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Charles Stuart Patterson
Louisiana State University and Agricultural & Mechanical College

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Avicennia germinans L., in a Louisiana mangal/salt marsh
community**

Patterson, Charles Stuart, Ph.D.

The Louisiana State University and Agricultural and Mechanical Col., 1991

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FACTORS CONTROLLING THE DISTRIBUTION OF THE
BLACK MANGROVE, *AVICENNIA GERMINANS* L.,
IN A LOUISIANA MANGAL/SALT MARSH COMMUNITY

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Marine Sciences

by
Charles Stuart Patterson
B.S., The University of Southern Mississippi, 1978
December 1991

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ABSTRACT

Mangroves are intertidal, halophytic trees limited to the tropics and subtropics because they are not cold-tolerant. In coastal Louisiana (29° N latitude), the black mangrove, *Avicennia germinans*, is the only mangrove found because *Avicennia* is the most cold-tolerant of mangrove genera. *Avicennia* intergrades with salt marsh cordgrass, *Spartina alterniflora*, with 3 observed zones: an *Avicennia* zone, a transition zone, containing both *Avicennia* and *Spartina*, and a *Spartina* zone. The purpose of this dissertation was to determine why *A. germinans* does not occur in the *Spartina* zone within a mangal/salt marsh ecotone. Three studies investigated the following zone differences in: (1) soil physicochemical variables (2) ability of *Avicennia* seedlings to survive and grow and (3) propagule dispersal, establishment and predation.

The transition and *Spartina* zones were similar across most soil physicochemical variables. However, the *Avicennia* zone was distinctly different, with higher elevation, soil bulk density, and redox potential, and lower sulfide levels in the interstitial water.

Although the zones differed in soil physicochemical variables, these differences did not impact the survival of *Avicennia* seedlings, although growth was reduced in the more inundated *Spartina* zone.

Since *Avicennia* seedlings can survive and grow in the *Spartina* zone, seedling success may be related more to the establishment capabilities and predation of *Avicennia* propagules. When propagules were prevented from being moved away by tides, *Avicennia* could establish in the *Spartina* zone. However, propagule predation rates were significantly higher in the *Spartina* zone and unaffected by propagule background density.

Since *Avicennia* seedlings have reduced growth in the *Spartina* zone, the long-term survival of *Avicennia* in the *Spartina* zone is questionable. However, the most probable causes for exclusion of *A. germinans* from the *Spartina* zone are related to the fate of the propagules. Most propagules dispersed into the *Spartina* zone are probably washed away by tides before establishment, and the few remaining propagules are probably damaged enough by predators to render them incapable of establishment.

INTRODUCTION

Plant communities in many areas of the world show distinct species zonation. Intertidal communities are harsh environments for most plants, and species richness is low. Intertidal plant communities provide plant ecologists ideal opportunities to study plant species zonation because the low species richness often causes obvious zonation, with zones dominated by only one or two species.

In the temperate zones of the world, low-energy coasts contain salt marsh communities. Salt marshes are comprised of rooted vegetation, mostly grasses, such as *Spartina* spp. and rushes, often *Juncus* spp. (Chapman 1960), forming distinct monospecific zones. The factors controlling plant species zonation have been investigated in salt marshes throughout the world.

In the tropics and subtropics, salt marshes are usually replaced with their ecological analog, mangrove swamps (Mitsch and Gosselink 1986). Mangroves are intertidal, halophytic plants (mostly trees) confined to the lower latitudes because they are not cold-tolerant. Mangrove species exhibit many interesting adaptations to flooded, saline environments, including internal oxygen transport (McKee et al. 1988) in red mangrove (*Rhizophora*) and black mangrove (*Avicennia*), aerial roots (pneumatophores) in *Avicennia* and white mangrove (*Laguncularia*), possibly for oxygen transport, and prop roots for anchoring and oxygen transport in deep water (*Rhizophora*). Most mangroves exhibit some form of vivipary, with seeds germinating on the parent plants before being dispersed. Because mangroves do not reproduce vegetatively, many researchers believe that vivipary is another adaptation to life in a flooded environment (Mitsch and Gosselink 1986). The young plants, termed propagules, exhibit varying degrees of buoyancy, depending on the species, and are dispersed by the tides. They do not require a period of dormancy and thus are able to exploit favorable habitats quickly upon arrival.

Mangrove swamps are also noted for exhibiting distinct species zonation. In a classic paper by Davis (1940) mangrove species zonation was discussed relative to tidal inundation, and the pattern of *Rhizophora* at the lowest elevations, *Avicennia* at intermediate elevations and white mangrove (*Laguncularia*) at the highest elevations was accepted as a "typical" zonation pattern in New World mangrove swamps for many years. However, since that time, many authors, such as Lugo and Snedaker (1974), Snedaker (1982) and Schaeffer-Novelli et al. (1990), have reported substantial variation in zonation patterns of mangrove swamps, so that the idea of "typical" mangrove species zonation is now not as widely accepted.

Zonation in mangrove swamps (mangals) has been studied by many scientists in different areas of the world. Most of the earlier work involved correlative studies and experiments on the relationship of various environmental factors to mangrove species zonation. Among environmental factors hypothesized to control mangrove species zonation were depth, duration and frequency of flooding, salinity, soil drainage (Chapman 1976), site-specific geomorphic characteristics (Thom 1967), and interstitial water sulfide and iron concentrations (Carlson et al. 1983, Nickerson and Thibodeau 1985, Gu et al. 1987).

Interspecific interactions, such as competition, have also been hypothesized as possible factors influencing mangrove species zonation (Ball 1980), although little research has been conducted.

Other studies have focused on the fate of mangrove propagules as a primary influence on species zonation. Rabinowitz (1978a,b) and Jimenez and Sauter (1991) hypothesized that tidal sorting of propagules controls mangrove species zonation. According to the tidal sorting theory, species with heavier propagules are found in more-inundated areas, and species with lighter propagules, which can be carried further by tides, are found at higher elevations. Differential propagule predation has also been proposed as a possible cause of mangrove species zonation (Osborne and

Smith 1990, Smith 1987a, Smith 1987b, Smith *et al.* 1989), with individual mangrove species absent or rare in zones where their propagules are most heavily preyed upon.

All of the previously mentioned hypotheses concerning mangrove species zonation are probably valid in the sense that they appear operative in the specific plant communities studied by their respective researchers.

In certain areas of the subtropics, often near 30° latitude, mangroves are at their latitudinal limits and intergrade with salt marsh plants within the same wetland, forming an ecotone. At the latitudinal limits of mangroves, *Avicennia* is the only mangrove found because it is the most cold-tolerant of mangrove genera (Lugo and Zucca 1977, McMillan and Sherrod 1986, Tomlinson 1986). Although many studies have been conducted on plant species zonation in salt marshes and in mangrove swamps, there is a paucity of studies investigating zonation in wetlands where mangroves and salt marsh plants co-occur. Some of these studies are correlative and speculative, instead of being based on experimental evidence (Detweiler *et al.* 1975, Kangas and Lugo 1990). Of the few experimental studies in mangal/salt marsh communities, none have addressed propagule establishment and dispersal (Clarke and Hannon, 1969, 1971).

This dissertation investigates several possible factors which may influence or control the distribution of *Avicennia germinans* in a mangal/salt marsh community in Louisiana. Because there are few studies dealing with mangrove zonation in this type of community, the information gained from this research will advance the present knowledge of factors controlling plant species distribution in ecotones. The study site for the research in this dissertation is located on the southeastern coast of Louisiana and is at the northern distributional limits of *A. germinans*. *Avicennia* plants in this community are stunted, usually not exceeding 2.5 m in height before being killed by occasional sub-freezing temperatures. Plant species diversity in this community is

very low, with two dominant species, *A. germinans* and salt marsh cordgrass, *Spartina alterniflora*, with sparse occurrences of *Batis maritima*, *Distichlis spicata* and *Salicornia* sp. When this research first began, there were three species zones at the study site: a zone dominated by *A. germinans* at the edge of a bay, a transition zone further inland containing both *A. germinans* and *Spartina alterniflora*, and a pure zone of *S. alterniflora* furthest inland. This dissertation addresses possible reasons why *A. germinans* is not found in the more inland marsh areas dominated by *S. alterniflora*.

Chapter 1 is a correlative study of possible environmental factors which have been shown to influence mangrove distribution in other communities. Zone differences in many soil physicochemical variables, such as interstitial water macronutrients, micronutrients, pH and sulfides, soil redox potential, soil texture, and elevation were determined.

Chapter 2 explores the possibility that *A. germinans* seedlings can survive in areas at the study site where they are not naturally found. Both greenhouse and field manipulative (transplant) experiments were used. Possible interspecific interactions between *A. germinans* and *S. alterniflora* are addressed.

In Chapter 3 propagule survival within enclosures and propagule predation were compared between the *Avicennia* and *Spartina* zones to investigate the possibility that factors acting at the level of propagule dispersal and establishment could be influencing the distribution of *A. germinans* in this community.

Chapter 1 has been published in a refereed scientific journal (Wetlands), and Chapters 2 and 3 have been prepared as manuscripts for journals, and hence there will be some redundancy among the introductions of each chapter.

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*Society of
Wetland Scientists*

July 30, 1991

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Dear Stuart:

This letter confirms that permission is granted to use your paper entitled, "A comparison of physicochemical variables across plant zones in a mangal/salt marsh community in Louisiana," in your dissertation. The paper appeared in Volume 11, No. 1, pages 139-161 of Wetlands.

Sincerely,

Doug Wilcox

Douglas A. Wilcox, Ph.D.
Project Leader, Habitat Assessment
Editor, Wetlands

CHAPTER 1

A COMPARISON OF PHYSICOCHEMICAL VARIABLES ACROSS PLANT ZONES IN A MANGAL/SALT MARSH COMMUNITY IN LOUISIANA

INTRODUCTION

The black mangrove, *Avicennia germinans* L., is a tropical- subtropical tree found in many mangrove swamps (mangals) throughout the New World. In the northern hemisphere, mangrove vegetation occurs on low-energy coasts from the equator to as far as 24 to 32 degrees north latitude (Chapman 1976, Teas 1977). The northern limits of individual mangrove species seem to be determined by the number of killing frosts (-2 to -4° C) per year (Chapman 1976, McMillan and Sherrod 1986), although chill-tolerant populations of *A. germinans* have been found at the northernmost part of its range (Lugo and Zucca 1977, Johnston 1983, McMillan and Sherrod 1986). At the extremes of the distributional range, *A. germinans* is the only mangrove found because it has a greater chilling tolerance than other mangrove genera (Sherrod *et al.* 1986).

Within any particular mangal, mangrove species often occur in monospecific zones parallel to the shoreline. In a "typical" New World mangal, red mangrove (*Rhizophora mangle*) inhabits the lowest elevations, often adjacent to a body of water, while *A. germinans* is more abundant further inland at higher elevations, followed by white mangrove (*Laguncularia racemosa*) at the highest elevations (Davis 1940, Dawes 1981, Snedaker 1982).

A number of hypotheses have been proposed to explain the distribution of mangrove species within a mangal. Thom (1967) suggested that geomorphic characteristics of an area in conjunction with subtle elevational differences are the main factors responsible for mangrove species zonation. Depth, duration and frequency of flooding, salinity, soil drainage, and soil composition also may affect zonation (Chapman 1976). *Avicennia* is the most salt-tolerant of New World mangroves, with high productivity in salinities greater than 40 parts per thousand (Chapman 1976). This genus has optimum growth in oxidized, well-drained soils (Chapman 1976), and hence it is usually found at higher elevations where duration and frequency of flooding are relatively low. Relative proportions of silt, sand, and clay fractions in the soil are important because they influence drainage (Chapman 1976). Differential establishment capabilities and stranding period requirements for propagules of six mangrove species in a Panama mangal have been studied by Rabinowitz (1978) and hypothesized to be the main factors controlling mangrove distribution. Ball (1980) found that interspecific competition between two mangrove genera determined distribution and zonation in a disturbed mangal/salt marsh habitat near Miami, Florida. Shade intolerance and seed predation controlled the distribution of *Avicennia marina* in an Australian mangal (Smith 1987).

At their extreme northern range in the western hemisphere, *Avicennia* swamps intergrade with salt marshes dominated by *Spartina alterniflora*. In southeastern Louisiana, we observed that mangroves dominated higher-elevation sites, such as creekbanks, bay shores and on barrier islands at higher elevations, while *Spartina alterniflora* occurred at lower elevations that experience greater depth and duration of inundation. Penfound and Hathaway (1938) noted similar trends in mangrove distribution in Louisiana 50 years ago.

The factors that control the distribution of mangroves and salt marshes in intertidal systems where both communities coexist have received little attention. Both salinity and waterlogging influenced species distribution patterns in a mangal/salt marsh system near Sydney, Australia (Clarke and Hannon 1969). In addition, competitive interactions between *A. germinans* and salt marsh plants may influence zonation (Penfound and Hathaway 1938). However, little research has been conducted to determine what controls the distribution of *A. germinans* where it intergrades with *S. alterniflora*.

The objective of this study was to determine if specific soil physicochemical variables are correlated with the distribution of *A. germinans* in a mangal/salt marsh system in southeastern Louisiana.

METHODS

We investigated a mangal / salt marsh community located on the edge of Bay Champagne on the southeastern coast of Louisiana at 29° 6' 35"N, 89° 11' 1"W, at the northern limit of the range of *Avicennia* in Louisiana (Figure 1.1). *Avicennia germinans* and salt marsh cord grass (*Spartina alterniflora*) are the dominant plant species found in this community. *Batis maritima*, *Distichlis spicata*, and *Salicornia* sp. are sparsely distributed within this community. Three plant zones can be delineated at the study site--an *Avicennia* -dominated zone starting at the edge of the bay and extending 20-60 m inland, a transition zone of mixed species composition (*Avicennia* and *Spartina*) further inland and ranging from 30-60 m wide, and a *Spartina* -dominated zone starting approximately 60 m from the bay and extending inland (Figure 1.1).

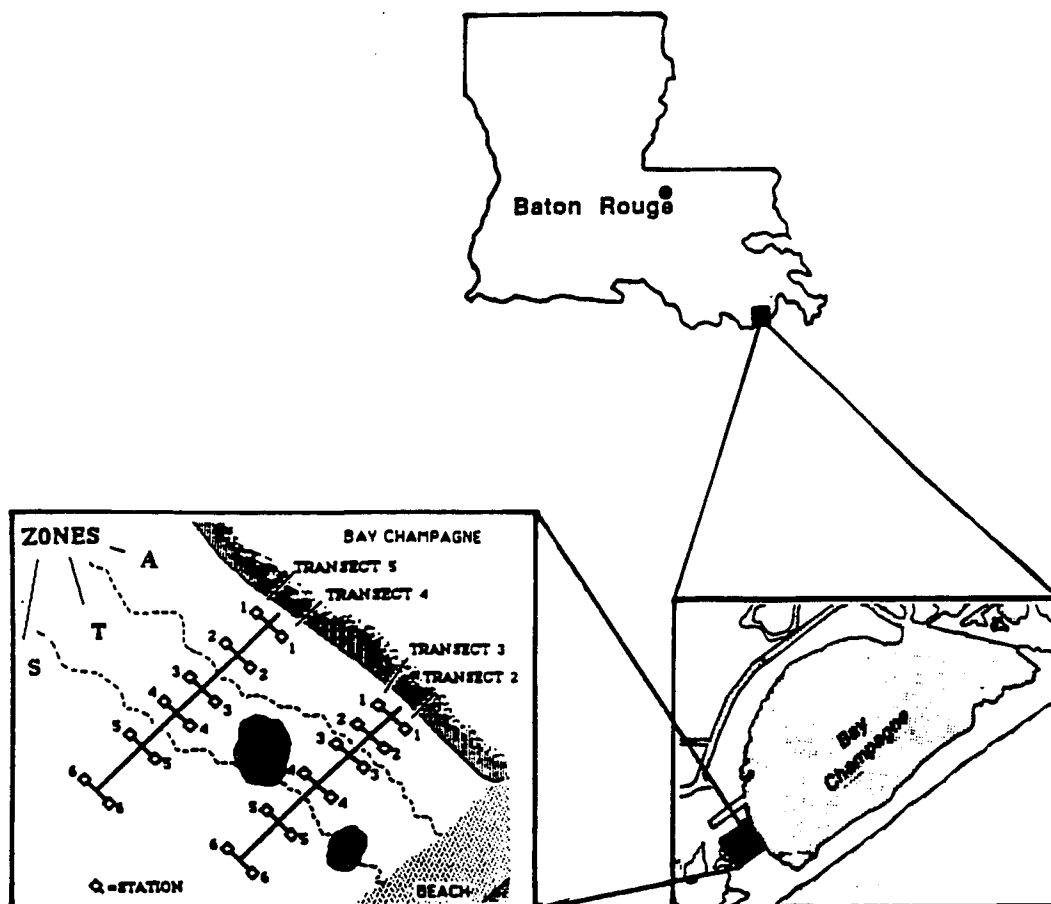


Figure 1.1. Location of transects and sampling stations adjacent to Bay Champagne, Lafourche Parish, Louisiana. A=Avicennia zone (*Avicennia germinans*), T=Transition zone, S=*Spartina* zone (*Spartina alterniflora*). North is to the top of the page. Dark areas are small ponds, not drawn to scale.

