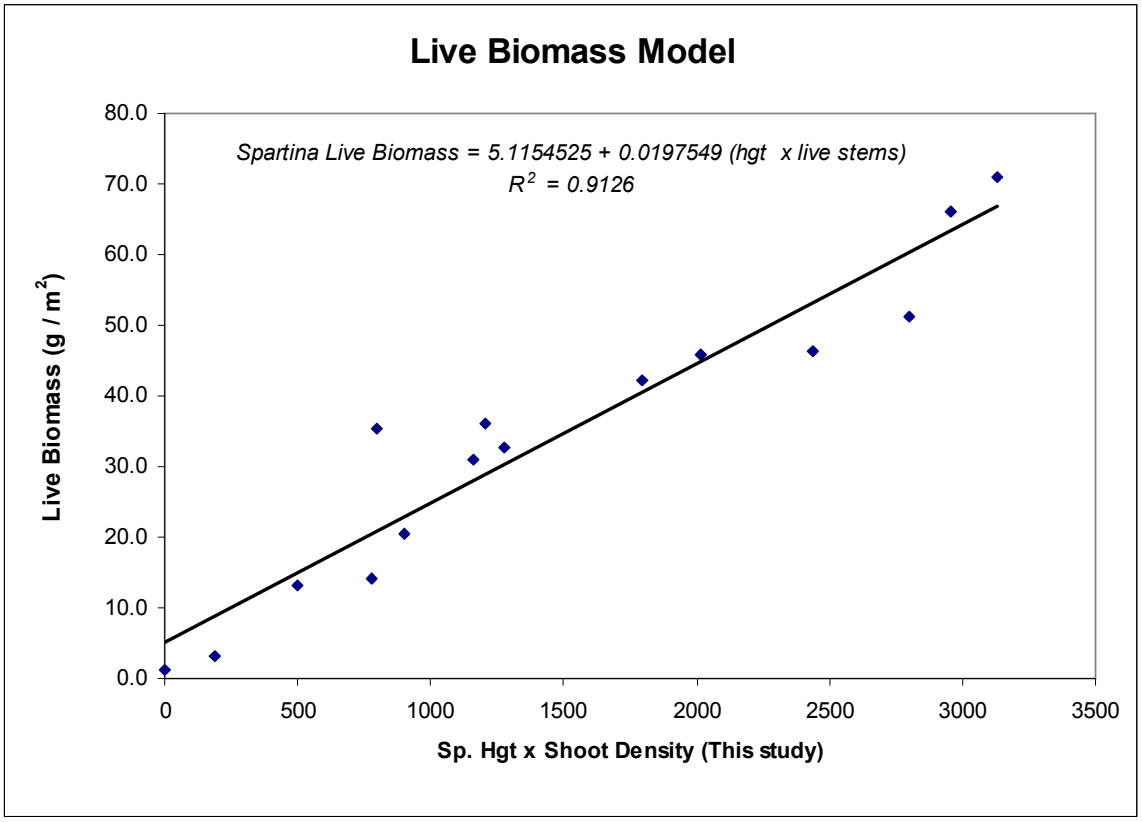


Table 4-Comparison of calculated biomass values (from Live Biomass Model above) versus actual live biomass values

Type	Source	Marsh position	Stem length or height (cm)	Stem density (per m2)	Hgt x density	Calculated Biomass (g/m^2)	Measured Biomass (g/m^2)
Control	Bertness 1985	Short	28.03	238.56	6686.8368	137.51	65.52
Control	Bertness 1985	Short Sp. (High)	47.8	92.4	4416.72	92.57	82.4
Control	Bertness 1985	Short Sp. (Low)	51.5	104.8	5397.2	111.98	125.6
Control	Bertness 1985	Edge (Low)	76.9	94.4	7259.36	148.85	272
Control	Bertness 1985	Flat (High)	98.4	137.2	13500.48	272.43	446
Control	Bertness 1985	Edge (Low)	96.8	3.056	295.8208	10.97	9.504
Control	Bertness 1985	Flat (High)	111.4	2.736	304.7904	11.15	9.904
Control	Bertness 1985	Short	38.7	7.12	275.544	10.57	3.712
Control	Silliman et al 2001	Intermediate	55.2	141	7783.2	159.22	155
Control	Silliman et al 2001	Intermediate	55.2	141	7783.2	159.22	155
Control	Silliman et al 2001	Intermediate	55.2	141	7783.2	159.22	155
Control	Silliman et al 2001	Intermediate	55.2	141	7783.2	159.22	155
Control	Silliman et al 2001	Intermediate	55.2	141	7783.2	159.22	155
Control	This study	Intermediate-Avicennia	34.28	64	2193.92	48.56	72.832
Control	This study	Intermediate-Mixed	68.72	63.2	4343.104	91.11	110.776
Control	This study	Intermediate-Spartina	81.62	130.4	10643.248	215.85	224.416
Treatment	Bertness 1985	Short	31.4	311.4	9777.96	198.72	96.6
Treatment	Bertness 1985	Short Sp. (High)	51.3	53.2	2729.16	59.15	62.8
Treatment	Bertness 1985	Short Sp. (Low)	55.7	63.6	3542.52	75.26	77.2
Treatment	Bertness 1985	Edge (Low)	85	78.8	6698	137.74	261.2
Treatment	Bertness 1985	Flat (High)	82.3	85.2	7011.96	143.95	234.8
Treatment	Silliman et al 2001	Intermediate	85.1	227	19317.7	387.61	726
Treatment	Silliman et al 2001	Intermediate	75.4	87	6559.8	135.00	147
Treatment	Silliman et al 2001	Intermediate	96.1	312	29983.2	598.78	1340
Treatment	Silliman et al 2001	Intermediate	52.2	73	3810.6	80.57	51
Treatment	Silliman et al 2001	Intermediate	56.8	178	10110.4	205.30	231

EXCLOSURE STUDY

Growth response to treatments

ANOVA test of *S. alterniflora* daily relative growth rate (Fig. 15) was not found to vary significantly between treatments ($F=2.5050$, $p<0.0687$). This result, however, was not illustrative of the observed response to treatments seen in the second and third field visits. ANOVA of *A. germinans* daily relative growth (Fig 16), however, did show a significant difference between treatments ($F=7.7418$, $p<0.01$). *A. germinans* exhibited a marked response to fertilization (Fig 16). With fertilization, *A. germinans* would over top *S. alterniflora* within one year versus almost three years at ambient conditions.

Fig 15-Spartina Shoot Growth

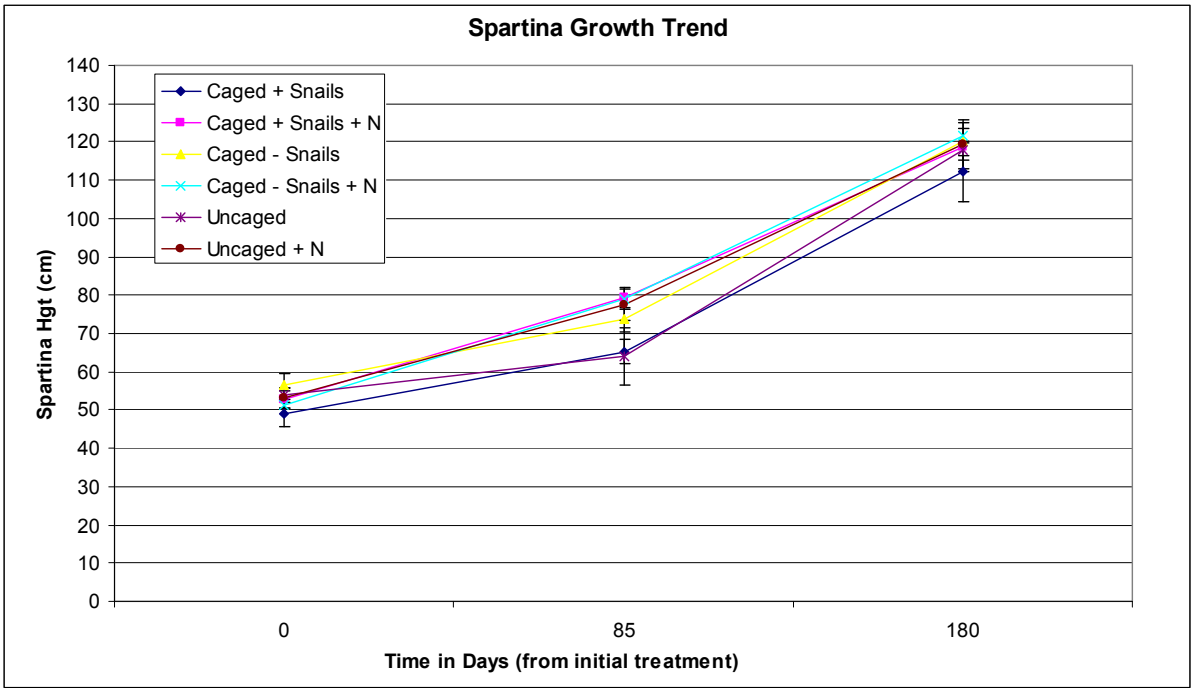
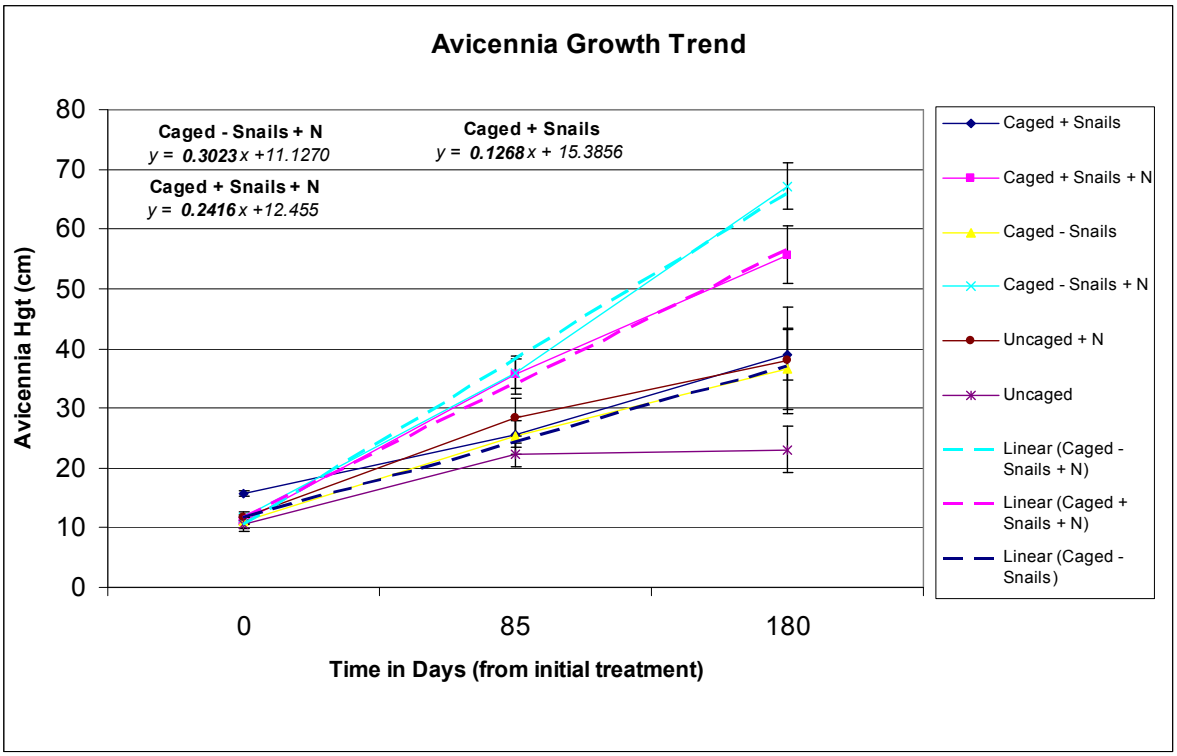


Fig 16-Juvenile Avicennia Growth



S. alterniflora Densities

Initial *S. alterniflora* densities (Fig 17) within the center 0.10 m^2 quadrat were not found to differ significantly during the time of the exclosure construction and treatment application. Live *S. alterniflora* densities, however, did vary significantly across the treatments on the second (Fig 18) and third (Fig R19) visits ($F=4.9533$, $p<0.01$; $F=3.3068$, $p<0.01$ respectively). Post hoc Tukey's HSD analysis on the second visit showed that (caged – snails) and (caged + snail) plots varied significantly from the (uncaged + nitrogen) plots. The (caged – snails) plots also varied significantly from (caged + snails + nitrogen) treatments. Post hoc Tukey's HSD analysis on data from the third visit showed that (caged + snail) and (caged + snails + nitrogen) treatments were significantly different.

Over the six month time period, an overall reduction in the number of stumps and dead shoots was observed.

Fig 17- Relative S. alterniflora Densities in Exclosures Initial Visit (April 2006)

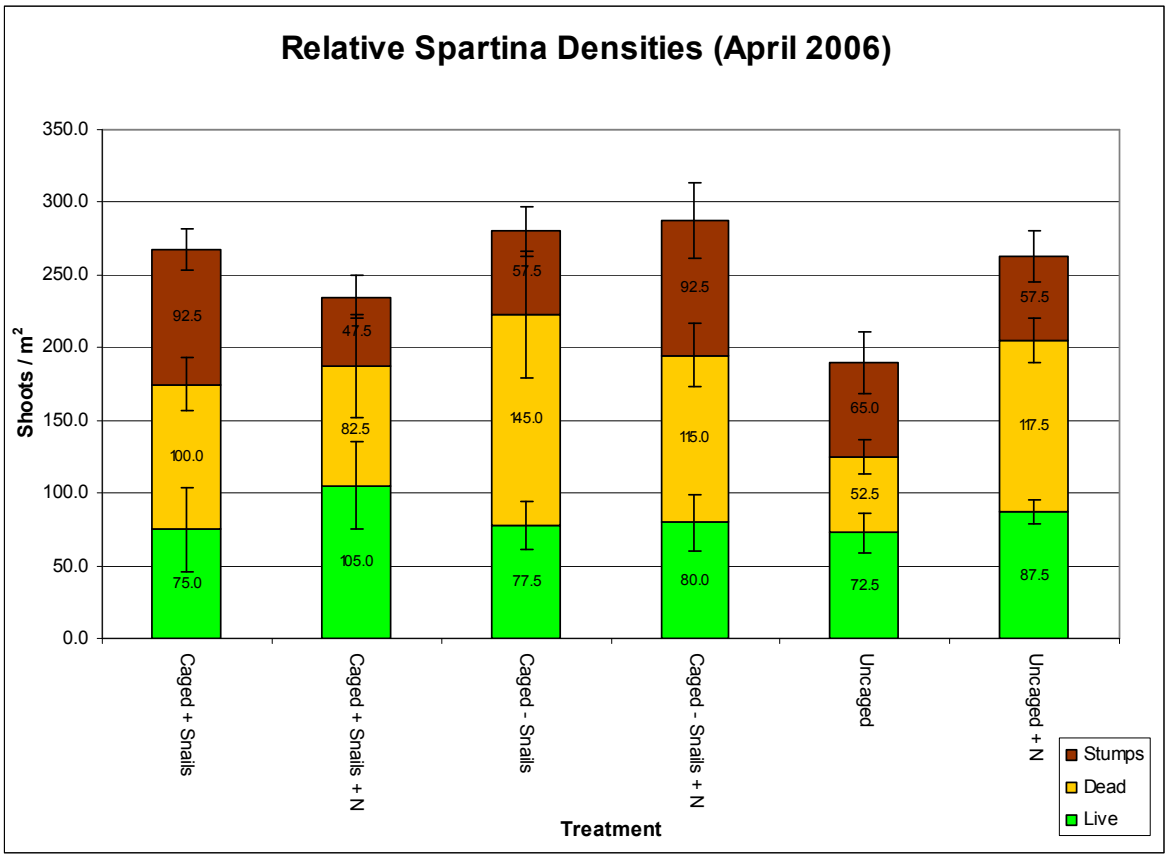


Fig 18-Relative S. alterniflora Densities in Exclosures Second Visit (June 2006)