In October 1985, we could clearly delineate the *Avicennia* and *Spartina*-dominated zones. The *Avicennia* zone contained large dead stumps and smaller, healthy plants. No *Spartina* was found in this zone. The *Spartina* zone, consisting of a monospecific stand of *S. alterniflora*, extended from the inland boundary of the transition zone several hundred meters further inland. There was no visible evidence that mangroves had ever occurred in the *Spartina* zone. The transition zone was more difficult to identify because it contained few living *Avicennia*. Severe winter weather in December 1983 and January 1985 had killed all above-ground *Avicennia* biomass at the study site. Although the trees in the *Avicennia* zone were resprouting vigorously from root stocks of frost-killed plants, few plants in the transition zone were re-growing. The transition zone contained a mixture of healthy *Spartina*, many *Avicennia* stumps, a few small living *Avicennia*, and a large amount of bare space. The open areas in the transition zone usually contained large *Avicennia* stumps, evidence that the bare spaces were once shaded by *Avicennia*.

Four replicate transects perpendicular to and intersecting the 3 vegetation zones were established at the study site (Figure 1.1). Six sampling stations, two in each zone were located along each transect. The total length of the *Avicennia* and transition zones were measured on each transect. Stations within a vegetative zone were located a distance of one-fourth of the total length of the zone from each border of the zone. This was done to control for possible gradients in the variables along a transect. Sampling was conducted 5 times during the 1986 growing season on the following dates (March 7, May 29, July 29, September 26, and November 7) to account for possible seasonal variation.

Interstitial Water Variables

On each sampling date, a sediment core 5 cm in diameter and 10 cm long was collected at each of the 24 stations and placed in a 500 ml centrifuge bottle. The bottles, containing air-tight septa, were then purged in the field with nitrogen gas for 2 minutes to create an anaerobic environment. Within 72 hours, the samples were centrifuged for 30 minutes at 25° C and 5,216 *g* to remove interstitial water from the sediment cores. Interstitial water for sulfide analysis was quickly removed from the centrifuge bottles after centrifugation and placed in a 50% solution of sample and antioxidant buffer (Lazar Research Labs 1986). The antioxidant buffer consisted of sodium salicylate, sodium hydroxide, and ascorbic acid in distilled deoxygenated water at concentrations of 250, 85, and 65 g/l, respectively. The antioxidant buffer prevented air oxidation of sulfides and adjusted the pH of the solution so that sulfides would be present in the sulfide ion form (S^{2-}). The sample solutions were then analyzed for free sulfides with a sulfide microelectrode (Lazar Research Labs 1986). The water from each centrifuge bottle was then filtered through a 0.45 micron filter and three additional aliquots were taken to measure salinity and pH, ammonium, and selected macronutrients and micronutrients. Salinity and pH were measured with the appropriate meters. The ammonium aliquot was frozen and later analyzed according to US EPA Method #350.1 (US EPA 1979). Any loss of ammonium due to freezing is insignificant relative to the concentrations of interstitial water ammonium measured in this study. The aliquot for macronutrients and micronutrients was acidified to less than pH 2 with reagent - grade nitric acid (suitable for trace metal analysis). Phosphorus, magnesium, calcium, potassium, copper, zinc, iron, and manganese

were determined by inductively coupled argon plasma emission spectrometry (Williams et al. 1986).

Soil Variables

Soil redox potential (Eh) was measured with brightened platinum electrodes and a digital pH/mV/temp meter. Measurements were taken at the soil surface (1 cm) and at 10 cm depths after a 30 minute equilibration period. The potential of a calomel electrode against a standard hydrogen electrode (+244 mV) was added to each value to calculate Eh.

Soil bulk density, percentage moisture, texture analysis, percentage organic matter, and surface elevation were determined once in November 1987. Elevational differences across transects and stations were measured with a level and stadia rod. Bulk density (oven-dry weight per volume) and percentage moisture (water weight/oven-dry soil weight * 100) were determined after drying soil samples of known volume and wet weight at 105° C for 24 hours (Hausenbuiller 1972). Particle size (texture) analysis was conducted by the pipet method (USDA 1984). Percentage organic matter was determined by combusting samples of known weight overnight at 425° C in a muffle furnace, allowing samples to cool for one hour in a desiccator, and calculating percentage weight lost (USDA 1984).

Data Analysis

Prior to the use of any statistical techniques, the data for interstitial water variables and Eh were tested for the necessary assumptions of homogeneity of variances and

normal distributions and found to be in violation of them. Several transformations were attempted, but none adequately met these assumptions. Consequently, a nonparametric ranking procedure (Proc Rank, SAS User's Guide 1985) was used, and all multivariate and univariate analyses on interstitial water variables and Eh in this study were performed on ranked variables.

The univariate analysis of variance used for those variables consisted of a randomized block design blocked on transect. Linear, quadratic, and cubic effects of sampling date were included in the model. Also, interactions of all date effects with zones were tested. Least squares means were used to determine zone differences overall and on individual sampling dates.

Many of the interstitial water variables and Eh were not expected to be independent, so a factor analysis was conducted on a correlation matrix of these variables to uncover common factors composed of multiple variables within this mangal / salt marsh community. Varimax factor rotation, an orthogonal rotation method, was used to clarify factor interpretation (Tabachnick and Fidell 1983, Dillon and Goldstein 1984). Factor scores for each observation were then used as variables in analysis of variance (ANOVA) to determine if factor scores differed across zones and sampling dates.

Textural variables, bulk density, percentage moisture, percentage organic matter, and surface elevation were all normally distributed, with the exception of percentage sand. Therefore, percentage sand was transformed by the nonparametric ranking procedure previously mentioned, while all other soil variables and elevation remained unchanged. Univariate analyses of variance were performed separately on all soil variables to test zone effects, using a randomized block design to remove transect

variation. Duncan's multiple range test was used to detect individual zone differences.

Unless specified, all results significant at $P < 0.05$ will be referred to as significant and results significant at $P < 0.01$ as highly significant.

RESULTS

Univariate Analysis of Soil Physicochemical Variables

Soil Texture, Organic Matter, and Elevation. Bulk density was significantly higher in *Avicennia* zone soils than soils of the transition and *Spartina* zones, but relative percentages of sand, silt, and clay were not significantly different among zones.

The only difference in percentage moisture occurred between the *Avicennia* and *Spartina* zones (Table 1.1), with a lower percentage moisture in the *Avicennia* zone ($P=0.02$).

Although zone effects for percentage organic matter were not significant (Table 1.1), the probability of 0.10 is suggestive of a trend toward higher levels of organic matter in *Avicennia* zone soils.

Relative elevation showed the most pronounced zone differences, with highly significant zone effects and three separate Duncan groupings (Table 1.1). The *Avicennia* zone was highest, the transition zone intermediate, and the *Spartina* zone lowest in elevation.

Table 1.1. Soil texture and physical variables measured once during 1986 across zones. Different superscript letters indicate significant zone differences (Duncan's test, n=8).

Variable	Zone		
	<i>Avicennia</i>	Transition	<i>Spartina</i>
Percentage sand	24.3 ± 20.1 ^a	17.1 ± 7.5 ^a	21.9 ± 5.5 ^a
Percentage silt	31.4 ± 12.2 ^a	32.3 ± 11.2 ^a	25.0 ± 11.5 ^a
Percentage clay	44.3 ± 19.0 ^a	50.6 ± 8.3 ^a	53.1 ± 10.9 ^a
Percentage moisture**	128.1 ± 32.8 ^b	156.6 ± 15.9 ^{a,b}	185.2 ± 42.9 ^a
Bulk density (g cc ⁻¹)**	0.57 ± 0.13 ^a	0.48 ± 0.06 ^b	0.43 ± 0.10 ^b
Relative elevation (cm)***	36.5 ± 0.6 ^a	33.1 ± 0.8 ^b	29.8 ± 1.2 ^c
Percentage organic matter*	10.9 ± 2.0 ^a	8.9 ± 3.7 ^{a,b}	7.2 ± 1.6 ^b

* P < .10.

** P < .05

*** P < .001.

Macronutrients. Although overall zone differences of interstitial water ammonium concentrations across dates were not significant, differences in ammonium between the *Avicennia* zone and the other zones occurred on some dates. In March and September, ammonium was significantly lower in the *Avicennia* zone than in the other zones, which had similar concentrations (Figure 1.2a). In May, the only difference occurred between the *Avicennia* and *Spartina* zones, with higher ammonium concentrations in the *Avicennia* zone. In July and November, all zones were similar. Trends across time differed in the three zones, indicated by a significant interaction of zone effects with sampling date. Ammonium in the *Avicennia* zone increased from March to May and then remained relatively stable. In the transition zone, ammonium levels were relatively stable from March through July, increased significantly from July to September, and stabilized from September to November. In the *Spartina* zone, ammonium decreased from March to May, increased from May to July, and then remained at stable levels.

Phosphorus concentrations were similar in the transition and *Spartina* zones on all sampling dates and in the *Avicennia* and *Spartina* zones on all dates except March, when concentrations were higher in the *Spartina* zone (Figure 1.2b). The transition zone had higher phosphorus levels than the *Avicennia* zone on all dates except November. All zones had different seasonal trends in phosphorus concentrations. The *Avicennia* zone showed a highly significant linear increase over the year. Concentrations in the transition zone followed a quadratic trend over time, with a peak in mid-summer to early fall. Phosphorus levels remained relatively constant in the *Spartina* zone.

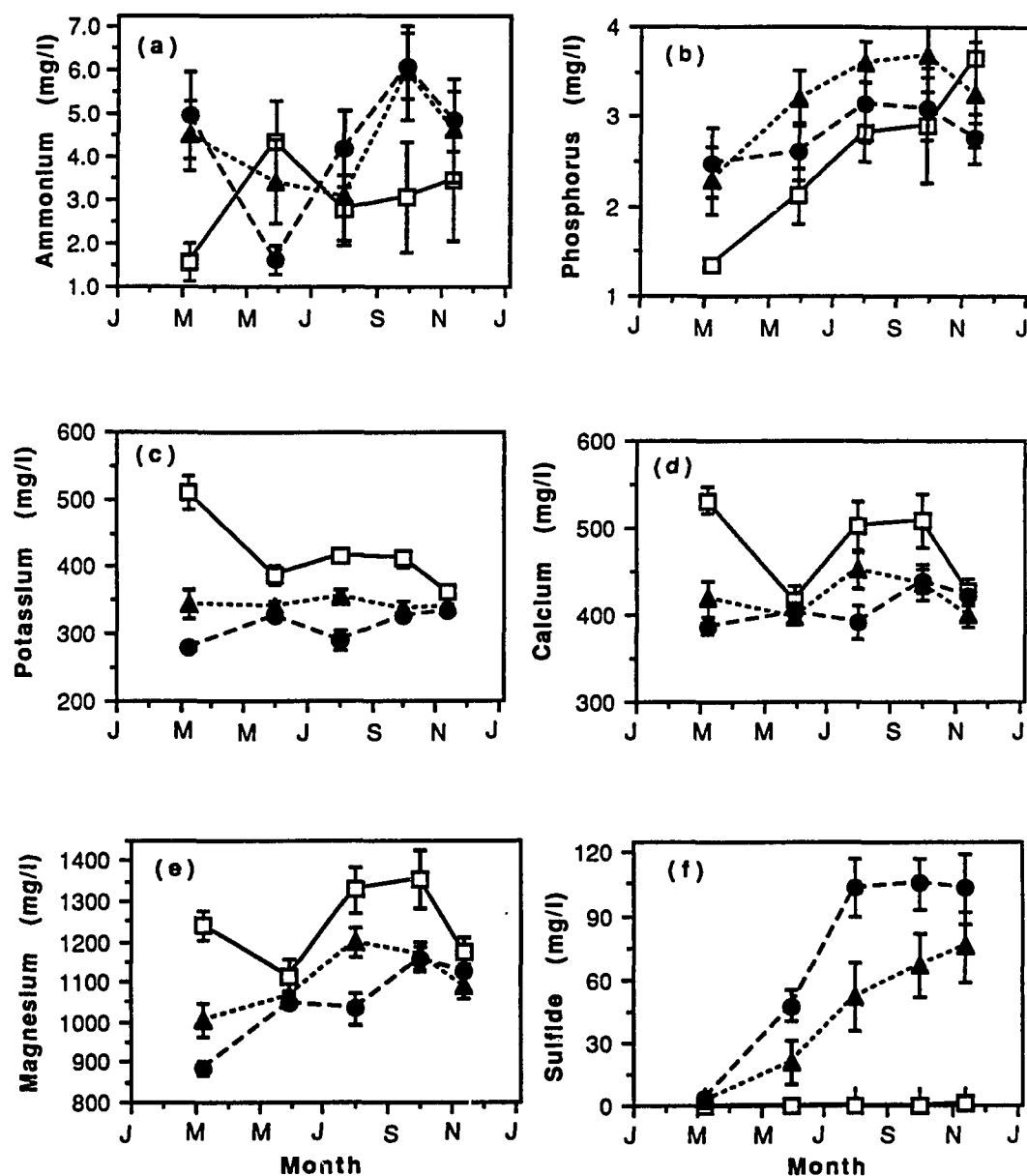


Figure 1.2. Macronutrient concentrations in the three vegetation zones across sampling dates; *Avicennia* zone (-□-), transition zone (-▲-), *Spartina* zone (-●-). Points are the means of replicate samples ± one standard error.

A highly significant interaction of zone effects with sampling date occurred for potassium. Concentrations were highest in the *Avicennia* zone, intermediate in the transition zone, and lowest in the *Spartina* zone from March through July (Figure 1.2c) but were similar in the transition and *Spartina* zones in September and November, while remaining higher in the *Avicennia* zone. Linear trends were also different in each zone. Potassium levels in the *Avicennia* zone decreased linearly from March to May, remained stable from May through September, and decreased again from September to November. There was no significant linear trend in the transition zone, where potassium concentrations remained relatively constant. In the *Spartina* zone, potassium fluctuated throughout the year, with lowest levels in the early part of the growing season and an overall increase for the year.

Calcium had a highly significant interaction of zone effects with sampling dates, indicating seasonal differences across zones. In March, the *Avicennia* zone had higher calcium levels than the transition and *Spartina* zones, which had similar levels (Figure 1.2d). In May and November, all zones were similar. In July, the *Spartina* zone had significantly lower calcium levels than the other zones, which did not differ, and in September, the only significant difference occurred between the *Avicennia* and transition zones, with highest and lowest levels, respectively. The transition and *Spartina* zones had similar calcium concentrations on all sampling dates except July, when levels were higher in the transition zone. The behavior of calcium across dates was different in each vegetation zone (Figure 1.2d). There were highly significant linear effects in the *Avicennia* and *Spartina* zones, with overall decreases and increases, respectively. Calcium levels in the transition zone were relatively constant.