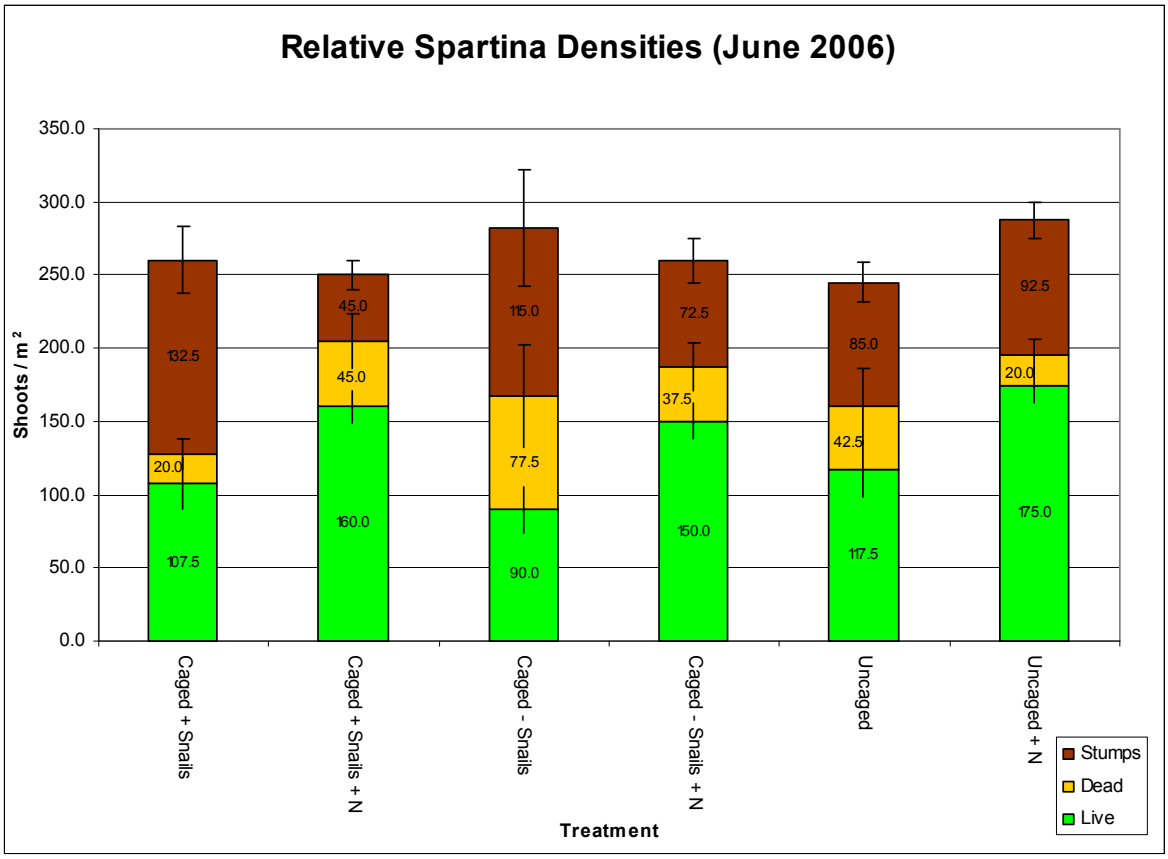
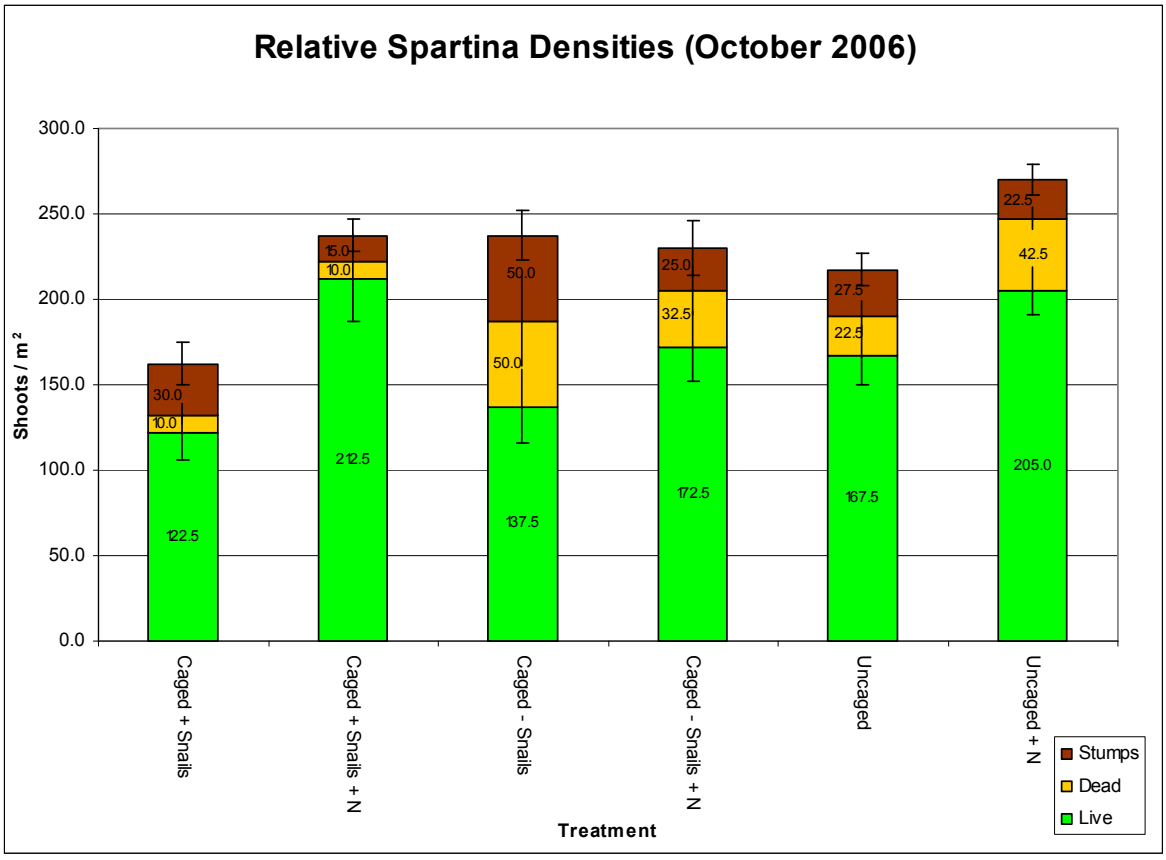


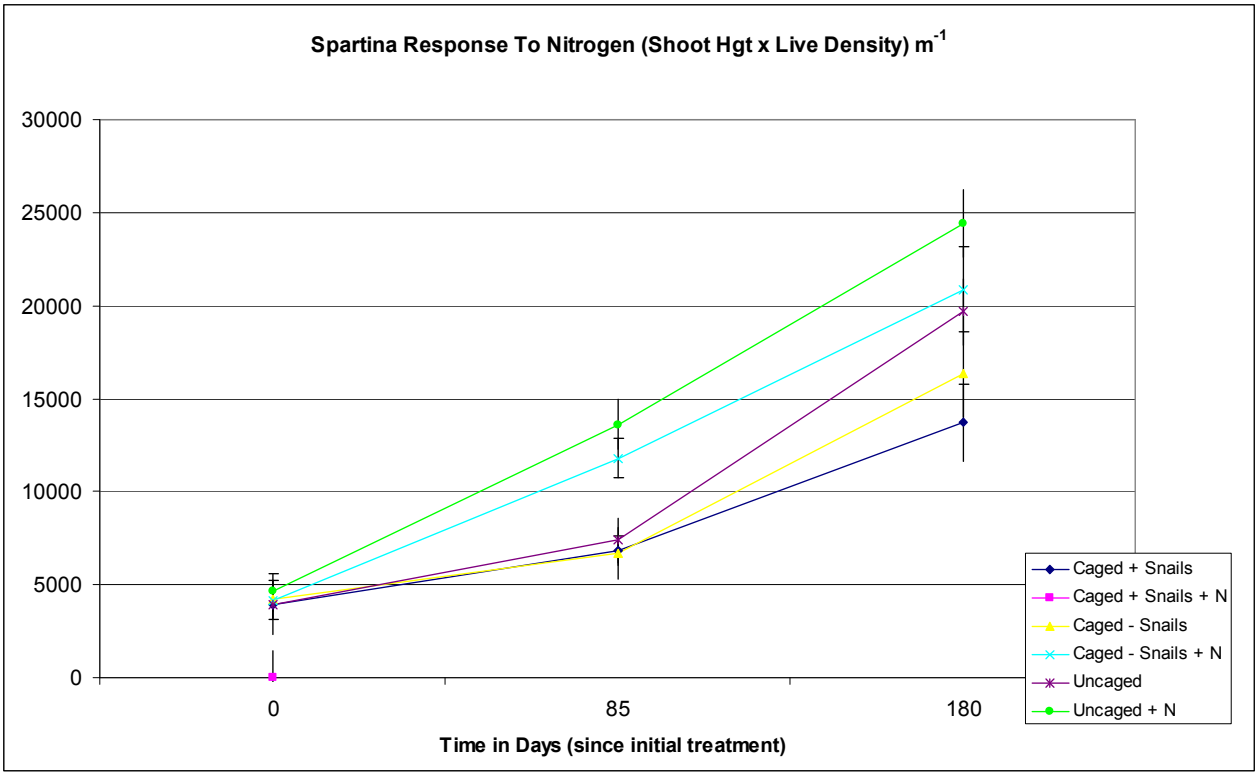
Fig 19-Relative S. alterniflora Densities in Exclosures Final Visit (October 2006)



Biomass Proxy Calculations

Although *S. alterniflora* height was not found to be significantly different across treatment levels, when a biomass proxy calculation was used (Mean shoot height x live stem count) a significant effect of fertilization was found. Figure 20 illustrates the response of *S. alterniflora* in fertilized plots (caged + snails + N), (caged – snails + N), and (uncaged + N) where live *S. alterniflora* biomass increases at a sharper rate in the fertilized plots than in the unfertilized plots. ANOVA analysis of the slopes for lines fitted to the data show a significant difference between plots receiving fertilization and those that did not ($F=9.9558$, $p<0.05$). Further, Figure 20 illustrates that there were no apparent cage effects on foliar response as the uncaged fertilized plots (UAN) are virtually indistinguishable from the caged fertilized plots (CAN).

Figure 20-Spartina Shoot Hgt x live shoot density



Predicting Live S. alterniflora Biomass

Using biomass model developed in the marsh density study

(y = 0.0198x+5.1155) results in predicted live *S. alterniflora* biomass (Fig. 21) results comparable to published studies with similar fertilization treatments (Table 5) and illustrates a 36% increase of live *S. alterniflora* biomass from N enrichment.

Figure 21-Predicted live Spartina biomass based on linear model from marsh density study

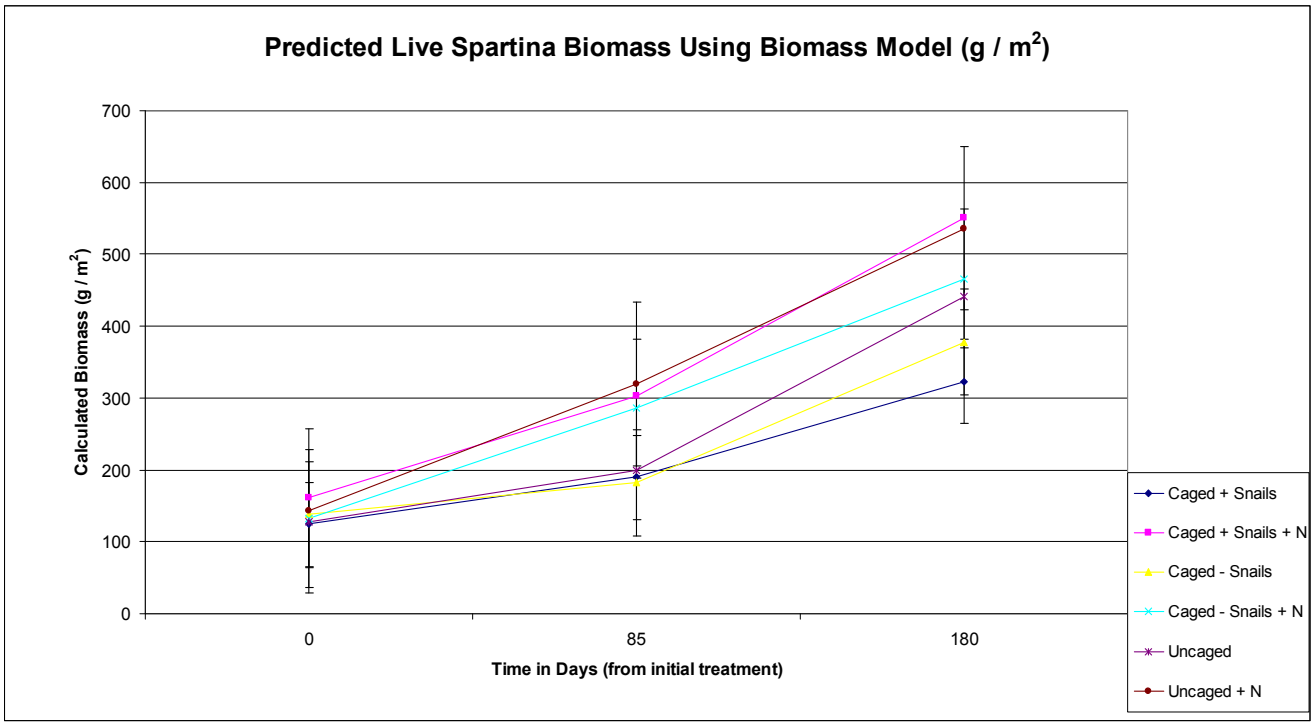


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Table 5- Nitrogen enrichment biomass studies

Source	Spartina Control Biomass (g/m^2)	Treatment	Spartina Treatment Biomass (g/m^2)	% Biomass Increase
Mendelssohn 1979	316	Broadcast, Ammonium, 280 kg/ha N	580	84%
Mendelssohn 1979	316	Broadcast, Ammonium, 560 kg/ha N	612	94%
Mendelssohn 1979	316	Broadcast, Ammonium, 1120 kg/ha N	680	115%
Mendelssohn 1979	320	Broadcast, Nitrate, 280 kg/ha N	464	45%
Mendelssohn 1979	320	Broadcast, Nitrate, 1120 kg/ha N	476	49%
Mendelssohn 1979	320	Broadcast, Nitrate, 560 kg/ha N	568	78%
Mendelssohn 1979	348	Band, Ammonium, 280 kg/ha N	644	85%
Mendelssohn 1979	348	Band, Ammonium, 560 kg/ha N	836	140%
Mendelssohn 1979	348	Band, Ammonium, 1120 kg/ha N	948	172%
Gallagher 1975	349	200 kg / ha N (1 y after treatment)	899	158%
Sullivan et al 1974	361	20g N/m2	1052	191%
Mendelssohn 1979	380	Band, Nitrate, 280 kg/ha N	568	49%
Mendelssohn 1979	380	Band, Nitrate, 560 kg/ha N	656	73%
Mendelssohn 1979	380	Band, Nitrate, 1120 kg/ha N	764	101%
This study (Predicted Biomass)*	381	urea, 149 g N/ m^2	518	36%
Dai et al 1996	404	219 kg/ ha N	953	136%
Gallagher 1975	471	200 kg / ha N	803	70%
Emery 2001	862	60 g NPK/m2/2weeks	1936	125%
Emery 2001	997	60 g NPK/m2/2weeks	1849	86%
Buresh et al 1980	1061	200 kg/ ha N	1357	28%
Gallagher 1975	1124	200 kg / ha N	1338	19%
Mendelssohn 1979	1248	Broadcast, Nitrate, 560 kg/ha N	1380	11%
Mendelssohn 1979	1248	Broadcast, Nitrate, 1120 kg/ha N	1404	13%
Mendelssohn 1979	1248	Broadcast, Nitrate, 280 kg/ha N	1412	13%
Mendelssohn 1979	1364	Band, Ammonium, 560 kg/ha N	1844	35%
Mendelssohn 1979	1364	Band, Ammonium, 280 kg/ha N	1860	36%
Mendelssohn 1979	1364	Band, Ammonium, 1120 kg/ha N	1968	44%

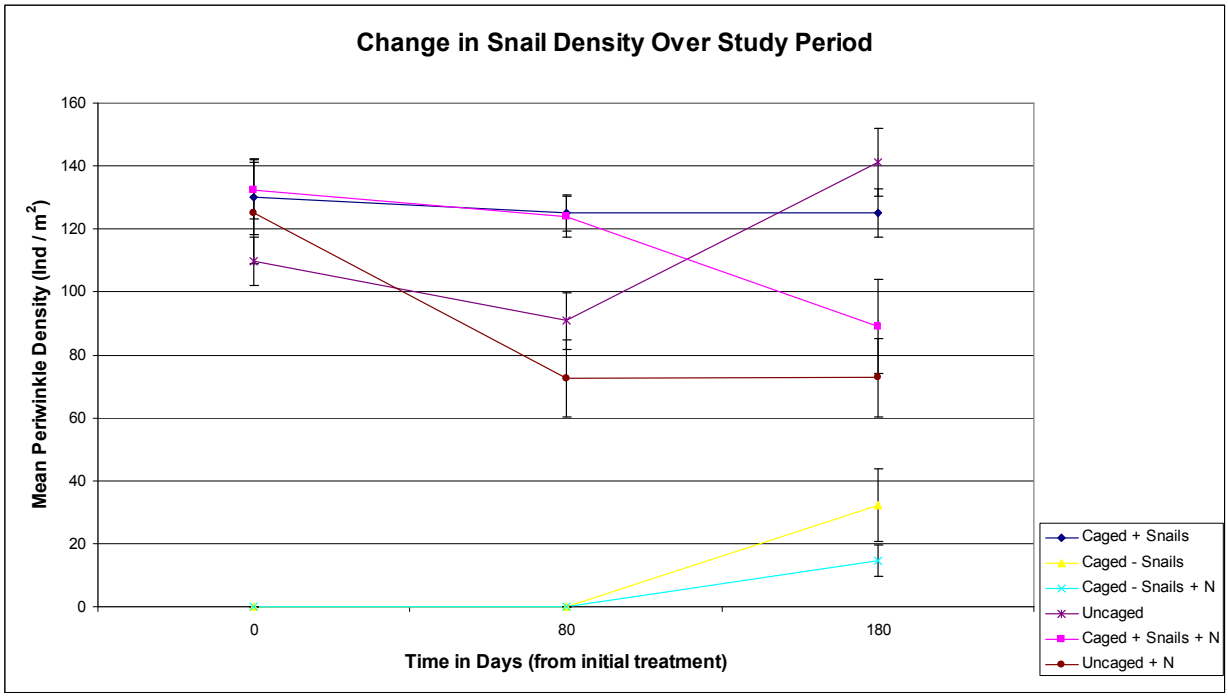
Mendelssohn 1979	1436	Broadcast, Ammonium, 560 kg/ha N	1272	-11%
Mendelssohn 1979	1436	Broadcast, Ammonium, 280 kg/ha N	1440	0%
Mendelssohn 1979	1436	Broadcast, Ammonium, 1120 kg/ha N	1512	5%
Mendelssohn 1979	1504	Band, Nitrate, 280 kg/ha N	1256	-16%
Mendelssohn 1979	1504	Band, Nitrate, 560 kg/ha N	1456	-3%
Mendelssohn 1979	1504	Band, Nitrate, 1120 kg/ha N	1640	9%

*Mean predicted biomass as of Day 3 with control (CA+UA+CO) and nitrogen addition as (CAN+CON+UAN)

Effect of periwinkles

While caging was not found to have an effect upon plant response to treatment, the caging did achieve the necessary result in maintaining periwinkle treatment densities over the length of the study (Fig 22).

Figure 22-Periwinkle Density



Silliman et al (2003a) have argued that *S. alterniflora* response to nitrogen has been historically under represented because prior studies have failed to account for grazing pressure exerted on *S. alterniflora.* Periwinkle pressure was not found to be a factor in *S. alterniflora* response to fertilization (Fig 23 and 24) in this study. A full factorial analysis of variance resulted in no significant effects on density changes of live, dead, or stumps of *S. alterniflora,* nor was there a significant effect on *S. alterniflora* growth rates across snail, fertilization, and

snail*fertilization factors. In no cases were snail*fertilizer effects significant. Table 6 details effect tests with significant results ($p<0.05$).

Table 6-Two factor analysis of variance

Effect Tests-live Spartina predicted biomass

Source	*Nparm*	*DF*	*Sum of Squares*	*F Ratio*	*Prob > F*
Snails	2	2	20470.77	1.3463	0.2852
Fertilizer	*1*	*1*	*110795*	*14.5737*	*0.0013*
Snails*Fertilizer	2	2	23036.39	1.5151	0.2465

Significant effect in italics

Effect Tests-Avicennia growth rate

Source	*Nparm*	*DF*	*Sum of Squares*	*F Ratio*	*Prob > F*
Snails	2	2	0.05534758	7.6999	0.0038
Fertilizer	1	1	0.08377246	23.3087	0.0001
Snails*Fertilizer	2	2	0.00783719	1.0903	0.3573

Significant effect in italics

Effect Tests-live Spartina density

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Snails	2	2	39.58333	1.2873	0.3003
Fertilizer	*1*	*1*	*176.04167*	*11.4499*	*0.0033*
Snails*Fertilizer	2	2	38.58333	1.2547	0.3089

Significant effect in italics

Live S. alterniflora biomass and density results listed are based upon measurements taken on the final field visit.