Magnesium had a highly significant interaction of zone effects with sampling dates. In March and September, the *Avicennia* zone had higher magnesium concentrations

than the other zones, which did not differ. In May, only the *Avicennia* and *Spartina* zones differed, with higher levels in the *Avicennia* zone (Figure 1.2e). In July, the *Spartina* zone had significantly lower magnesium concentrations than the other zones, which were similar. In November, the only difference in magnesium concentration occurred between the *Avicennia* and transition zones, with higher levels in the *Avicennia* zone.

Zone differences in sulfide concentrations varied throughout the year (highly significant interactions of zone and date effects). In March, sulfide concentrations were low and similar in all zones (Figure 1.2f). After March, during the growing season, sulfide levels were highest in the *Spartina* zone, with intermediate levels in the transition zone and lowest levels in the *Avicennia* zone. In late fall, sulfide concentrations in the transition zone had reached levels equal to those in the *Spartina* zone. A highly significant linear date by zone interaction ($P=0.0003$) indicated separate linear effects for zones. In the *Avicennia* zone, sulfide levels were low and constant over time. However, in the transition zone, sulfide levels increased linearly from March through November. Sulfide levels in the *Spartina* zone rapidly increased in a linear fashion from March through July and then reached a plateau, staying at higher levels than those of the other zones.

Micronutrients. Iron had a significant interaction of zone effects with time, and seasonal trends differed among zones. Interstitial water iron concentrations were higher in the *Avicennia* zone than in the other two zones except in March, when the *Avicennia* and transition zones had similar values (Figure 1.3a). The transition and *Spartina* zones were similar except in May and July, when the transition zone had iron concentrations intermediate between those of the *Avicennia* and *Spartina* zones. In the

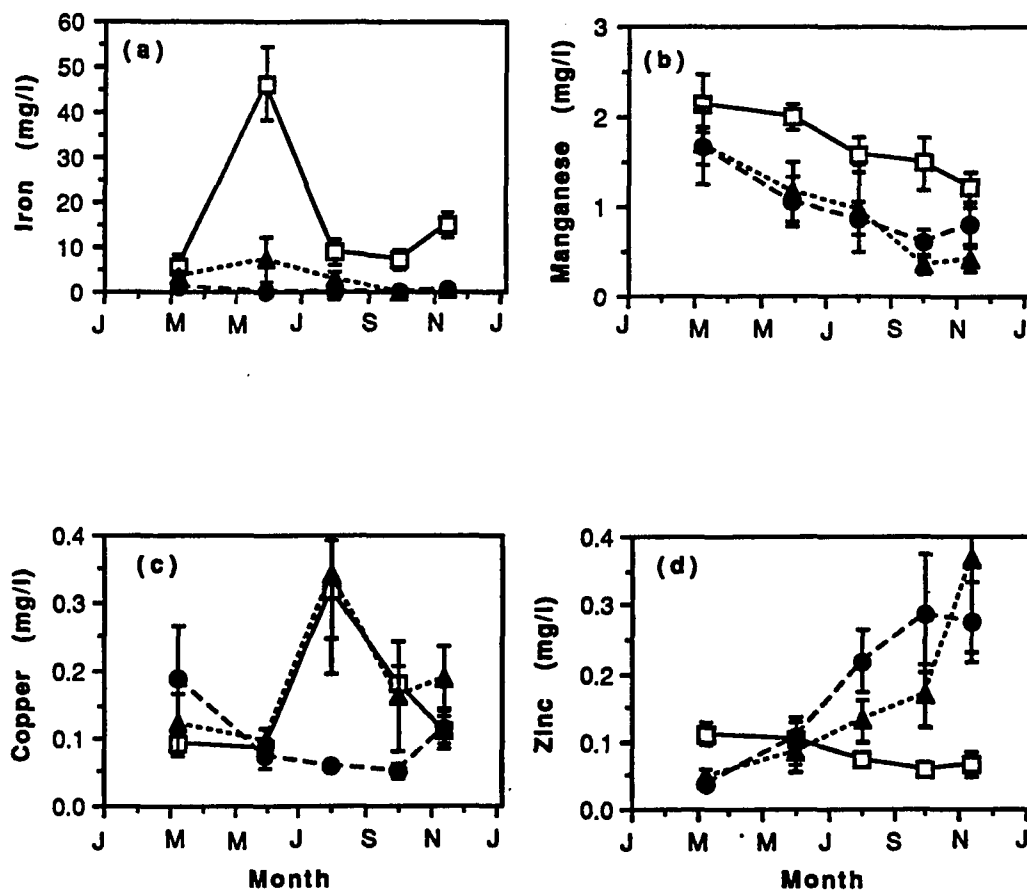


Figure 1.3. Micronutrient concentrations in the three vegetation zones across sampling dates; *Avicennia* zone (\square), transition zone ($\cdot\blacktriangle\cdot$), *Spartina* zone (\blacksquare). Points are the means of replicate samples \pm one standard error.

transition and *Spartina* zones, iron was always low and showed linear (horizontal) trends. In the *Avicennia* zone, iron concentrations followed a cubic trend throughout the year, with a peak in May.

Zone effects for manganese were highly significant, with non-significant interactions with time. Overall, manganese was highest in the *Avicennia* zone (Figure 1.3b). Manganese levels in the transition and *Spartina* zones were different only in November, with higher levels in the *Spartina* zone. The overall linear trend across sampling dates was highly significant, with no significant interactions with zone. Therefore, all vegetation zones showed a linear decrease in mean manganese levels from March through November.

Zone effects for copper were non-significant, but a significant interaction of zone effects with time indicated that zone differences occurred on some sampling dates. In March, May, and November, all zones had similar interstitial water copper concentrations (Figure 1.3c). In July and September, the *Spartina* zone had significantly lower levels than those of the other two zones. Trends in copper concentration were similar in the *Avicennia* and transition zones from March through September, both having a peak in July. Copper concentrations in the *Spartina* zone remained relatively constant throughout the year, with no significant changes across dates.

Zinc did not show overall zone differences (non-significant zone effect). However, there was a highly significant interaction of zone effects with sampling dates. In March, zinc was higher in the *Avicennia* zone than in the other two zones (Figure 1.3d). In May, all zones had similar levels. In July, the only difference occurred between the *Avicennia* and *Spartina* zones, with higher levels in the *Spartina* zone. In September and November, zinc was lower in the *Avicennia* zone than in the

other two zones, which had similar concentrations. A highly significant linear interaction effect for interstitial water zinc indicated different behavior of zinc across zones for the year. In the *Avicennia* zone, mean zinc levels decreased slightly from March until November. Zinc concentration in the *Spartina* zone increased rapidly from March through July and then remained stable. In the transition zone, mean zinc levels increased linearly but less rapidly than in the *Spartina* zone from March through July and then increased rapidly from September to November.

Soil Eh, pH, and Salinity. Zone effects for surface Eh were highly significant. Surface Eh was highest in the *Avicennia* zone (Figure 1.4a), with no differences between the transition and *Spartina* zones. Over time, surface Eh was generally higher in the *Avicennia* zone, but in May, all zones had similar levels. In November, the only difference occurred between the *Avicennia* and transition zones, with higher levels in the *Avicennia* zone. All zones had a similar significant quadratic trend over time (non-significant quadratic by zone interaction) (Figure 1.4a). Surface Eh was highest in March, reached its lowest point in May, increased until September, and remained relatively stable in all zones through November.

A significant interaction of zone effects with time for Eh at 10 cm depth indicated that there were inconsistent differences between zones over the year. Any differences that occurred were between the *Avicennia* zone and the other two zones, which were similar on all sampling dates (Figure 1.4b). In March, July, and November, levels were higher in the *Avicennia* zone, with similar values in all zones in May and September. Also, all zones showed different trends over time. In the *Avicennia* zone, Eh at 10 cm depth decreased sharply from a high point in March to a low level in May, increased until September, and stabilized through November. In the

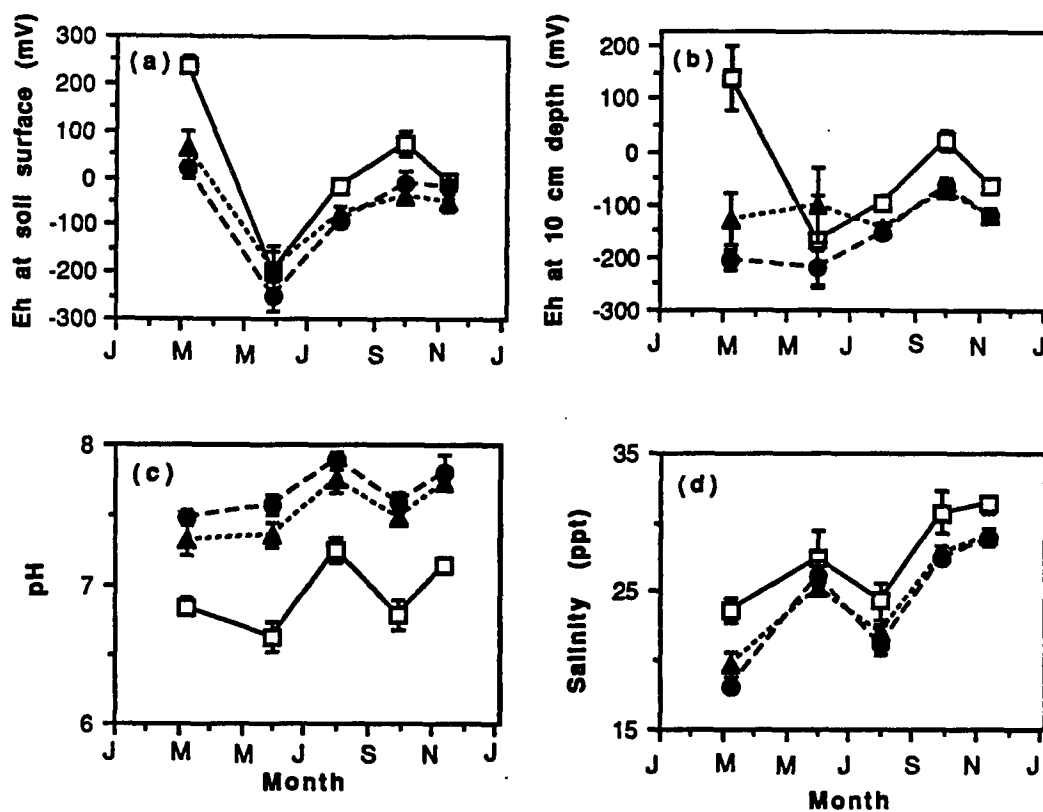


Figure 1.4. Eh, pH and salinity in the three vegetation zones across sampling dates; *Avicennia* zone (—□—), transition zone (···▲···), *Spartina* zone (—■—). Points are the means of replicate samples ± one standard error.

transition zone, levels stayed relatively constant, with the highest level in September. In the *Spartina* zone, Eh was low in the spring and summer, reached a peak in September, and decreased in the fall.

Zone effects for pH were highly significant, with non-significant interactions of zone with sampling date. Overall, pH was lowest in the *Avicennia* zone, intermediate in the transition zone, and highest in the *Spartina* zone. pH was always lower in the *Avicennia* zone, but pH levels in the transition and *Spartina* zones were not different on any sampling date (Figure 1.4c). Overall linear effects were highly significant, and none of the interactions with date were significant, indicating similar trends in pH over time in all zones. There was a slight linear increase in pH over the year, with highest levels in all zones in July and November, and lower levels in the other months.

Salinity levels were similar in the transition and *Spartina* zones on all sampling dates (Figure 1.4d). In May, September, and November, all zones were similar, but in March and July, the *Avicennia* zone had higher levels. Overall linear and cubic trends over time were highly significant, with non-significant interactions of the above effects with time. Salinity in all zones increased from late winter to spring, decreased from spring to mid-summer, and increased again from mid-summer through fall (Figure 1.4d).

Factor Analysis

Many of the interstitial water variables and Eh had correlations that exceeded 0.5 (Table 1.2), indicating that factor analysis would be appropriate. The first five factors constructed by the factor analysis had eigenvalues greater than 1, a criterion

Table 1.2. Correlations of Eh and interstitial water variables. Correlations with absolute value greater than 0.200 are significant; greater than 0.250 are highly significant. E1=Eh at surface. E2=Eh at 10 cm depth. Sal=salinity.

	E1	E2	S	Cu	Zn	Fe	Mn	Ca	Mg	P	K	pH	Sal	NH4
E1	1.000	0.501	-0.439	0.257	-0.175	0.257	0.328	0.375	0.283	-0.184	0.288	-0.264	0.007	-0.119
E2		1.000	-0.247	0.090	0.069	0.177	-0.005	0.462	0.535	-0.084	0.418	-0.294	0.355	-0.098
S			1.000	-0.349	0.584	-0.794	-0.660	-0.375	-0.291	0.433	-0.593	0.818	0.044	0.404
Cu				1.000	-0.246	0.372	0.236	0.254	0.314	-0.018	0.360	-0.190	0.140	-0.279
Zn					1.000	-0.485	-0.409	0.065	0.162	-0.010	-0.091	0.419	0.179	0.200
Fe						1.000	0.625	0.348	0.361	-0.233	0.591	-0.797	0.132	-0.306
Mn							1.000	0.429	0.225	-0.164	0.339	-0.558	-0.113	-0.360
Ca								1.000	0.908	-0.152	0.675	-0.363	0.289	-0.399
Mg									1.000	-0.089	0.724	-0.340	0.464	-0.343
P										1.000	-0.244	0.368	0.061	0.488
K											1.000	-0.600	0.299	-0.329
pH												1.000	-0.163	0.261
Sal													1.000	-0.120
NH4														1.000

commonly used in deciding on the number of factors to extract (Dillon and Goldstein 1984). Those five factors accounted for 79.1 percent of the total variation in the data. The sixth factor had an eigenvalue of 0.837, indicating that the five-factor solution would be best.

After Varimax rotation, all factors had at least one variable with a loading whose absolute value exceeded 0.5. Only one variable, Eh at 10 cm depth, loaded on more than one factor (Table 1.3).

Analysis of variance of factor scores showed highly significant interactions of zone effects with dates for the first two factors. Consequently, these scores will be discussed reflecting zone differences on individual sampling dates. Factor scores from the other three factors showed few zone differences, so only factor interpretations will be mentioned for factors 3-5.

The first factor was interpreted as a sulfide factor. Sulfide, pH, and zinc had high positive loadings on this factor, while iron and manganese had substantial negative loadings (Table 1.3). The interpretation follows that sulfide, pH, and zinc increased as reducing conditions increased, while iron and manganese decreased. In March, scores of factor 1 were low and similar in all zones (Figure 1.5a). In May, all zones had highly significant factor 1 score differences--lowest in the *Avicennia* zone, intermediate in the transition zone, and highest in the *Spartina* zone. During July through November, *Avicennia* zone scores were lower than scores in the other two zones ($P=0.0001$), which did not differ.

The second factor was interpreted as a salinity factor. Magnesium, calcium, salinity, potassium, and Eh at 10 cm depth all had high positive loadings on this factor (Table 1.3). The four elements listed above would be higher in higher salinity water relative to less saline water. In March and July, this factor was highest in the

Table 1.3. Correlations of Eh and interstitial water variables with factors. E1 = Eh at soil surface. E2=Eh at 10 cm depth. Sal=salinity.

Variable	FACTOR				
	1	2	3	4	5
S	0.863	-0.090	0.297	-0.260	-0.112
pH	0.860	-0.309	0.178	-0.103	0.160
Zn	0.729	0.323	-0.124	-0.007	-0.247
Mn	-0.664	-0.012	-0.222	0.142	0.330
Fe	-0.869	0.272	-0.093	0.021	0.127
Mg	-0.076	0.850	-0.175	0.269	0.268
Sal	0.030	0.774	0.144	-0.136	-0.064
Ca	-0.136	0.684	-0.282	0.359	0.319
K	-0.449	0.670	-0.207	0.186	0.145
P	0.197	0.015	0.865	-0.108	0.234
NH ₄	0.177	-0.184	0.746	0.061	-0.383
E1	-0.212	0.011	-0.068	0.888	0.173
E2	-0.059	0.527	0.037	0.682	-0.174
Cu	-0.232	0.177	0.017	0.070	0.782

Percent variance explained by each factor

1	2	3	4	5	Total
25.80	20.46	11.98	11.62	9.25	79.12

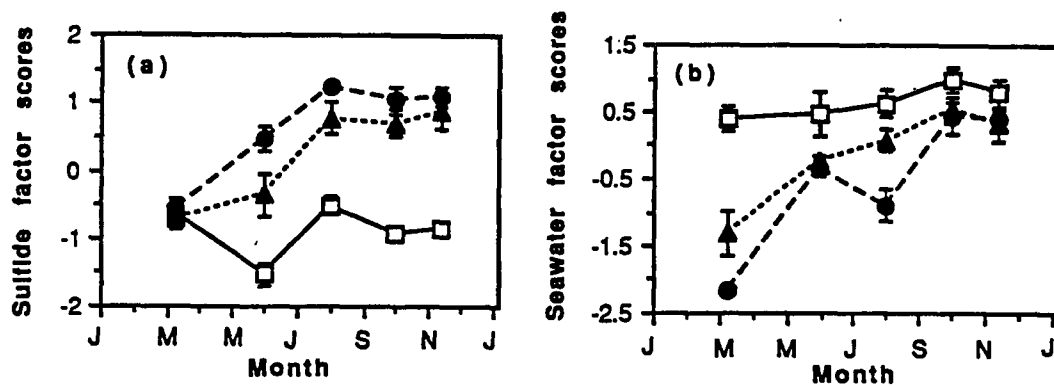


Figure 1.5. Factor scores in the three vegetation zones across sampling dates; *Avicennia* zone (□), transition zone (Δ), *Spartina* zone (●). Points are the means of replicate samples \pm one standard error.

Avicennia zone, intermediate in the transition zone, and lowest in the *Spartina* zone, all with highly significant differences (Figure 1.5b). On all other dates, factor 1 scores in the transition and *Spartina* zones were not different. In May, the *Avicennia* zone had higher scores than the other two zones. In September and November, scores were similar in all zones.

The third factor was interpreted as a nitrogen/phosphorus factor. Ammonium and phosphorus had high positive loadings on this factor (Table 1.3). The fourth factor had high positive loadings of both Eh measurements, and thus was an Eh factor (Table 1.3). The fifth factor was a copper factor. Copper was the only variable with a significant loading on this factor, a high positive loading (Table 1.3).

DISCUSSION

The analyses of soil physicochemical variables across three vegetative zones, *Avicennia* -dominated, *Spartina* -dominated, and transition, demonstrated significant zone differences. The *Avicennia* zone differed from the other zones for all variables except copper, while the transition and *Spartina* zones were similar for all variables except potassium and sulfide. When the univariate data (Eh and interstitial water variables) were analyzed simultaneously via factor analysis, the resultant factor scores, which are linear combinations of the univariate data, also exhibited zone differences. Significant differences in factor scores occurred between the *Avicennia* zone and the other two zones for the sulfide and salinity factors.

The sulfide factor, which accounted for 26 percent of the variation in the data, was comprised of sulfide, zinc, pH, iron, and manganese. This factor was significantly

higher in the transition and *Spartina* zones than in the *Avicennia* zone after March (Figure 1.5a), indicative of stronger soil reducing conditions in the transition and *Spartina* zones.

Textural Differences

Although differences in percentages of sand, silt and clay were not significant among the soils of the three zones, there was a tendency for higher sand in the *Avicennia* zone. This may explain the significantly higher bulk density of the *Avicennia* zone soils relative to the soils of the other two zones. This would be expected because the *Avicennia* zone is located closer to Bay Champagne and sediments would be reworked more by waves. Heavier sediments would settle out of suspension first, while lighter silts and clays would be transported further inland of the bay shoreline.

Differences in Anaerobic Conditions

Influence of soil water. Bradley and Morris (1990b) found that bulk density is a good predictor of sediment water percolation rate in marsh soils, with greater percolation velocities in soils with greater bulk densities. The higher elevation and bulk density of the *Avicennia* zone, in conjunction with its location nearest Bay Champagne, would promote better soil water drainage than in the other zones (Mendelssohn *et al.* 1982), also explaining the lower soil moisture in the *Avicennia* zone relative to the *Spartina* zone. Better soil water drainage would cause *Avicennia* zone soils to be more oxidized than soils of the other two zones, which explains the

higher Eh usually found in the *Avicennia* zone. The Eh factor derived from the factor analysis did not show significant differences among zones, apparently because of the influence of other variables loading on this factor. The univariate Eh data are not confounded by the other variables and therefore better elucidate the differences in soil oxidation among zones. Seasonal differences in Eh were apparent in all zones. Other studies of marsh systems in Louisiana have shown yearly trends in Eh similar to those found in this study, with high Eh in the winter and early spring and low Eh in the summer and fall (Brannon 1973, Feijtel *et al.* 1988). High Eh levels in the winter and spring have been attributed to dominant northwesterly winds that move water out of the marshes. Low Eh in the summer and fall is caused by onshore water transport by southern winds and high levels of precipitation, which increase water levels in the marsh. On the May sampling date, when water levels were high at the study site, Eh of the *Avicennia* zone decreased and reached levels as low as those of the other two zones, possibly indicating sustained flooding conditions at that time.

In general, flooding, with subsequent anaerobic soil conditions, causes pH to approach 7 (Ponnamperuma 1972). Reduction of iron, manganese, and sulfate would consume hydrogen ions under reducing conditions and cause increases in pH (Giblin and Howarth 1984). Therefore, the higher pH of the transition and *Spartina* zone soils may have resulted from the more reduced conditions that occurred in those zones, substantiated by high sulfide concentrations in those zones for most of the year.

Sulfides. Anoxic conditions are essential for sulfate reduction to occur (Gambrell and Patrick 1978). Sulfate reduction by bacteria, *Desulfovibrio*, is also influenced by temperature, with higher rates at higher temperatures (Ponnamperuma 1972). The low sulfide concentrations in all zones in March were due to oxidized soil

conditions and low soil temperatures. From spring to mid - summer, the rapid linear increase in sulfide production in the transition and *Spartina* zones was probably caused by increased temperatures and soil flooding. Sulfide production reached a plateau in the *Spartina* zone after July, possibly because it had reached a maximum rate possible for the system (Howarth and Giblin 1983). Although *Spartina* zone sulfide levels were high, similar levels have been found in other salt marshes (King *et al.* 1982, King *et al.* 1985, Bradley and Morris 1990a). However, interstitial water sulfide concentrations reported in the literature are highly variable. Although the cause of this variation is unknown, differences in sample processing as well as sulfide standardization are likely reasons. Also, the slightly lower Eh levels in the *Spartina* zone relative to the transition zone substantiated the higher sulfide levels in the *Spartina* zone in late spring and summer. Measurable levels of sulfide were never found in the *Avicennia* zone during the year, substantiated by negative correlations between Eh measurements and sulfide (Table 1.2), and the higher Eh of *Avicennia* zone soils.

Iron and manganese. Interactions of pH, Eh, and sulfide strongly influence concentrations of soluble iron and manganese. Persistent reducing conditions cause the release of significant amounts of Mn^{2+} and Fe^{2+} in solution (Gambrell and Patrick 1978). However, much of the hydrogen sulfide produced under reducing conditions causes these metals to precipitate as sulfides (Feijtel 1988). Iron and manganese were highly correlated (Table 1.2), and both had significant negative correlations with sulfide and pH. Therefore, low levels of iron and manganese were found with high levels of interstitial water sulfide and pH. Similar results have been obtained in other studies. In a comparative study between salt marshes in

Massachusetts and Georgia, Giblin and Howarth (1984) found that sites with lower pH had higher concentrations of iron and manganese and lower concentrations of sulfides. Areas with better drainage had more dissolved iron, and sulfide concentrations were lower. In a comparative study of interstitial water variables of *Avicennia* and *Rhizophora* zones in a Florida mangal, Carlson *et al.* (1983) demonstrated that high concentrations of dissolved iron were found in the *Avicennia* zone during periods of frequent inundation, while dissolved iron was consistently low in the *Rhizophora* zone due to iron sulfide precipitation. At our study site, the better drainage, greater oxidation, and lower sulfide of the *Avicennia* zone may have caused dissolved iron and manganese to be higher than in the other zones. The sharp peak in iron concentration in the *Avicennia* zone in May (Figure 1.3a) resulted from the combination of low redox, pH, and sulfide levels. Iron was probably in its more soluble ferrous form (Gambrell and Patrick 1978), but there was not enough sulfide present to cause precipitation as iron monosulfides or pyrite (Feijtel *et al.* 1988). Although iron and manganese should have been in their reduced forms in the transition and *Spartina* zones, sulfide concentrations were high and probably caused precipitation of iron and manganese in the interstitial water (Carlson 1983, Gu *et al.* 1987).

Zinc. Reducing conditions favor the release of zinc from Fe^{3+} and Mn^{4+} oxyhydroxides (Ponnamperuma 1972), but the presence of sulfide favors precipitation of zinc sulfide from solution (Ponnamperuma 1972, Feijtel 1986). In this study, zinc had almost identical negative correlations with iron and manganese (Table 1.2) and a relatively high positive correlation with sulfide. These correlations are opposite of what would be expected, since sulfide would also precipitate zinc,

with zinc behaving similarly to iron and manganese. Consequently, the zone and seasonal differences of zinc seen in this study are difficult to interpret.

Salinity-Related Nutrients

The salinity factor, which accounted for 20 percent of the variation in the data, was comprised of calcium, magnesium, potassium, salinity, and Eh at 10 cm depth. The nutrients are highly intercorrelated (Table 1.2) and have similar zone and seasonal responses (Figures 1.3, 1.4). Concentrations of these nutrients are similar to their respective concentrations in sea water at 35 ppt (Tchernia 1980) and are probably responsible for zone and seasonal differences in salinity. Behavior of nutrients loading highly on the salinity factor and salinity *per se* can be summarized by the seasonal and zone responses of salinity factor scores. The factor scores were usually higher in the *Avicennia* zone and similar in the other two zones. This may have been caused by greater soil water evaporation in the higher elevation and better drained *Avicennia* zone soils.

Nitrogen and Phosphorus

Although the nitrogen/phosphorus factor did not show significant zone differences, univariate zone differences were seen for both ammonium and phosphorus. Ammonium is the dominant form of nitrogen available for plant uptake in anaerobic soils (Gambrell and Patrick 1978, Mendelssohn 1979). Plant nitrogen requirements are greater for aerobic than anaerobic metabolism, so ammonium could accumulate in reduced soils relative to aerobic soils (Ponnamperuma 1972). Also, in aerobic soils,

ammonium is oxidized to nitrite and then to nitrate. In reduced soils, ammonium is removed by plant uptake, bacterial assimilation, or diffusion to an overlying aerobic soil (Gambrell and Patrick 1978). A positive correlation between interstitial water sulfide and ammonium concentrations has been observed (DeLaune *et al.* 1983, Mendelssohn and McKee 1988, Bradley and Morris 1990a). We found similar results in our study (Table 1.2). This correlation is hypothesized to be the result of sulfide inhibiting nitrogen uptake in *S. alterniflora* (Bradley and Morris 1990a, Koch *et al.* 1990). Therefore, ammonium levels should be lower in the *Avicennia* zone, which had negligible sulfide and usually higher Eh than the transition and *Spartina* zones. However, an exception occurred in May, when ammonium was highest in the *Avicennia* zone. At that time, the *Avicennia* zone had its lowest Eh levels, similar to those found in the other zones. In May, the sharp decrease in ammonium in the *Spartina* zone was probably due to uptake by *Spartina* (Casselman *et al.* 1981) because the highest net production by *S. alterniflora* occurs in the spring (Kirby 1976). Overall increases in ammonium concentration in the transition and *Spartina* zones from May through September and also subsequent decreases from September through November were probably temperature-influenced, since ammonium release in flooded soils is directly related to temperature (Ponnamperuma 1972, Brannon 1973).

Phosphorus availability increases under reducing conditions and increased pH due to (1) reduction of ferric phosphate to more soluble ferrous phosphates (Gambrell and Patrick 1978), (2) reaction of ferrous iron with sulfides, releasing phosphate into solution (Brannon 1973), and (3) release of phosphorus adsorbed to clays and hydrous oxides by anion exchange processes (Gambrell and Patrick 1978). Although the *Spartina* zone had lower or equal redox potentials relative to the transition zone and higher or equal pH levels and higher sulfide concentrations, phosphorus was

usually higher in the transition zone. *S. alterniflora* was healthier and much denser in the *Spartina* zone than the transition zone (data not presented), similar to results found by Kangas and Lugo (1990). Reimold (1972) demonstrated that *S. alterniflora* can act as a nutrient pump for phosphorus, possibly reducing phosphorus levels in the *Spartina* zone compared to the transition zone. Lower phosphorus levels in the *Avicennia* zone from early spring to late summer were probably due to the more oxidized condition of the soils of that zone. The sharp increase in *Avicennia* zone phosphorus levels in the fall may have occurred due to soluble organic phosphorus released from litter fall in the form of leaves and propagules (Lopez-Portillo and Ezcurra 1985).

CONCLUSIONS

Results of this study show that the *Avicennia* zone was markedly different from the transition and *Spartina* zones, which were similar across all variables except potassium, sulfide, and relative elevation.

The *Avicennia* zone was higher, better-drained, more oxidized and had higher levels of ions associated with sea water. It is unlikely that salinity would control the plant zonation observed at this study site because both *A. germinans* and *S. alterniflora* are known to grow well within a wide range of salinities that include the levels found in this study (Chapman 1974, 1976).

The relationships among variables measured in this study suggest that the species zonation seen at Bay Champagne was influenced by (1) elevational differences, (2) degree of anaerobic conditions, or (3) the combination of both elevational and anaerobic effects. The elevational differences may be of sufficient magnitude that

Avicennia propagules do not have enough time to be in contact with the *Spartina* zone substrate because of flooding and are prevented from successful rooting and establishment in the *Spartina* zone (Rabinowitz 1978). Also, the *Avicennia* propagules may not establish well in the *Spartina* zone because of anaerobic/high-sulfide conditions.

The possibility of interspecific competition should also be considered. *S. alterniflora* may exclude *A. germinans* in the anaerobic, frequently flooded soils of the *Spartina* zone, with the opposite trend in the *Avicennia* zone (Kangas and Lugo, 1990).

Since many differences in physicochemical variables have been shown between the *Avicennia* zone and the inland zones, further research, emphasizing the manipulation of some of those variables, needs to be conducted to determine if survival is possible for *A. germinans* in the more anaerobic, poorly drained, lower elevation *Spartina* zone.

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CHAPTER 2

GROWTH AND SURVIVAL OF *AVICENNIA GERMINANS* SEEDLINGS IN A MANGAL/SALT MARSH COMMUNITY IN LOUISIANA

INTRODUCTION

Plant species zonation has been studied by plant ecologists in many different communities, with intertidal communities, such as salt marshes and mangrove swamps (mangals) receiving much attention because of their simplicity (Snow and Vince 1984, Pidwirny 1990). Although earlier studies usually focused on environmental influences on species zonation, more recent interest has focused on biotic factors, such as competition, methods of propagation, herbivory, etc., in combination with environmental factors (Bertness 1991a).