S. alterniflora's growth rate was greater than that of *A. germinans* in all plots with periwinkles present and no nitrogen addition. When periwinkles were removed and nitrogen was added however, *A. germinans* growth rate is equal to that of *S. alterniflora (Fig 25).*

Figure 23-Live Spartina Response to Nitrogen Enrichment

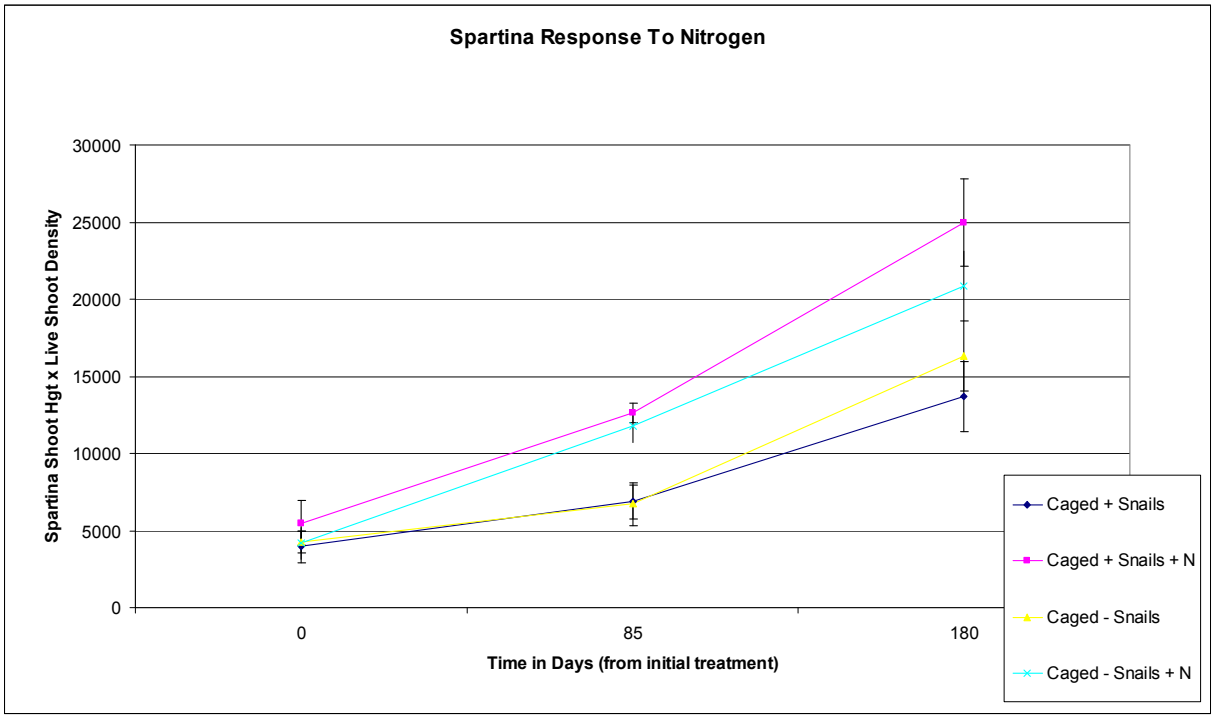


Figure 24-Live Biomass Using Live Biomass Model

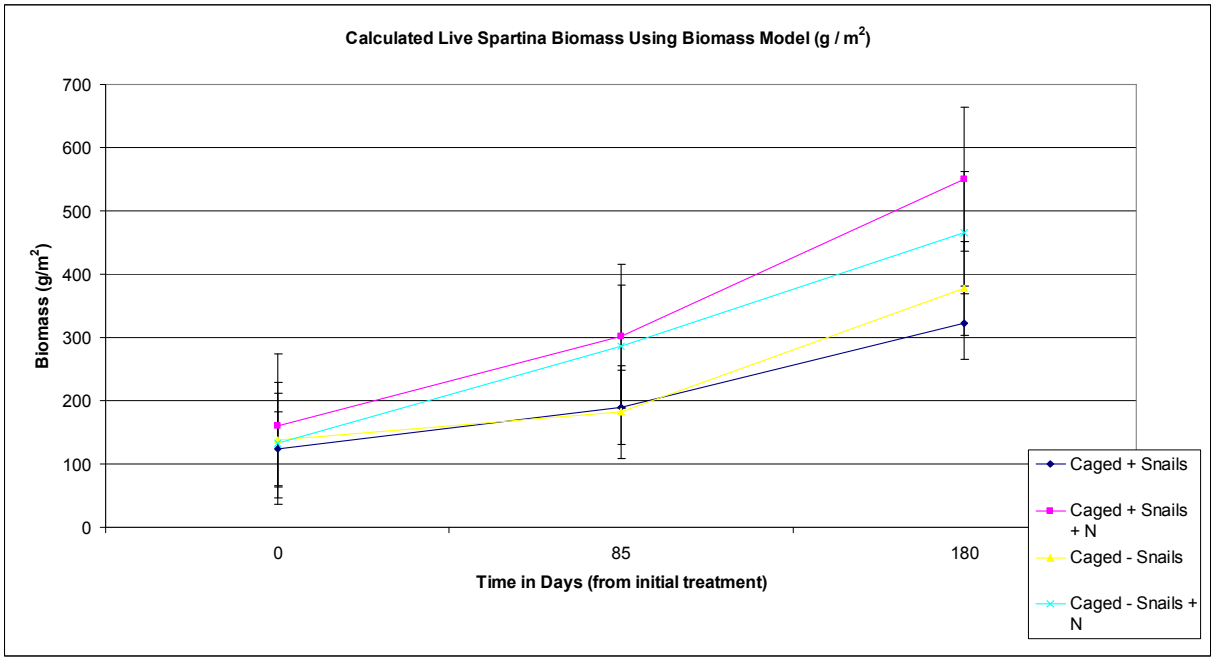
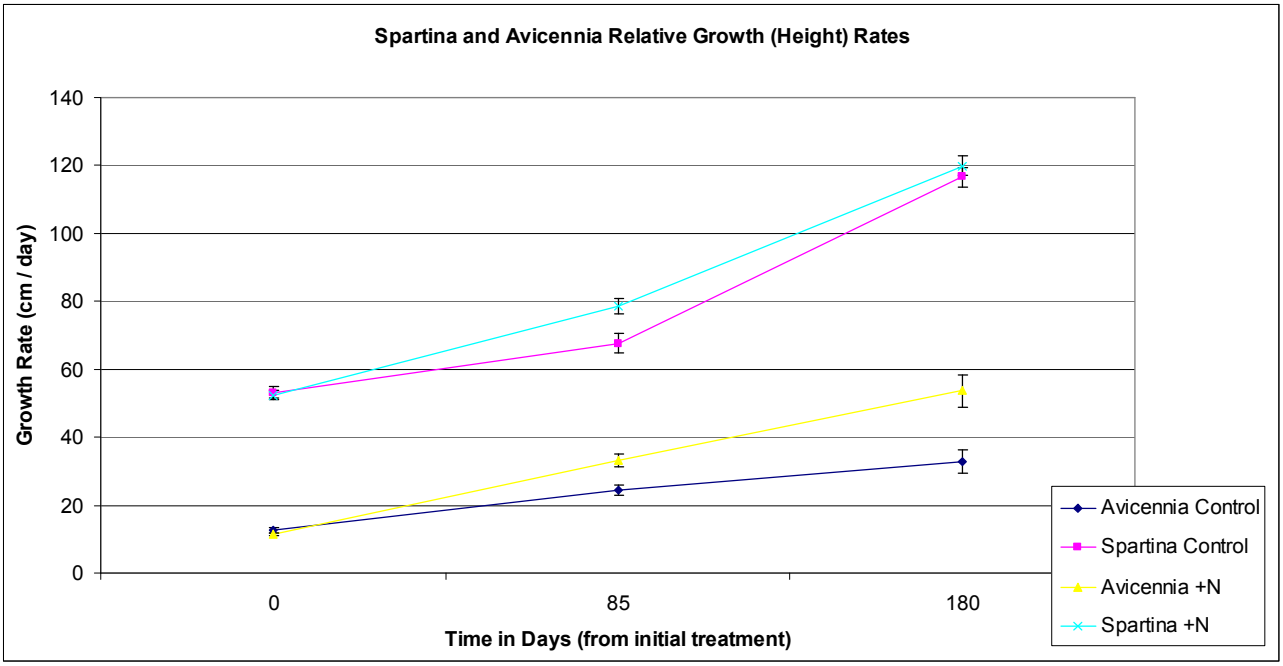
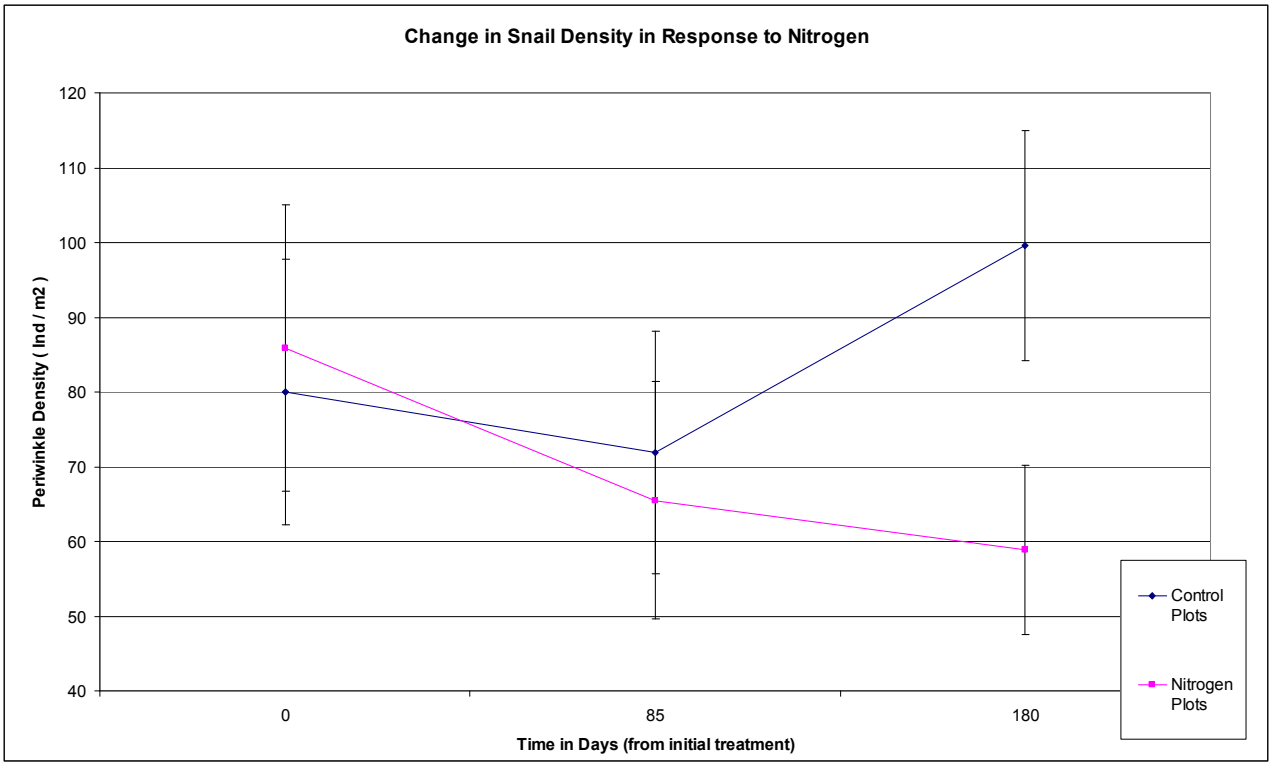