Mangroves are intertidal trees found on low-energy coasts in the tropics and subtropics, with their latitudinal limits determined by the number of freezing events (-2 to 4° C) per year (Chapman 1976, McMillan and Sherrod 1986). An interesting example of plant zonation in the coastal zone occurs at the latitudinal limits of mangroves, where their boundaries constitute an ecotone with salt marshes (Clarke and Hannon 1969, 1971, Detweiler et. al. 1975, Lopez-Portillo and Ezcurra 1989). At latitudes between $26-30^{\circ}$ N in the western hemisphere, the black mangrove, *Avicennia germinans*, is the only mangrove found because *Avicennia* has a greater chilling tolerance than other mangrove genera (Lugo and Zucca 1977, Johnston 1983, Sherrod *et al.* 1986). In southeastern Louisiana, as well as Florida and Texas, *A. germinans* swamps intergrade with salt marshes dominated by *Spartina alterniflora*. *Avicennia* usually dominates higher-elevation sites, such as creekbanks, bay shores and on barrier islands at higher elevations, while *S. alterniflora* occurs at lower

elevations which I would expect to experience greater depth and duration of inundation (Patterson and Mendelssohn 1991). Penfound and Hathaway (1938) noted similar trends in mangrove distribution in Louisiana 53 years ago. I have observed that during events of extremely cold conditions, *A. germinans* is killed and *S. alterniflora* invades areas previously dominated by the mangroves. *A. germinans* later grows back, either from root stock or in more extreme cases, when both above and below-ground structures are killed, from propagules which can survive more extreme conditions than the parent plants, similar to populations on the Texas coast (Sherrod and McMillan 1985).

Factors controlling the distribution of mangroves and salt marsh plants in intertidal communities where both types of plants coexist have received little attention. Both salinity and waterlogging influenced species distribution patterns in a mangal/salt marsh community near Sydney, Australia (Clarke and Hannon 1969). Some authors (Penfound and Hathaway 1938, Kangas and Lugo 1990) have thought that competitive interactions between *A. germinans* and salt marsh plants may influence plant species zonation in mangal/salt marsh communities. Kangas and Lugo (1990) hypothesized that in temperate areas salt marsh vegetation is competitively superior to mangroves due to adaptations to cold stress, but that mangroves are competitively superior in the tropics, and mentioned the need for reciprocal transplant experiments to test these hypotheses. Lopez-Portillo and Ezcurra (1989) concluded that physicochemical characteristics, the response of species to the environment, and interspecific relations controlled the distribution of mangroves and salt marsh plants in a mangal/salt marsh community in Mexico. However, they did not conduct field manipulative experiments. Detweiler *et. al.* (1975) stated that *A. germinans* excludes *S. alterniflora* in Florida by shading, but did not present experimental evidence to substantiate their statement.

Greenhouse experiments investigating the possibility of interspecific interactions have been conducted with several species of salt marsh plants in Alaska (Snow and Vince 1984) and with salt marsh plants and mangroves from a mangal/salt marsh community in Australia (Clarke and Hannon 1971). In addition, field transplant experiments have been conducted to study interspecific interactions in mangrove communities (Teas 1977, Rabinowitz 1978a) and salt marshes (Snow and Vince 1984, Bertness 1991a,b). However, to my knowledge, transplant experiments have not been conducted with mangroves in areas transitional with salt marshes to investigate survival success of mangroves in areas normally dominated by salt marsh plants nor to explore the possibility of interspecific interactions.

In this paper, I tested the ability of *A. germinans* seedlings to grow in the *Spartina* zone and compete with *S. alterniflora* with a combination of greenhouse and transplant experiments. I did not test hypotheses concerning the success of *S. alterniflora* growth and survival in the zone dominated by *Avicennia* because my interest is in factors controlling the distribution of mangroves in mangal/salt marsh communities and also because I have observed robust growth of *S. alterniflora* in the *Avicennia* zone when light gaps became available.

A greenhouse experiment tested the following hypotheses: (1) Can *A. germinans* seedlings survive and grow under controlled, permanently flooded conditions? (2) Do *A. germinans* seedlings exhibit increased growth rates in the absence of *S. alterniflora* under permanently flooded conditions in comparison to seedlings grown under the same conditions in the presence of *Spartina*, i.e. does *Spartina* inhibit growth of *A. germinans* seedlings?

A field transplant experiment was conducted to test the following hypotheses: (1) Can *A. germinans* survive in the low areas of a mangal/salt marsh community, which are usually monospecific zones of *S. alterniflora*? (2) If it can survive in these areas,

does *Avicennia* exhibit increased growth rates when above-ground competition from *Spartina* is removed?

In conjunction with the transplant experiment, I also collected inundation and temperature data to determine if these environmental variables could be influencing *Avicennia* survival and growth along this vegetation gradient.

METHODS

Greenhouse Experiment

A greenhouse experiment was conducted to determine the relative success of *A. germinans* growing in monoculture (control) and mixed-species treatments with *S. alterniflora* under permanently flooded conditions. Because *A. germinans* is not found in the lowest areas of the *Spartina* zone (most inundated), I investigated the possibility that *A. germinans* cannot grow under permanently flooded conditions or is competitively excluded by *S. alterniflora* under these conditions.

Experimental Design

Experimental units were 56.6-liter pots, 40 cm deep, which were filled to about 25 cm with a homogeneous soil mixture of equal proportions of salt marsh clay, sand, loam, and a commercial potting soil (jiffy mix, Jiffy Products of America, Inc.). The pots were permanently flooded with at least 10 cm of water overlying the sediment surface. Young plants of both species (*A. germinans* and *S. alterniflora*) used in this experiment had been purchased from a nursery in Florida. Upon receipt of the plants, I observed a relatively large variation in the sizes of plants of both species and

subsequently divided them into 3 size classes. *Avicennia* plants were randomly assigned to one of two possible treatments, *Avicennia* control or *Avicennia/Spartina* 50% species mix, and numbered so that growth increments on an individual plant could be monitored. All plants within a pot were members of the same size class. On 15 sampling dates height (cm) and diameter (mm) of *Avicennia* plants were measured. Height and diameter were analyzed by a repeated measures randomized block design, blocking on size class (Gurevitch and Chester 1986). Where treatment differences were found, height and diameter growth rates were compared by regression. Above and below-ground biomass differences at harvest were analyzed within a split-plot randomized block design, with above/below ground biomass type in the sub-plot and size class as a block.

Transplant Experiment

Study Site

I investigated a mangal / salt marsh community located on the edge of Bay Champagne on the southeastern coast of Louisiana at 29° 6' 35"N, 89° 11' 1"W, at the northern limit of the range of *Avicennia* in Louisiana (Figure 2.1). *Avicennia germinans* and *S. alterniflora* are the dominant plant species found in this community, with sparse occurrences of *Batis maritima*, *Distichlis spicata*, and *Salicornia* sp. Three plant zones can be delineated at the study site--an *Avicennia*-dominated zone starting at the edge of the bay and extending 20-60 m inland, a transition zone of mixed species composition (*Avicennia* and *Spartina*) further inland and ranging from 30-60 m wide, and a *Spartina*-dominated zone starting at the inland border of the transition zone and extending several hundred meters inland (Figure 2.2).

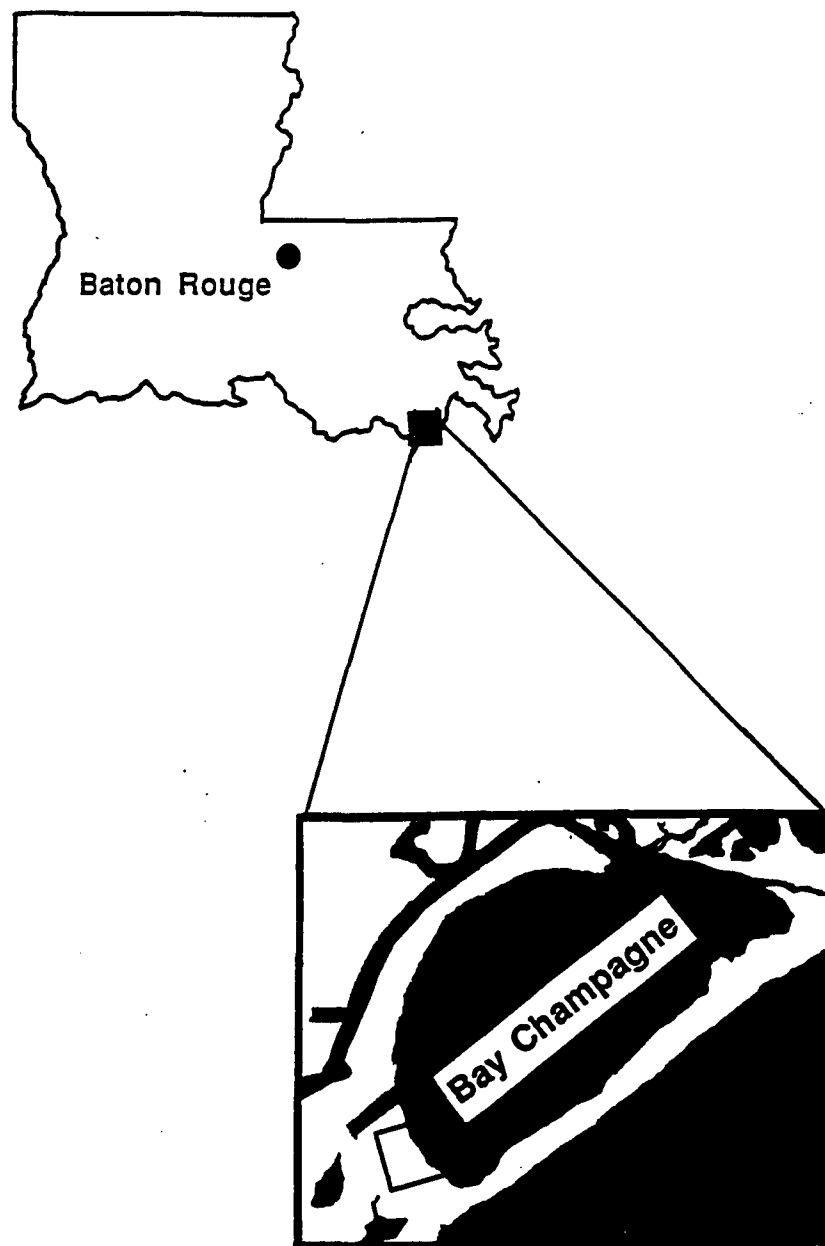


Figure 2.1. Location of the study site at Bay Champagne, Louisiana.

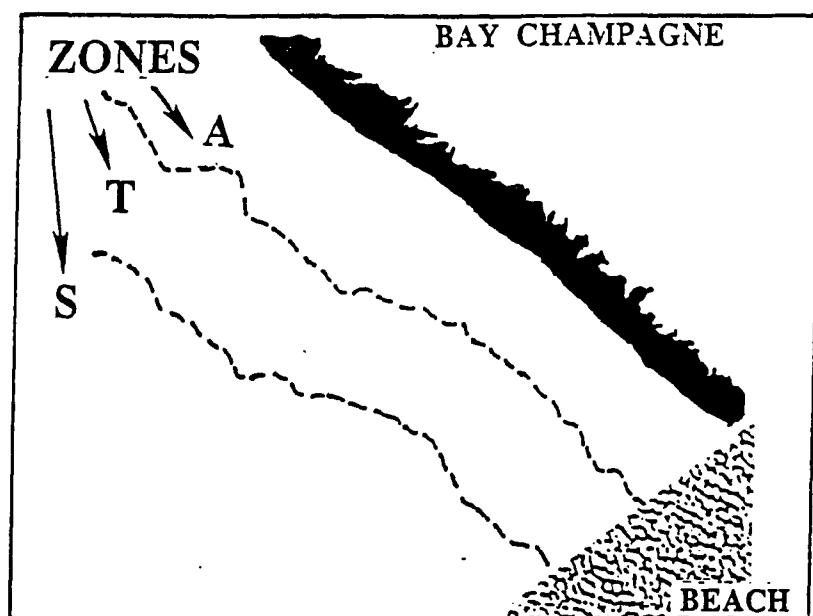


Figure 2.2 Location of plant species zones at the study site.

In December 1989 a severe freeze killed all above and below-ground *A. germinans* biomass at the site, except for propagules which had been produced by the parent plants prior to the freeze. The propagules may have been protected by ice coating or debris, similar to the situation described by Sherrod and McMillan (1985) after a severe freeze on the Texas coast in December, 1983. Some propagules in the *Avicennia* and transition zones successfully established and are now 20-50 cm in height. Also, with extensive light gaps created by the death of the parent mangroves, *S. alterniflora* invaded the *Avicennia* zone, as seen in Florida (Detweiler, *et al.* 1975), and I observed that *Spartina* plants grew taller in the *Avicennia* zone than in the transition or *Spartina* zones.

In a previous study I found that the *Avicennia* zone differed from the transition and *Spartina* zones across many soil physicochemical variables, while the transition and *Spartina* zones were similar across all variables except elevation, with the *Spartina* zone lower (Patterson and Mendelssohn 1991). The transition and *Spartina* zones were lower, more reduced, had higher interstitial water sulfide levels and lower concentrations of ions associated with seawater relative to the *Avicennia* zone. Also, I observed that some *A. germinans* propagules had become established in one area of the *Spartina* zone, after the initial descriptive study had been completed, and on subsequent analysis of the elevational data found that this area of the *Spartina* zone was higher than areas of the *Spartina* zone where *Avicennia* was not observed. All *A. germinans* plants found in this area of the *Spartina* zone were less than 30 cm in height and too young to reproduce.

Experimental Design

A. germinans propagules were collected from trees at the study site in the fall of 1989 and grown in a greenhouse under saturated soil conditions until the time of transplantation to the field (May 10, 1990). Seedlings in the greenhouse were selected so that the sizes of the plants were as homogeneous as possible. The plants were then randomly selected for each treatment, measured (height and diameter) and tagged so that individual plants could be identified throughout the study.

Experimental units were 1 m² plots, randomly located for each treatment combination, containing 4 seedlings which were equally - spaced. The experiment was designed as a 3*2 factorial treatment arrangement (3 plant zones, plots either clipped, to eliminate above-ground competition, or unaltered) in a completely randomized design with repeated measures of height (cm) and diameter (mm) on individual plants on 3 sampling dates (initial, intermediate, harvest) and measurements of interstitial water variables and redox potential in each plot on the same dates, with 4 plots per treatment combination. The three zones were the *Avicennia* zone, the higher part of the *Spartina* zone (*Spartina* high), where *Avicennia* has occasionally been observed, and the lower part of the *Spartina* zone (*Spartina* low). The *Spartina* high was chosen as a treatment instead of the transition zone because it represents the most extreme conditions (high sulfides, low elevation and Eh) in which *Avicennia* has been observed at the study site. In both *Spartina* zone treatments, half of the plots were clipped to remove all above-ground *Spartina*. In the *Avicennia* zone, the equivalent of clipped plots were plots located in areas where there was little or no shading from above-ground, older *Avicennia* plants. Unaltered treatments, as implied, were plots in which I planted seedlings with no alterations in the environment. Above-ground biomass of each surviving *Avicennia* seedling was determined at harvest.

Interstitial Water Variables

On each growth sampling date, a sediment core 5 cm in diameter and 10 cm long was collected at each of the 24 plots and placed in a 500 ml centrifuge bottle. The bottles, containing air-tight septa, were then purged in the field with nitrogen gas for 2 minutes to create an anaerobic environment. Within 48 hours, the samples were centrifuged for 30 minutes at 25° C and 5,216 g to remove interstitial water from the sediment cores. Interstitial water for sulfide analysis was quickly removed from the centrifuge bottles and placed in a 50% solution of sample and antioxidant buffer (Lazar Research Labs 1986). The antioxidant buffer consisted of sodium salicylate, sodium hydroxide, and ascorbic acid in distilled deoxygenated water at concentrations of 250, 85, and 65 g/l, respectively. The antioxidant buffer decreased air oxidation of sulfides and adjusted the pH of the solution so that inorganic sulfides were present in the sulfide ion form (S^{2-}). The sample solutions were then analyzed for free sulfides with a sulfide microelectrode (Lazar Research Labs 1986). The water from each centrifuge bottle was then filtered through a 0.45 micron filter and three additional aliquots were taken to measure salinity, ammonium, and selected macronutrients and micronutrients. Salinity was measured with a meter. The ammonium aliquot was frozen and later analyzed according to US EPA Method #350.1 (US EPA 1979). The aliquot for macronutrients and micronutrients was acidified to less than pH 2 with reagent - grade nitric acid (suitable for trace metal analysis). Phosphorus, magnesium, calcium, potassium, iron, and manganese were determined by inductively coupled argon plasma emission spectrometry (Williams et al. 1986).

Redox Potential

Soil redox potential (Eh) was measured in each plot on each growth measurement sampling date with brightened platinum electrodes and a digital pH/mV/temp meter. Measurements were taken at the soil surface (1 cm) and at 10 cm depths after a 30 minute equilibration period. The potential of a calomel electrode against a standard hydrogen electrode (+244 mV) was added to each value to calculate Eh. All soil interstitial water variables and Eh were analyzed simultaneously in a multivariate analysis of variance (Gurevitch and Chester 1986, Bertness 1991b) within a 3*2 factorial design identical to the one used for the growth variables.

Survival Analysis

On 4 sampling dates after the beginning of the experiment, all plots were monitored for survival. The last 2 dates coincided with the intermediate and final growth measurement dates. Transplant survival for the 2 monitoring periods before the intermediate (second) growth sampling date was recorded to determine if mortality occurred early in the experiment, before significant growth differences would be evident. Survival counts were analyzed by a categorical modelling procedure (Proc Catmod, SAS 1985). Where treatment differences were found in CATMOD, Fisher's Exact Test was used to determine the probabilities of the differences between individual treatments and times because it gives more accurate and robust values when some treatment cell counts are zero (Agresti 1990).

Growth Variables

Height and diameter measurements were analyzed by a repeated measures analysis of variance to determine treatment differences (Gurevitch and Chester 1986), and

growth rates were determined by regression, similar to the analysis of height and diameter in the greenhouse experiment. Above-ground biomass of each surviving *A. germinans* seedling was determined at harvest, and zone differences were determined by analysis of variance.

Water Level Measurements

A tide gauge was installed on a bulkhead over a canal about 250 m from the study site. Water levels and time of measurement were recorded in each plot during a high tide. These water level measurements were then related to their simultaneous tide gauge readings. From these data I was able to determine the depth and duration of flooding in each plot from hourly tide gauge readings which were taken throughout the time of the experiment, similar to the methods used by Eleuterius and Eleuterius (1979).

Temperature Measurements

To determine if a possible winter temperature gradient exists from the *Avicennia* zone to the *Spartina* zone, maximum-minimum thermometers were placed on the substrate and at a height of one meter in the *Avicennia*, transition and *Spartina* zones. Since my objective was to determine if a temperature gradient exists from the *Avicennia* zone into the interior of the marsh (Figure 2.2), it was necessary to use the transition zone as a treatment site. The ground level thermometers were anchored to the substrate with metal wire 4 mm thick driven into the substrate. The aerial thermometers were nailed to the tops of 1m wooden stakes. The thermometers were monitored three times during the winter season following the harvest of the transplant experiment, with only the minimum temperatures recorded.

RESULTS AND DISCUSSION

Greenhouse Experiment

Both above and below-ground biomass (per plant) were significantly lower in the 50% *Avicennia-Spartina* mix than in the *Avicennia* control, suggesting growth suppression of *Avicennia* by *Spartina* under permanently flooded conditions (Table 2.1, Figure 2.3).

Avicennia exhibited highly significant increases in height and diameter in both treatments over the course of the experiment, as shown by significant time (week) effects in the repeated measures analysis (Table 2.2) and growth rates significantly greater than zero (Table 2.3). Height growth (linear) was significantly greater in the *Avicennia* control than in the 50% *Avicennia-Spartina* species mix, with height growth rates of 0.40 and 0.16 cm/week, respectively (Table 2.3). Height growth was apparently similar during the first few months of the experiment, but leveled off in the 50% species mix while continuing in the *Avicennia* control (Figure 2.4a), evidenced by a non-significant overall treatment effect coupled with a highly significant treatment * week interaction in the repeated measures analysis (Table 2.2). This suggests that height growth may have been suppressed by *Spartina*. Changes in diameter over time did not differ between treatments, as indicated by non-significant treatment effects and interactions in the repeated measures analysis (Table 2.2) and equal growth rates (Table 2.3, Figure 2.4b).

Table 2.1. Analysis of Variance of above and below-ground biomass differences in the greenhouse experiment. The two treatments are *Avicennia* control and *Avicennia/Spartina* 50% mix. Blocks represent size classes.

Main Plot

<u>Source</u>	<u>df</u>	<u>Mean Square</u>	<u>F</u>	<u>Pr>F</u>
Treatment	1	37.46	8.79	0.0251
Block	2	11.84	2.78	n. s.
Error 1	6	4.26		

Sub Plot

Above/Below	1	1.20	1.10	n. s.
Above/Below*Tmt	1	0.04	0.04	n. s.
Above/Below*Class	2	0.28	0.26	n. s.
Error 2	6	1.09		

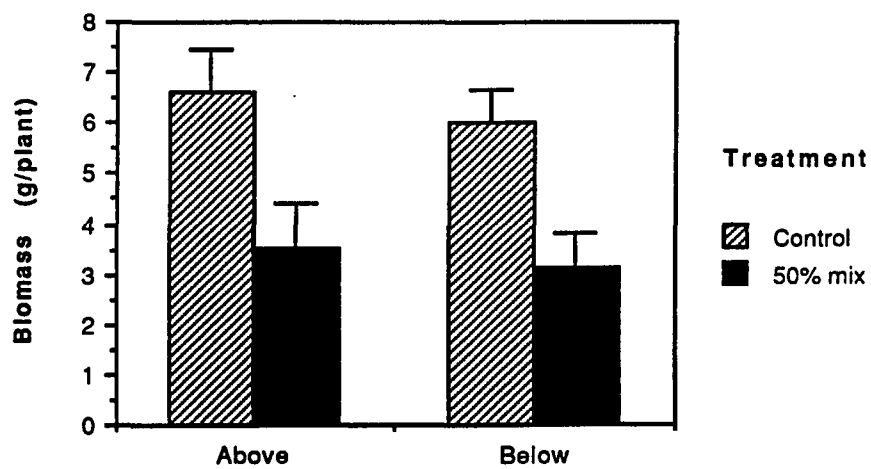


Figure 2.3. Above and below-ground biomass of *A. germinans* in treatments of the greenhouse experiment.

Table 2.2. Repeated measures analysis of variance of height (cm) and diameter (mm) in the greenhouse experiment. Blocks represent size classes.

Height				
Whole Plot				
<u>Source</u>	<u>df</u>	<u>MS</u>	<u>F</u>	<u>Pr>F</u>
Treatment	1	2315.50	3.18	n. s.
Block	2	9660.12	13.25	0.0063
Error 1	6	729.25		
Sub Plot				
Week	14	1436.14	34.35	0.0001
Treatment*Week	14	225.00	5.38	0.0001
Block*Week	28	45.73	1.09	n. s.
Error 2	84	41.81		
Diameter				
Whole Plot				
Treatment	1	2.16	0.14	n. s.
Block	2	83.34	5.31	n. s.
Error 1	6	15.70		
Sub Plot				
Week	14	49.67	32.34	0.0001
Treatment*Week	14	1.91	1.24	n. s.
Block*Week	28	1.17	0.76	n. s.
Error 2	84			

Table 2.3. Linear height growth rates (cm/week) and diameter growth rates (mm/week) in the greenhouse experiment.

Height

<u>Treatment</u>	<u>Growth Rate</u>	<u>Standard Error</u>
Avicennia control	0.404	0.014
Species Mix	0.158	0.021

<u>Contrast</u>	<u>Mean Square</u>	<u>F</u>	<u>Pr>F</u>
Control vs. Mix	3958.86	6.08	0.0488
Error	651.34		

Diameter

<u>Treatment</u>	<u>Growth Rate</u>	<u>Standard Error</u>
Avicennia control	0.069	0.003
Species Mix	0.042	0.004

<u>Contrast</u>	<u>Mean Square</u>	<u>F</u>	<u>Pr>F</u>
Control vs. Mix	46.31	3.51	n. s.
Error	13.19		

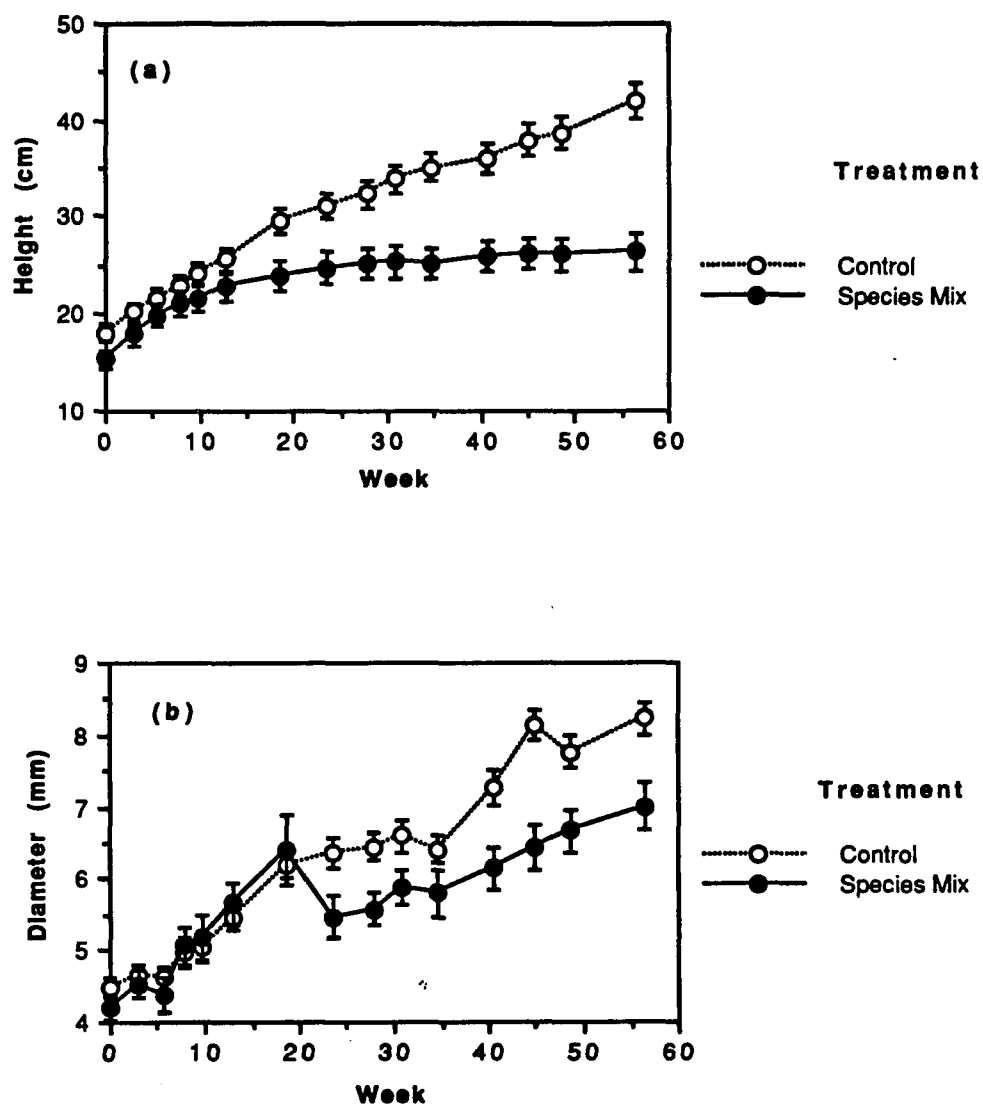


Figure 2.4. Height and diameter growth of *A. germinans* seedlings over a 13-month period.

The above results show that *A. germinans* can grow under permanently flooded conditions, since significant growth occurred over a 13-month period. Also, it appears that growth of *A. germinans* may have been inhibited by *S. alterniflora*, because both above and below-ground biomass and height growth per plant were significantly lower in the 50% species mix than in the *Avicennia* control. However, the conditions of the greenhouse experiment were not identical to field conditions. Sulfides, which are potentially toxic to wetland plants (Koch and Mendelssohn 1989), were much lower in the soils of the greenhouse experiment. Also, the permanently flooded conditions of the greenhouse experiment represent an extreme in percent of time flooded which would not be likely to occur in the field. Therefore, although valuable information has been gained from the greenhouse experiment investigating two possible factors which may influence species zonation at the study site (flooding and interspecific interactions), the survival and growth of *A. germinans* seedlings under field conditions must be investigated with a transplant experiment to further elucidate the observed zonation.

Transplant Experiment

Survival

The effect of clipping plots on survival of *A. germinans* seedlings was different among the zones (zone*clipping interaction significant at $P=0.0045$). All other interactions were non-significant in Proc Catmod. However, even though zone*clipping*time interactions were non-significant, it is informative to present treatment survival percentages for each time period (Table 2.4) because percent survival changed over the course of the experiment (overall time effects significant at $P=0.0001$). Fisher's Exact Test was used to determine zone*clipping differences in percent survival for all treatment and time combinations.

Table 2.4. Survival differences of *Avicennia* seedlings between unaltered and clipped treatment cells by time and zone.

		<u>Avicennia</u>		<u>Spartina High</u>		<u>Spartina Low</u>	
Days	Treatment	% Survival	P	% Survival	P	% Survival	P
11	Unaltered	100.00	n. s.	93.75	n. s.	93.75	0.015
	Clipped	100.00		100.00		50.00	
40	Unaltered	100.00	n. s.	93.75	n. s.	81.25	0.029
	Clipped	93.75		93.75		37.50	
90	Unaltered	81.25	n. s.	87.50	n. s.	62.50	0.0002
	Clipped	68.75		62.50		0.00	
184	Unaltered	75.00	n. s.	81.25	0.0002	43.75	0.007
	Clipped	50.00		12.50		0.00	

Survival differences were observed between unaltered and clipped treatments in the *Spartina* low zone 11 days after the experiment started, with 50 percent survival in the clipped plots vs. 93.75 percent in the unaltered treatments (Table 2.4). After 90 days, at the midpoint of the experiment, all seedlings had died in the *Spartina* low clipped treatments. In the *Spartina* high there were no differences in percent survival between unaltered and clipped treatments until harvest, when survival was 12.5 percent in the clipped vs. 81.25 percent in the unaltered treatments (Table 2.4). In the *Avicennia* zone, there were no significant differences in percent survival between clipped and unaltered treatments throughout the experiment (Table 2.4). Within clipped treatments, survival was significantly lower in the *Spartina* low than in the other zones on the first four sampling dates (Table 2.5), and significantly higher in the *Avicennia* zone than in the two *Spartina* zones on the final date (harvest) due to high mortality of seedlings in the *Spartina* high zone.

None of the interstitial water variables or Eh exhibited differences between unaltered and clipped treatments which could explain the high mortality in both *Spartina* zone clipped plots. I did not find hypersaline conditions in the *Spartina* zone clipped plots as seen in a recent study by Bertness (1991b). However, he noted that the lower-elevation bare patches in his study were buffered from evaporative salinity increases by frequent tidal inundation, and I expect the same effects to be operative in this community because of the relatively low elevation of the *Spartina* zone. The high mortality probably occurred due to direct effects of cutting *Spartina* in the clipped plots. The soils of the *Spartina* zone have lower bulk density than the *Avicennia* zone soils (Patterson and Mendelssohn 1991). In most of the *Spartina* zone clipped plots, the *Spartina* above-ground material did not grow back, suggesting that the below-ground material may have been decomposing. Decomposition of the below-ground *Spartina* could cause the sediments to become less stable. Also, the above-ground *Spartina* could provide a physical buffer against the movement of the tides.

Table 2.5. Zone differences in percent survival by time within clipped treatments. Treatments with the same letter are not significantly different. *Significant at 0.05. **Significant at 0.01. ***Significant at 0.001.