Fig 25-Relative growth rates of S. alterniflora and A. germinans



While caging was effective in maintaining periwinkle densities in the unfertilized plots, periwinkle densities in the caged fertilized plots unexpectedly dropped an average of 32.8% from original densities (Fig 22). This translates to a drop in snail density at a rate of 0.14 per day versus an increase of 0.11 periwinkles per day increase in unfertilized plots. A similar drop (41.8%) in density was seen in the uncaged fertilized plots from initial densities indicating caging was not the cause for the drop in densities. Periwinkle densities on the final date varied significantly ($F=20.1427$, $p<0.05$) between fertilized and unfertilized plots (Fig 26).

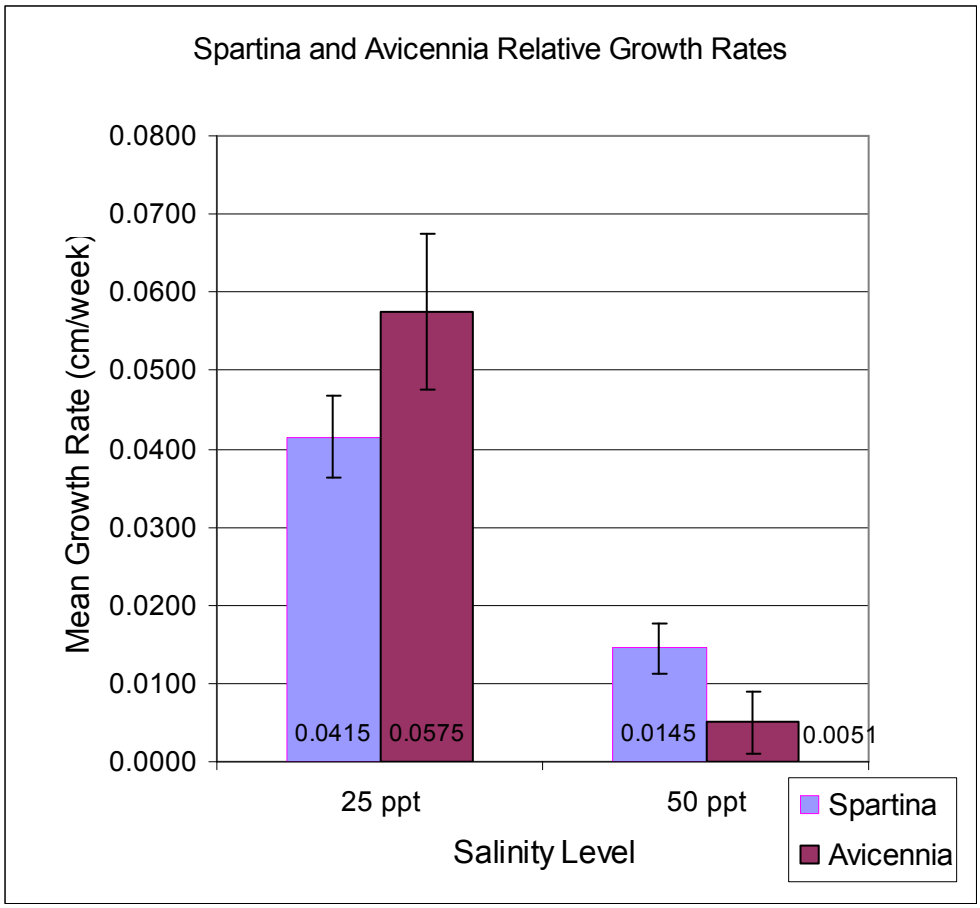
Figure 26-Periwinkle Response To Nitrogen



GREENHOUSE STUDY

The relative growth rates for *A. germinans* and *S. alterniflora* growth rate were significantly different between high and low levels of salinity ($F=23.9566$, $p<0.01$; $F=19.7846$, $p<0.01$ respectively). The number of new *S. alterniflora* shoots was significantly different between salinity levels ($F=70.2715$, $p<0.01$). The number of additional *A. germinans* nodes from the originally identified terminal node was also found to be significantly different between salinity levels ($F=17.3197$, $p<0.01$). In low salinity levels, *A. germinans* mean growth rate was higher than *S. alterniflora* (Fig 27) but in high salinity levels *S. alterniflora* growth rates were higher.

Fig R27-Greenhouse Growth Rates of Avicennia and Spartina at 2 Salinity Levels



DISCUSSION

The results of this study suggest that periwinkles do not play a role in the interplay between *A. germinans* and *S. alterniflora*. The marsh census revealed that the Mixed zone had highest periwinkle densities yet a positive correlation was found with total periwinkle density and overall shoot height, while the *S. alterniflora* zone had the greatest amount of dead and live *S. alterniflora* and the lowest density of periwinkles. These results indicate that periwinkles were not suppressing *S. alterniflora* growth in the two most likely areas to exhibit the effects of periwinkle grazing. Furthermore, the exclosure study found that periwinkle presence had no effect on the live shoot biomass, the number of live and dead shoots or the overall height of the shoots. More significant to the competition between *S. alterniflora* and *A. germinans* was the strong *A. germinans* response to nitrogen, indicating that, in the presence of nitrogen, *A. germinans* could overtop *S. alterniflora* in one growing season.

Our findings are contradictory to a prior study using similar periwinkle densities, 144 individuals/m^2 versus our 125 individuals/m^2, where nitrogen fertilization and periwinkle removal resulted in a 189% increase in *S. alterniflora* biomass over fertilized plots at ambient periwinkle densities (Silliman et al. 2001). A later study reports periwinkle densities of 78 individuals/m^2 were not sufficient enough to completely denude vegetation and was not likely to cause marsh die-off (Silliman et al. 2005) so the periwinkle levels in our experiment should have produced similar effects to the 2001 fertilization study. In addition to a lack of

periwinkle effect on *S. alterniflora* biomass, there was also an unexpected decrease in periwinkle densities in fertilized plots (both caged and uncaged).

In order to ascertain whether our results are anomalous, a literature review of *S. alterniflora* biomass was done encompassing twenty-seven separate studies across eleven states and combined with periwinkle data that has been collected from twenty-one studies across seven states.

S. alterniflora biomass and nitrogen response

Because dead stalks of *S. alterniflora* are known to remain standing estimations of biomass in the literature may or may not include dead matter. In order to ensure a similar comparison with our study's live biomass figures, only studies that differentiated and reported live biomass were used in the initial comparison (Table 7). The resulting comparison indicates that our figures are conservative for those reported for the state but still within the published ranges for live *S. alterniflora* biomass. When similar fertilization studies are compared, our results fall well within previously published results. Comparison of varying forms of *S. alterniflora* across fertilization studies confirm prior findings that nitrogen response will vary based upon form with the intermediate form of *S.alterniflora* responding at a level closer to the tall form than the short (Table 8). Several studies concluded that the significantly higher response in the short form of *S. alterniflora* indicates that this growth form is at least partially dictated by nitrogen availability (Gallagher 1975, Valiela et al. 1978, Mendelssohn 1979, Bertness

1991) .