<u>Days</u>	<u>Zone</u>	<u>% Survival</u>
11	Avicennia	100.00 a
	Sp. High	100.00 a
	Sp. Low	50.0 b***
40	Avicennia	93.75 a
	Sp. High	93.75 a
	Sp. Low	37.50 b***
90	Avicennia	68.75 a
	Sp. High	62.50 a
	Sp. Low	0.00 b***
184	Avicennia	50.00 a
	Sp. High	12.50 b*
	Sp. Low	0.00 b**

Therefore, the high mortality of *Avicennia* seedlings in the *Spartina* zone clipped plots probably occurred because the seedlings were being pushed over by the tides due to removal of above-ground buffers and reduced sediment stability.

In the unaltered treatments there were no significant survival differences among zones on any sampling date (Table 2.6), although the probability of 0.069 on the last sampling date suggests a trend toward a lower survival rate in the *Spartina* low zone than in the *Avicennia* and *Spartina* high zones, which had equal survival percentages. However, even though the survival rate tended to be lower in the *Spartina* low unaltered treatments, the survival rate of 43.75% is ecologically significant considering the fact that *Avicennia* does not naturally occur in that zone, and also because this survival rate is much higher than survival rates of *A. germinans* in other transplant studies, even in zones where it is naturally found (Davis 1940, Rabinowitz 1978a). In a reciprocal transplant experiment in a two-species mangrove forest on the Pacific coast of Costa Rica (Jimenez and Sauter 1991) *Avicennia bicolor* had significantly higher survival in a lower-elevation zone dominated by *Rhizophora racemosa* (73.6%) than in its own zone (47.3%), the opposite of the results of this study (Table 2.6). However, the fact that the survival rate of 43.75% in the *Spartina* low in this study is comparable to the survival rate of *A. bicolor* seedlings in their own zone in the study by Jimenez and Sauter adds further evidence to show that *A. germinans* can survive in the *Spartina* low zone.

Both the inability of *A. germinans* to survive in clipped plots in both *Spartina* zone treatments coupled with a marginally significant survival difference among all zones in the unaltered treatments at harvest can be interpreted as contradictory to the original purpose of having clipped plots in the *Spartina* high and low treatments, i.e. that elimination of *S. alterniflora* should enhance survival and growth of *A. germinans*. I would have expected opposite trends in both unaltered and clipped treatments based on the apparent trend in the greenhouse experiment for growth of *A. germinans* to be

Table 2.6. Zone differences in percent survival by time within unaltered treatments. Treatments with the same letter are not significantly different. *P=0.069.

<u>Days</u>	<u>Zone</u>	<u>% Survival</u>
11	Avicennia	100.00 a
	Spartina High	93.75 a
	Spartina Low	93.75 a
40	Avicennia	100.00 a
	Spartina High	93.75 a
	Spartina Low	81.25 a
90	Avicennia	81.25 a
	Spartina High	87.50 a
	Spartina Low	62.50 a
184	Avicennia	75.00 a
	Spartina High	81.25 a
	Spartina Low	43.75 b*

inhibited in the presence of *S. alterniflora* under permanently flooded conditions. However, the physical effects of the tides, which probably caused the mortality in the clipped plots, were not simulated in the greenhouse experiment.

Because one clipped plot treatment had no survivors and another had minimal survival at harvest (Table 2.4), all original treatment combinations were analyzed for differences in survival and soil physicochemical variables, but only the unaltered treatments were analyzed for zone differences in growth rates and biomass of the *Avicennia* seedlings.

Growth Differences

The *Avicennia* seedlings increased in height and diameter over the course of the transplant experiment, evidenced by a significant date effect in the repeated measures ANOVA (Table 2.7) and growth rates significantly different from zero (Table 2.8). Diameter growth rates were similar in the *Spartina* high and low (Table 2.8), and were approximately half the rate seen in the *Avicennia* zone (Figure 2.5a). Height growth rates were similar among all three zones (Figure 2.5b, Table 2.8), as seen in a study by Rabinowitz (1978a) in which mangrove seedlings showed similar height growth in all zones of a mangal. However, these results differ from those of the greenhouse experiment. In the greenhouse experiment, diameter growth rates were similar for *Avicennia* seedlings in the *Avicennia* control and in the presence of *Spartina*, but height growth rates were significantly greater in the *Avicennia* control.

Above-ground biomass showed similar trends to diameter growth rates, consistent with another study (Clough and Scott 1989), which noted a log-log relationship between above-ground biomass and diameter in mangroves. Mean biomass per plant in both *Spartina* zone treatments was approximately half of the value of the *Avicennia* zone (Figure 2.6). These results are consistent with those of the greenhouse experiment, which had half the biomass per plant (above and below-ground) in the

Table 2.7. Repeated measures analysis of variance of height and diameter in the transplant experiment.

Height				
<u>Source</u>	<u>df</u>	<u>Mean Square</u>	<u>F</u>	<u>Pr>F</u>
Whole Plot				
Zone	2	5.35	0.08	n. s.
Error 1	7	59.63		
Sub Plot				
Date	2	1628.58	137.67	0.0001
Date*Zone	4	31.05	2.63	n. s.
Error 2	14	11.83		
Diameter				
Whole Plot				
Zone	2	0.71	0.29	n. s.
Error 1	7	2.51		
Sub Plot				
Date	2	41.97	95.83	0.0001
Date*Zone	4	4.80	10.97	0.0003
Error 2	14	0.44		

Table 2.8. Linear height and diameter growth rates (cm/week) in the transplant experiment.

Height

<u>Zone</u>	<u>Growth Rate</u>	<u>Standard Error</u>
Avicennia	0.768	0.081
Spartina High	0.602	0.080
Spartina Low	0.613	0.094

<u>Contrast</u>	<u>Mean Square</u>	<u>F</u>	<u>Pr>F</u>
Avicennia vs. Sp. High	67.00	2.13	n. s.
Avicennia vs. Sp. Low	48.63	1.55	n. s.
Sp. High vs. Sp. Low	0.26	0.01	n. s.

Diameter

<u>Zone</u>	<u>Growth Rate</u>	<u>Standard Error</u>
Avicennia	0.156	0.014
Spartina High	0.081	0.014
Spartina Low	0.076	0.017

<u>Contrast</u>	<u>Mean Square</u>	<u>F</u>	<u>Pr>F</u>
Avicennia vs. Sp. High	13.84	14.23	0.0003
Avicennia vs. Sp. Low	12.95	13.34	0.0004
Sp. High vs. Sp. Low	0.04	0.04	n. s.

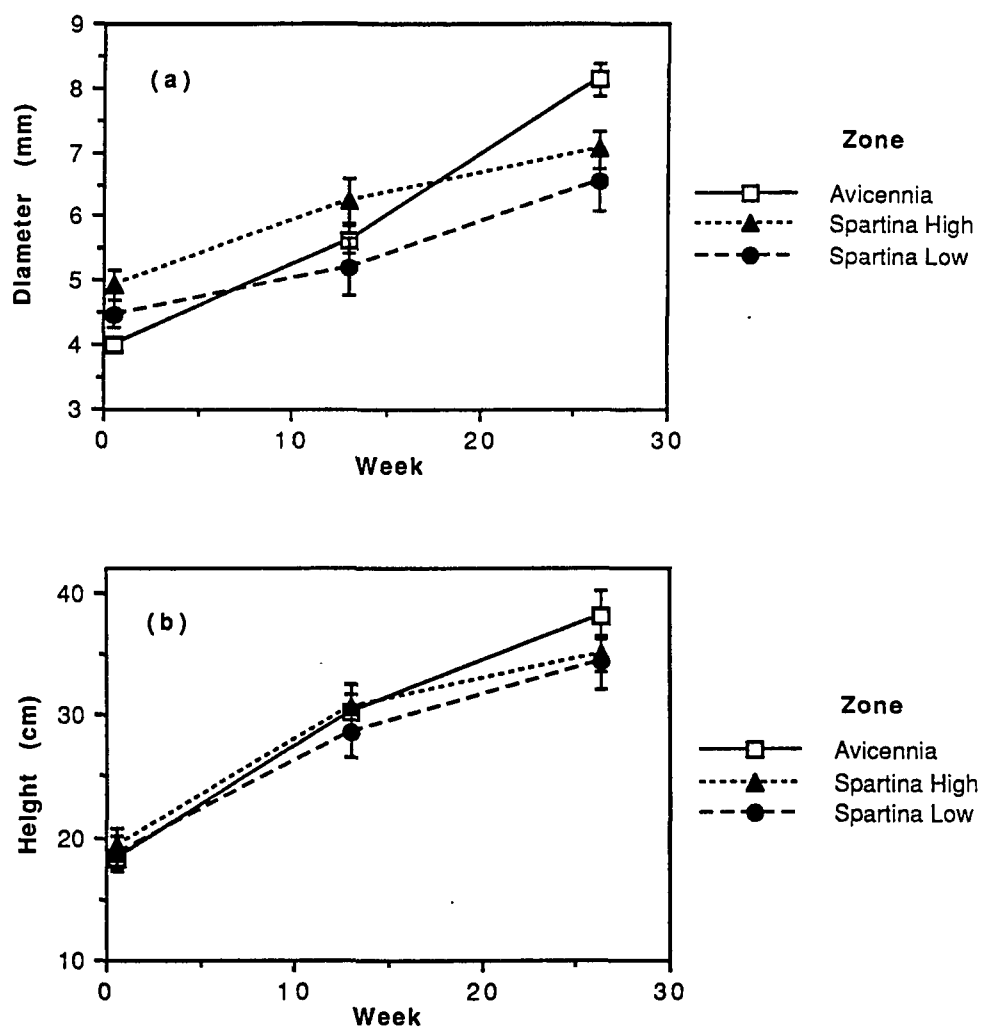


Figure 2.5. Diameter and height growth of *A. germinans* seedlings in the transplant experiment.

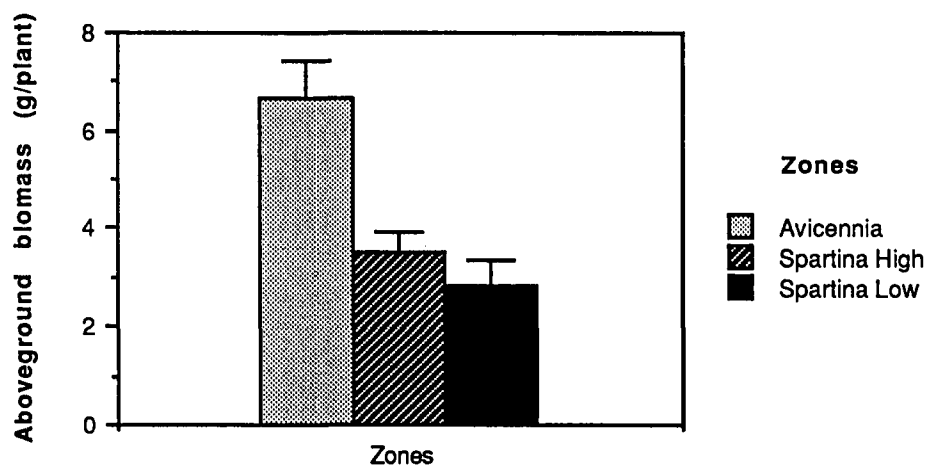


Figure 2.6. Above-ground biomass (g/plant) in the zones of the transplant experiment.

50% species mix compared to the *Avicennia* control, and show that *A. germinans* has reduced growth in the *Spartina* zones relative to the *Avicennia* zone, similar to the results from a mangal/salt marsh community in Australia (Clarke and Hannon 1971).

Within the unaltered treatments, sulfide levels were usually similar in the two *Spartina* zone treatments and always higher than in the *Avicennia* zone (Figure 2.7). This may have caused diameter growth rates and biomass to be lower in the *Spartina* zones, because sulfides have been shown to reduce the growth of salt marsh plants (King et al. 1982), and *A. germinans* (K. L. McKee, personal communication). However, the flooding regimes of the different zones probably exert a stronger influence on growth rate differences and may also control sulfide levels at the study site, as seen in a mangrove system in Florida (Carlson *et al.* 1983).

There were highly significant differences in flooding regimes for all zone comparisons. The tests of significance represent differences in zone means of the water level measurements in each plot, with 8 plots per zone. Figure 2.8 is a summary of meaningful parameters in monthly increments which were derived from the tide gauge data as it related to those water level measurements. Error bars were omitted from the points in Figure 2.8 because all standard errors would actually represent the standard errors of the original water level measurements in each plot. The *Spartina* low had the highest levels of mean flooding, maximum flooding, and percent of time flooded, with intermediate levels in the *Spartina* high and lowest levels in the *Avicennia* zone (Figure 2.8). Higher levels of mean flooding would cause the plants to be subjected to higher water levels than plants growing in areas with a lower mean flooding (Figure 2.8a). *Avicennia* seedlings growing in areas with a higher maximum flooding level have a greater chance of being completely submerged (Figure 2.8b). I observed some *Avicennia* seedlings in both *Spartina* zone treatments which had all of their leaves completely covered with sediment after being submerged, and these plants died within a short period of time. This is consistent with the findings of

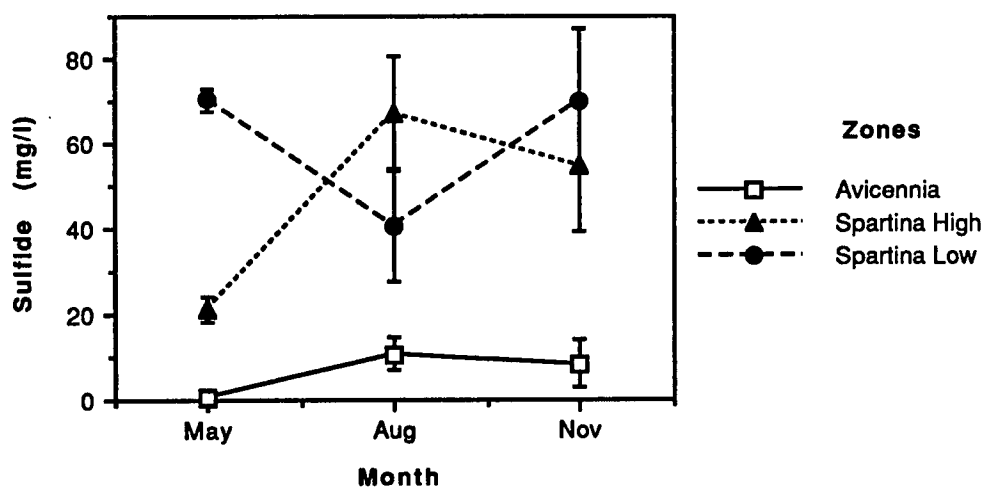


Figure 2.7. Sulfide levels in unaltered plots in the transplant experiment.