Table 7-Comparison of Live Biomass Ranges By State and Source

Peak/Live	State	Source	Min	Mean	Max
Live	DE	Sullivan et al 1974	361.0	361.0	361.0
	DE Total		**361.0**	**361.0**	**361.0**
	GA	[1]Chalmers 1979	396.0	396.0	396.0
		Gallagher 1975	349.0	648.0	1124.0
		Turner 1987	344.0	344.0	344.0
	GA Total		**344.0**	**424.3**	**1124.0**
	LA	Hopkinson et al 1980	469.0	469.0	469.0
		Kirby et al 1976	343.0	462.0	581.0
		This study	110.8	167.6	224.4
	LA Total		**110.8**	**345.6**	**581.0**
	ME	Linthurst et al 1978	246.0	338.5	431.0
	ME Total		**246.0**	**338.5**	**431.0**
	NC	[1]Broome et al 1975	450.0	450.0	450.0
	NC Total		**450.0**	**450.0**	**450.0**
	VA	Reidenbaugh 1983	162.2	381.8	627.8
	VA Total		**162.2**	**381.8**	**627.8**
Live Total			**110.8**	**392.2**	**1124.0**

[1] as reported by Silliman et al (2003a)

Table 8-Nitrogen Addition-Mean Percent Change in Biomass by Spartina Growth Form

State	Source	Spartina Type				Grand Total
		Not Reported	Short	Intermediate	Tall	
DE	Sullivan et al 1974		191%			191%
DE Total			**191%**			**191%**
GA	[1]Chalmers 1979		64%			64%
	[2]Chalmers et al 1976	64%				64%
	Gallagher 1975		114%		19%	82%
GA Total		**64%**	**97%**		**19%**	**75%**
LA	Buresh et al 1980			28%		28%
	[1]Patrick et al 1977	15%	15%			15%
	This study			37%		37%
LA Total		**15%**	**15%**	**35%**		**28%**
MA	Howes et al 1986		204%			204%
	Valiela et al 1976	97%				97%
MA Total		**97%**	**204%**			**168%**
NC	[1]Broome et al 1975	300%	300%			300%
	Mendelssohn 1979		88%		11%	48%
NC Total		**300%**	**106%**		**11%**	**68%**
VA	Silliman et al 2001		354%	376%		365%
VA Total			**354%**	**376%**		**365%**
Grand Total		**119%**	**147%**	**181%**	**12%**	**112%**

[1]as reported by Silliman et al (2003a), [2]as reported by Chalmers (1982)

Periwinkle Density

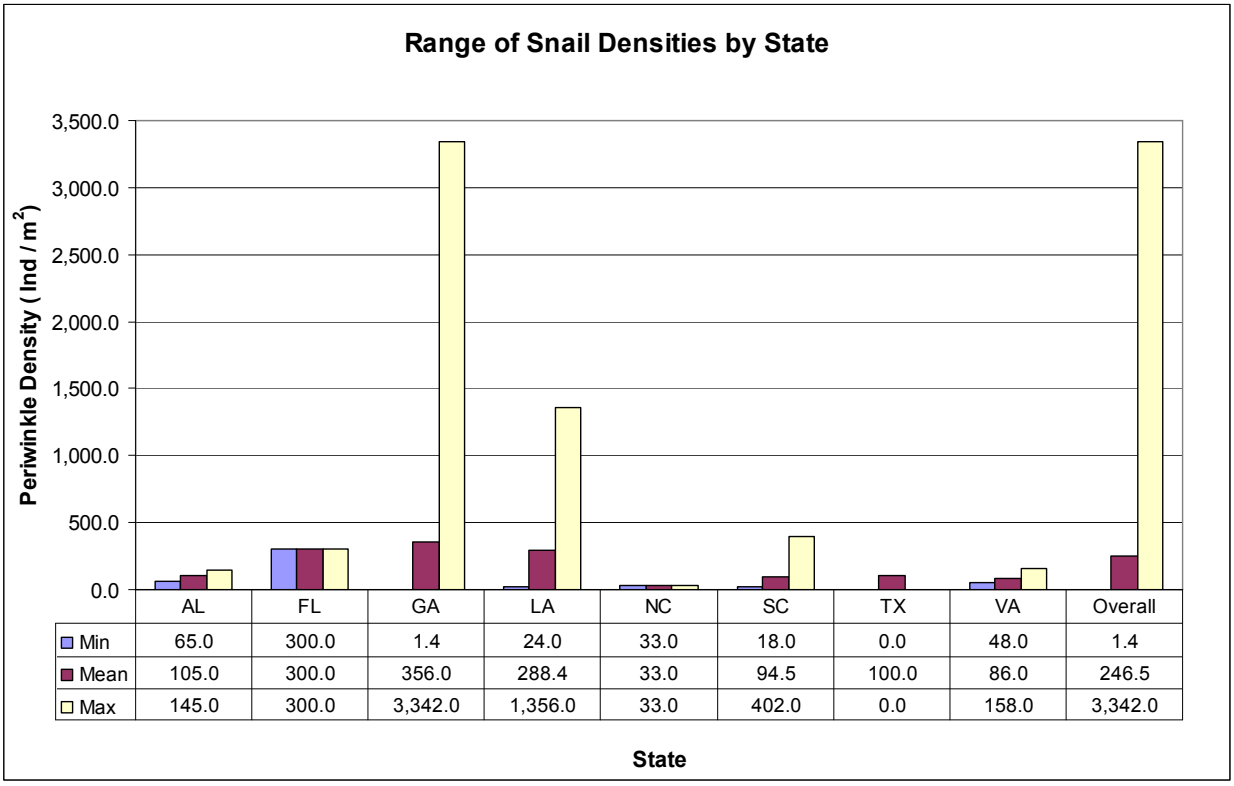
The periwinkle densities reported for Louisiana illustrate that our numbers are within published ranges-although considerably lower than found in Sapelo Island, Georgia- and were at a sufficient density to have exhibited a periwinkle top-down control response had there been one (Table 9). The lack of response and loss of periwinkles in nitrogen enriched plots found by this study suggests that other factors must be considered when evaluating the ability of periwinkles to exert control over *S. alterniflora.*

Table 9- Range of Periwinkle Density by State

State	Source	Min	Mean	Max
AL	[1]West et al 1985	65.0	105.0	145.0
AL Total		**65.0**	**105.0**	**145.0**
FL	Warren 1985	300.0	300.0	300.0
FL Total		**300.0**	**300.0**	**300.0**
GA	[2]Newell et al 1993	460.0	460.0	460.0
	[1]Pomeroy et al1981	700.0	700.0	700.0
	Schindler et al 1994	22.0	46.0	66.0
	Silliman et al 2002	5.4	305.2	605.0
	Silliman et al 2003a	243.0	1311.0	3342.0
	Silliman et al 2003b	220.0	220.0	220.0
	Silliman et al 2005	1.4	284.3	1575.3
	Turner 1987	146.6	146.6	146.6
GA Total		**1.4**	**356.0**	**3342.0**
LA	[2]Alexander 1979	24.0	24.0	24.0
	Silliman et al 2003a	323.0	323.0	323.0
	Silliman et al 2005	45.0	447.6	1356.0
	This study	43.0	107.0	180.0
LA Total		**24.0**	**288.4**	**1356.0**
NC	Cammen et al 1980	33.0	33.0	33.0
NC Total		**33.0**	**33.0**	**33.0**
SC	Hutchens et al 2006	18.0	62.3	115.0
	Silliman et al 2005	32.0	151.3	402.0
	[2]Tucker et al 1995	43.0	43.0	43.0
SC Total		**18.0**	**94.5**	**402.0**
VA	Crist et al 1983	48.0	48.0	48.0
	Silliman et al 2003a	88.0	88.0	88.0
	Silliman et al 2001	48.0	98.0	158.0
VA Total		**48.0**	**86.0**	**158.0**
Grand Total		**1.4**	**246.5**	**3342.0**

[1]as reported by Silliman et al (2003a),[2]as reported by Silliman et al (2001)

Fig 28- Periwinkle Density Ranges by State (from ranges reported in Table 9)



	AL	FL	GA	LA	NC	SC	TX	VA	Overall
Min	65.0	300.0	1.4	24.0	33.0	18.0	0.0	48.0	1.4
Mean	105.0	300.0	356.0	288.4	33.0	94.5	100.0	86.0	246.5
Max	145.0	300.0	3,342.0	1,356.0	33.0	402.0	0.0	158.0	3,342.0

Table 10-Mean periwinkle density (ind/m^2) by S. alterniflora height

Spartina Type	Source	Average
Short	Hutchens et al 2006	63.7
	Schindler et al 1994	55.0
	Silliman et al 2002	605.0
	Turner 1987	146.6
Short Total		**124.4**
Intermediate	Newell et al 1993	460.0
	Silliman et al 2005	447.6
	[1]West et al 1985	65.0
Intermediate Total		**401.3**
Tall	Hutchens et al 2006	59.7
	[2]Schindler et al 1994	37.0
	Silliman et al 2002	5.4
Tall Total		**43.1**
Grand Total		**196.4**

[1]as reported by Silliman et al 2003, [2]Hutchens et al 2006

Effects of latitude-All of the studies reporting high periwinkle densities and strong top down pressure exerted by *L. irrorata* on *S. alterniflora* were conducted in Georgia (30-31ºN lat) and North Carolina (33ºN) while this study was located at a latitude of 29ºN. This latitudinal difference may translate to several factors, e.g. plant palatability or increased temperature and salinity stress that would alter the effect of *L. irrorata* on *S. alterniflora.*

Plant Palatability-Palatability studies have shown that grazers sourced from both northern and southern latitudes preferentially choose northern plants over

southern conspecifics (Bolser et al. 1996, Pennings et al. 2001, Siska et al. 2002, Goranson et al. 2004). Bolser and Hay (1996) also found variations in resistance to herbivory within a population which could hint at the differences in periwinkle densities between tall and short forms of *S. alterniflora.* Foliar analysis of *S. alterniflora* collected in Georgia was found to have 30% more phenolic compounds and significantly less nitrogen than its Rhode Island conspecific, (Siska et al. 2002) which would suggest, assuming a latitudinal increase in phenols and decrease in nitrogen concentrations with increased latitude, that *S. alterniflora* in Louisiana would be even less palatable than its Georgian counterpart.

Temperature and salinity stress- Vaughn (1992) found a strong correlation between substratum temperature and *L. irrorata* shell temperature and suggested that vertical migration up *S. alterniflora* was in a response to thermoregulation particularly in juvenile periwinkles. In the same study, conducted at similar latitude as our study, found seasonal circumtidal variation was found to be correlated with *L. irrorata* position with majority of the periwinkles being found on the substratum during low tide and warm periods. The snail survey conducted in this study supports this with more periwinkles being located on the ground in the Spartina and Mixed zones than on live *S. alterniflora.* Additionally, in our greenhouse study, higher periwinkle mortality was seen in the high salinity mesocosms. This suggests that temperature and or higher salinity (perhaps as a by-product of increased temperatures) was a factor in periwinkle densities. Using the ground as a method to thermoregulate however, would

result in a higher vulnerability to predation by crabs.

S. alterniflora type and drop in periwinkle densities- As of the second field visit, *S. alterniflora* shoot height in the fertilized plots had only achieved an average height of 78.6 cm. By the third visit however, shoot height had reached 120.0 cm across caged and uncaged plots. Thus the *S. alterniflora* in the fertilized plots reached a shoot height on par of that of tall form *S. alterniflora*. Distribution of shoots in the tall form of *S. alterniflora* is found, when compared to the short form, to bemore uniform with the diameter of the shoots increasing but the density of shoots decreasing allowing for greater insolation (Valiela et al. 1978). This finding was supported by this study where the live shoot densities from the fertilized plots (ranging from 172-212 m^{-2}) is compared to published short form shoot densities (ranging from 370-1,100 m^{-2}) (Valiela et al. 1978, Bertness 1985). Previous studies have found that the tall form of *S alterniflora* (1-1.5 m height) not only has significantly fewer periwinkles per m^2 (Table 10) than its short counterpart, (Silliman et al. 2002, Hutchens et al. 2006) but suggest that the lower periwinkle densities are due to predation (due mainly to blue crab) in a tethered *L. irrorata* study (Silliman et al. 2002). Another consumer, the black-clawed crab (*Panopeus herbstii),* was found in tall *S. alterniflora* in densities eight times greater than that in intermediate *S. alterniflora* and was found to consume 12% of the periwinkles in test plots (based upon periwinkle density of 50 periwinkles/m^2) (Silliman et al. 2004). Further, Bertness (1985) found that tall form *S. alterniflora* contained a greater number and larger mud fiddler crab

burrows (*Uca pugnax)* while Cammen (1980) found both biomass and densities of *U. pugnax* and *U. minax* were greater in the intermediate and tall forms of *S. alterniflora* than in the short form. Thus predation stress by crabs is greater in taller forms of *S. alterniflora,* and could explain the loss of periwinkles in our study.

Nutrient availability and herbivore defense-Still another potential causative factor for the lack of any response to periwinkle grazing is the effects of nutrient availability and herbivore defense in *S. alterniflora*. Coley et al (1985) argued that a plant's investment of resources in defense can be predicted based upon its potential growth rate. If short forms *S. alterniflora* are truly stunted based upon nitrogen stress and its potential growth rate are high, then it would be less likely to invest limited nitrogen resources in defense mechanisms leaving it vulnerable to grazing or fungal inoculation by *L. irrorata.*

Selective feeding on S. alterniflora- Finally, *L. irrorata's* dependence upon *S. alterniflora* as a sole food source should be examined further. When offered 4 species of common salt marsh plants, *L. irrorata* was found to consume not just *S. alterniflora* but *J.roemerianus* and *Q. viriginiana (Valiela et al. 1978, Zimmer et al. 2004).* In our study, *L. irrorata* density was higher in the *A. germinans* zone than in the *S. alterniflora* zone which is contrary to the assertion that *L. irrorata* is dependent upon *S. alterniflora* as a food source (Silliman et al. 2003b). Similar to our findings, a study in a South Carolina marsh also found *L. irrorata* biomass higher in the high marsh than would be expected given the scarcity of *S.*

alterniflora in this zone (Hutchens et al. 2006). All of which suggests that *L. irrorata* is truly a detritivore that is not solely dependent upon *S. alterniflora* as a food source and less likely to exert strong control on *S. alterniflora* production.

CONCLUSION

Whether the variation between this study and Silliman and Zieman's (2001) study is due to latitudinal differences, *S. alterniflora* form variation, or nutrient stress, it is clear that *L. irrorata* does not influence *S. alterniflora* and thus has no role in the competition between *A. germinans* and *S. alterniflora.* Instead, environmental factors and the ability of *S. alterniflora* and *A. germinans* to adapt to those factors appear to be the determinant in the interplay between the two species.

These findings are in line with other studies that have found that temperature (McMillan 1971, Forbes et al. 2006, Stuart et al. 2007), nutrient availability (Sullivan et al. 1974, Gallagher 1975, Mendelssohn 1979, Buresh et al. 1980, Howes et al. 1986, Chen et al. 1998, Bertness et al. 2002, Alexander et al. 2006), soil redox potential (Howes et al. 1986, Bertness 1991), tidal amplitude (Patterson et al. 1997, Allen et al. 2003, Roland et al. 2005), inundation periods (Wiegert et al. 1983, Patterson et al. 1997), and exposure to toxins (Koch et al. 1989) can affect *S. alterniflora* and *A. germinans* viability and fecundity. As evidenced by the lack of temperature limiting conditions that has pushed the range of *A. germinans* northward. (Stevens et al. 2006, Stuart et al. 2007) the alteration of any of these factors can lead to a shift in dominance in the vegetation. This was also seen in our study where *A. germinans'* response to nitrogen was a significant increase to its rate of growth allowing it to overtop *S. alterniflora* in one third of the time.

Succession models often show the transition from herbaceous to forest systems as a linear pathway. The interplay between *S. alterniflora* and *A. germinans* is not so simple. Without barriers, like stands of *S. alterniflora*, preventing the tide from washing away the buoyant propagules of *A. germinans,* reproduction in low elevations is unlikely (Patterson et al. 1997, Stevens et al. 2006). Conversely, mangal systems have long been thought to trap sediments (Lugo et al. 1974) and given *S. alterniflora's* wave tolerance of <0.1m (Roland et al. 2005), *A. germinans* can provide necessary buffers between the tide and *S. alterniflora.* Long term evidence of this cyclical dominance regime is seen in Florida where mangal systems are re-establishing in areas that are currently *S. alterniflora* dominated but were previously *A. germinans* dominated (Stevens et al. 2006).

Global climate change models however with predict changes in temperature, precipitation patterns, and sea level rise may cause this mangal/marsh dynamic to falter. The apparent drought induced *S. alterniflora* dieback along the Mississippi deltaic plain in 2000, where dead stands of *S. alterniflora* were found adjacent to healthy *A. germinans* (McKee et al. 2004), may serve as a preview of things to come. Global climate change, and specifically nutrient availability, has been shown to affect plant interactions and caused shifts in dominant plant species in hypersaline marshes (Forbes et al. 2006), New England salt marshes (Bertness et al. 2002), as well as in alpine communities (Klanderud 2005). If temperatures and sea levels do rise as predicted, *A. germinans* with its high salinity tolerance and water use efficiency (Lopez-Hoffman et al. 2007) may

prove to be the dominant species in light of greater environmental stressors (Emery et al. 2001). This shift in dominance would have an upward cascading effect on not just marsh community but feasibly on the near shore marine and upland watershed as well.

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ABSTRACT

EFFECTS OF SNAIL GRAZING AND ENVIRONMENTAL FACTORS ON THE EXPANSION OF MANGROVES INTO SALT MARSHES

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Coastal wetlands are ecosystems that provide goods and services critical to our way of life. As dependent as we are upon these features, our understanding of their responses to global factors such as climate, sea-level rise, and eutrophication is limited. The transitional community where tropical mangrove meets temperate salt marsh is an ideal setting to test hypotheses about vegetative shifts caused by environmental changes. Black mangrove (*Avicennia germinans)* is at its northernmost boundary within the Gulf of Mexico where it commingles with smooth cordgrass (*Spartina alterniflora).* The purpose of this study was to examine what role grazing by the marsh periwinkle *(Littoraria irrorata)* plays in the competitive interactions between smooth cordgrass and black mangrove. This study centers on coastal Louisiana where black mangroves have been expanding for the past fifteen years. Our results indicate that environmental stressors such as nutrient deficiency or salinity have a greater impact on mangrove-marsh competition than snail grazing in

healthy cordgrass stands, but that grazing effects are important in stands already stressed by environmental factors. These findings are consistent with recent observations that mangrove expansion increased following large-scale dieback of salt marsh in Louisiana due to drought-related stress.