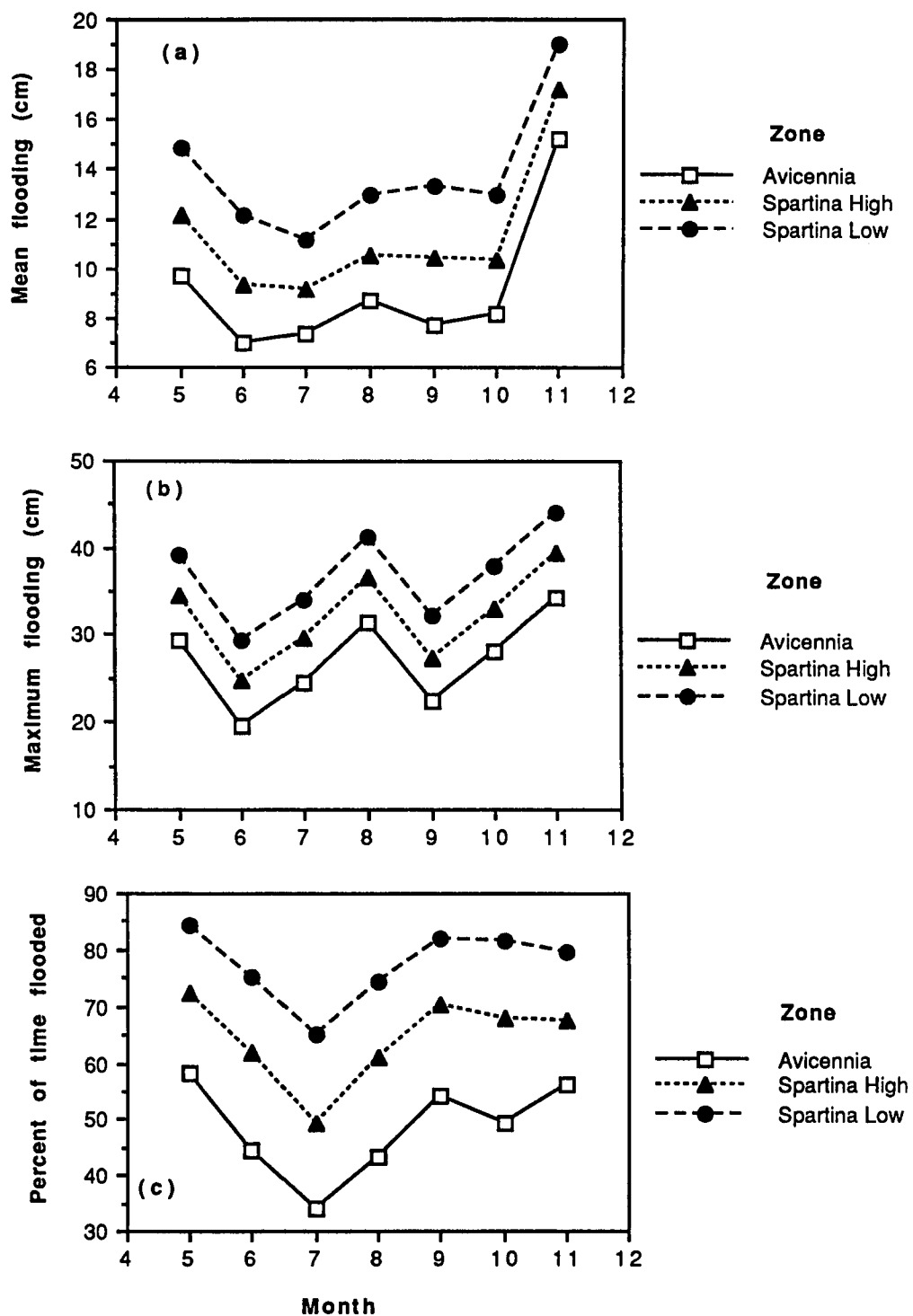


Figure 2.8. Flooding regimes of the zones during the transplant experiment.

Teas (1977), where mangrove seedling transplants in Florida were intolerant of mud and silt deposition. Also, I would expect that during submergence the *Avicennia* seedlings would have decreased rates of photosynthesis and lower growth rates, so that plants growing in areas with a greater maximum flooding level would be expected to have lower biomass production over a growing season. It is known that elevational differences of a few centimeters can cause different flooding regimes in mangals (Carlson *et al.* 1983) and salt marshes (Eleuterius and Eleuterius 1979). At Bay Champagne, even though the zones only differ in elevation by approximately 5 cm, each 5 cm decrease in elevation from the *Avicennia* to the *Spartina* high and from the *Spartina* high to the *Spartina* low represents an increase of 15 percent time flooded (Figure 2.8c). Percent of time flooded is important, since the plants would have less photosynthetic tissue above water and decreased photosynthetic rates when submerged. In general, the areas which are flooded for longer durations should be more reduced and have higher levels of sulfides than areas which experience less flooding (Gambrell and Patrick 1978), and it has been shown that oxygen concentrations in the roots of *A. germinans* decrease significantly within one hour after exposure to hypoxic conditions (McKee and Mendelssohn 1987). Therefore, in the areas which experience a greater percent of time flooded, the *Avicennia* seedlings might be stressed by low root oxygen concentrations more often than seedlings in less-inundated areas and would probably have decreased growth rates.

There were no differences in ground level or aerial minimum temperatures among the *Avicennia*, transition and *Spartina* zones during the winter season following the transplant experiment (Figure 2.9). Therefore, microclimatic differences proceeding from the water to the inland areas, as found in some other mangrove communities (Schaeffer-Novelli *et al.* 1990), probably do not exist at this site since the distance of this gradient is less than 100 meters.

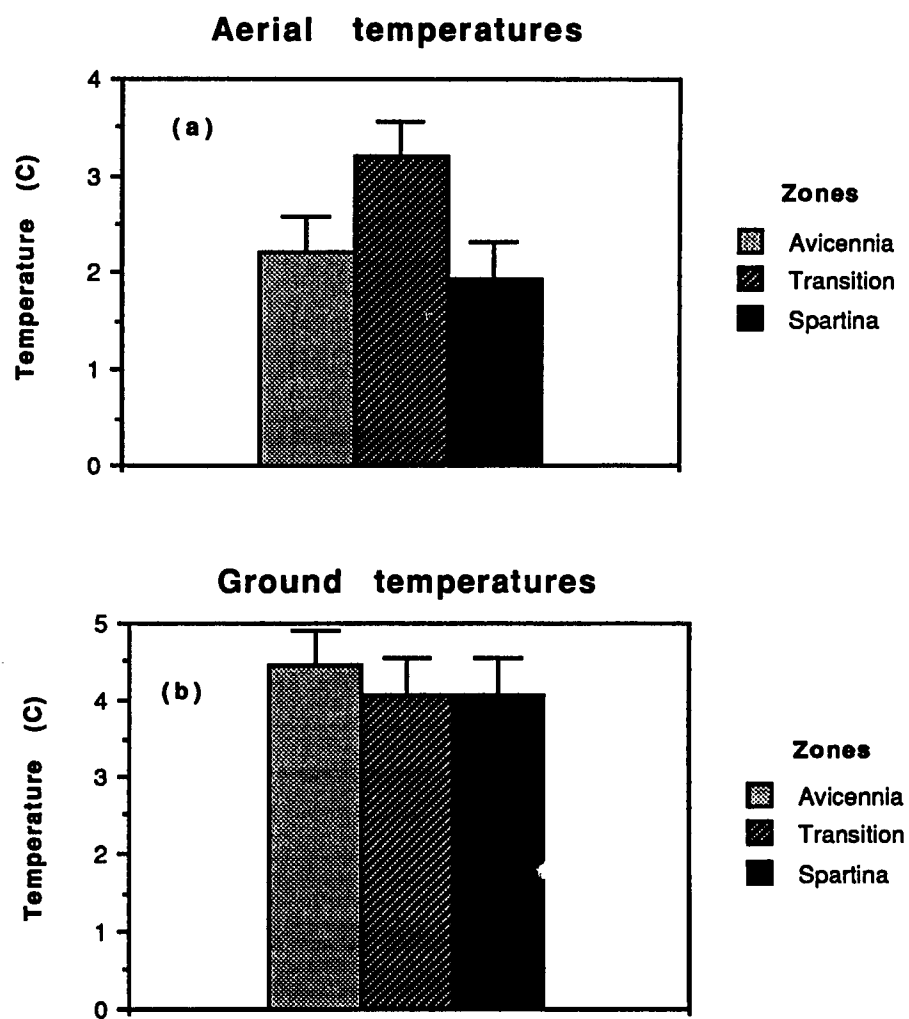


Figure 2.9. Mean minimum aerial and ground temperatures at the study site during the winter (November-March).

Although some environmental variables of the *Spartina* zones, such as sulfides and flooding regimes, are less conducive to growth of *A. germinans* seedlings than these same variables in the *Avicennia* zone, the results of the greenhouse experiment suggest that *S. alterniflora* may also be inhibiting growth of the *Avicennia* seedlings in the *Spartina* zones. Another reason for considering the possibility of growth inhibition by *Spartina* is that even though there were highly significant differences in flooding regimes between the *Spartina* high and low, growth rates and biomass of the *Avicennia* seedlings in those zones were similar. If only the environmental variables were causing *A. germinans* to have reduced growth in the *Spartina* zones, I would have expected growth rates to be greater in the *Spartina* high, because it has lower levels of mean, maximum and percent time flooded than the *Spartina* low (Figures 2.8b,c).

CONCLUSIONS

Results of the greenhouse experiment demonstrated that *A. germinans* seedlings can grow under permanently flooded conditions, and that *S. alterniflora* may inhibit the growth of *Avicennia* under these conditions.

In the transplant experiment, *A. germinans* survived in the low areas of the *Spartina* zone, where it has not been observed naturally. This is consistent with the results of the greenhouse experiment, where *Avicennia* seedlings survived under permanently flooded conditions in the presence of *Spartina*, and in agreement with other studies (Rabinowitz 1978a, Jimenez and Sauter 1991) in which mangrove seedlings grew in zones where they were not naturally found. In fact, survival differences between the *Spartina* low and the other two zones were marginally significant over one growing season. Almost half of the seedlings survived in the

Spartina low, and the percentage of seedlings surviving in the *Spartina* high (81.25%) was equal to the percentage of seedlings surviving in the *Avicennia* zone (Table 2.6), suggesting that the *Spartina* high may be a suitable site for *A. germinans*. It is possible that a successional trend exists, with *A. germinans* beginning to colonize the *Spartina* high and eventually becoming more common there, similar to successional trends documented in Florida (Detweiler *et al.* 1975, Teas 1977, Kangas and Lugo 1990). However, the diminished growth rates of *Avicennia* seedlings in the presence of *Spartina* in the greenhouse experiment and in both *Spartina* zone treatments in the transplant experiment suggest that physicochemical conditions, competition, or both are stressful to *A. germinans* seedlings, and may reduce its ability to exist in the *Spartina* zone over a number of years. This hypothesis can only be tested with a transplant experiment similar to the one conducted in this study which lasts over several growing seasons. Although there were no zone differences in minimum winter temperatures, so that the hypothesis of a warmer *Avicennia* zone due to proximity to the bay is rejected, it is possible that *A. germinans* is healthier in the *Avicennia* zone than it would be if growing in the *Spartina* zone, and could withstand colder winter temperatures in the *Avicennia* zone. Again, a long-term transplant experiment is needed to further understand the ability of *A. germinans* to grow in the *Spartina* zones.

I was unable to determine if *Avicennia* would show increased growth rates when above-ground *Spartina* was removed because of the high mortality in the *Spartina* zone clipped plots. Therefore, it would be informative to devise an experiment which could test this hypothesis.

Another important area of further research is propagule dispersal and establishment, which is essential for further understanding the observed species zonation at the study site since it has been shown that *Avicennia* seedlings can grow in areas outside their usual range within this mangal/salt marsh community. It is

possible that *A. germinans* could survive and grow in areas of this intertidal community where it does not naturally occur, but an inability of propagules to be dispersed to those areas or an inability of propagules to strand and establish in those areas may cause *Avicennia* to be excluded (Snow and Vince 1984, Rabinowitz 1978a,b). Chapter 3 addresses these points.

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CHAPTER 3

FATE OF *AVICENNIA GERMINANS* PROPAGULES AND POSSIBLE EFFECTS ON ZONATION IN A LOUISIANA MANGAL/SALT MARSH COMMUNITY

INTRODUCTION

Plant species zonation has been the focus of much research in plant ecology. Factors such as competition, seed dispersal and predation, herbivory, and environmental tolerance limits may play an important role in controlling species distribution along environmental gradients. Intertidal communities, such as mangrove swamps (mangals) and salt marshes have been ideal sites for research on plant zonation because they usually contain low numbers of species and thus are relatively simple (Chapman 1976, Snedaker 1982, Snow and Vince 1984, Mitsch and Gosselink 1986, Pidwirny 1990).

In mangrove swamps, both biotic and abiotic factors have been investigated in an attempt to explain plant species zonation. Mangroves exhibit vivipary, with seeds germinating on the parent plants (Chapman 1976, Tomlinson 1986). Since the young plants (propagules) have varying degrees of buoyancy and are dispersed by the tides, several studies have investigated the relationship between mangrove zonation and the dispersal and stranding period requirements of propagules. If a propagule becomes stranded and is not disturbed by tides for an adequate period of time, it can become rooted in the substrate. Rabinowitz (1978a) found that the time required for establishment of *Avicennia germinans* propagules is less than 3 weeks and that the

propagules can survive while floating for at least 16 weeks. McMillan (1971) found that *A. germinans* propagules did not require absolute freedom from inundation to establish, but could establish while floating in water of a wide range of salinities at depths less than 5 cm.

Several studies have shown that mangrove propagules can establish in zones where they are not usually found if held in place by enclosures and thereby prevented from being carried away by the tides (Rabinowitz 1978b, Smith 1987b, Jimenez and Sauter 1991). Some of these studies have led to wide acceptance of the idea that tidal sorting of propagules is a major factor controlling species zonation in mangals. Rabinowitz (1978a,b) noted a negative correlation between propagule size and location of the adult trees in a mangrove swamp, with mangroves at the higher elevations having smaller propagules which float and possibly require freedom from tidal inundation for several days. Rabinowitz (1978a), observed that since *Avicennia* propagules always float, they can not establish in lower elevation areas which are never free of flooding. Jimenez and Sauter (1991) found that if *A. bicolor* propagules were anchored to the substrate they were able to survive and grow in a lower elevation, more inundated zone normally dominated by *Rhizophora racemosa*, a mangrove with heavier propagules, and concluded, similar to Rabinowitz (1978a), that tidal sorting of propagules determined zonation of mangroves in a Costa Rican mangal. All of these studies involved comparisons among propagules of several mangrove species to investigate zonation in mangals.

Propagule predation may be an important factor in controlling mangrove species zonation in many different areas of the world, with possible predators including insects (Robertson *et al.* 1990), crabs (Smith 1987a, Smith *et al.* 1989, Osborne and Smith 1990) and snails (Smith *et al.* 1989), depending on the community. In a

number of mangrove systems, predation is often highest where a species does not naturally occur (Smith 1987a, Smith *et al.* 1989), and predators often prefer propagules of one species over another (Smith 1987a).

Mangroves, confined to the tropics and subtropics because they are not cold-tolerant (Chapman 1976, Lugo and Zucca 1977, McMillan and Sherrod 1986), often form ecotones with salt marshes at their latitudinal limits (Detweiler *et al.* 1975, Kangas and Lugo 1990). Whether these same processes, tidal sorting and predation, are important in controlling the distribution of mangroves where they form ecotones with salt marsh vegetation has not been investigated (Clarke and Hannon 1969, 1971, Lopez-Portillo and Ezcurra 1989, Kangas and Lugo 1990, Patterson and Mendelssohn 1991). I have been studying a mangal/salt marsh ecotone with 3 plant zones: a zone dominated by the black mangrove, *A. germinans*, the only mangrove species found between 26-30° N in the western hemisphere due to its greater cold tolerance than other mangrove genera (Lugo and Zucca 1977, Johnston 1983, Sherrod *et al.* 1986), a transition zone containing both *A. germinans* and salt marsh cord grass, *S. alterniflora*, and a *Spartina* zone. Previously, I found that the transition and *Spartina* zones were similar across many soil physicochemical variables (Patterson and Mendelssohn 1991), but that the *Avicennia* zone differed, having a higher elevation and redox potential and lower interstitial water sulfide levels. In a field transplant experiment (Chapter 2), I found that the *Spartina* zone experienced a greater depth and duration of flooding, but these factors did not prevent survival and growth of one year old *A. germinans* seedlings in that zone. Since mangroves can only colonize new areas by propagule dispersal (Chapman 1976, Rabinowitz 1978a), a study of the fate of mangrove propagules in any mangrove community exhibiting

zonation is an essential contribution to understanding the observed plant species zonation.

The goal of this study was to determine if establishment capabilities and predation of propagules could effect mangrove species zonation along a mangrove/salt marsh ecotone. Specifically, I addressed the following questions: (1) can *A. germinans* propagules held by enclosures establish in the more-inundated, lower-elevation areas (*Spartina* zone), where it is not normally found?, (2) does propagule predation occur?, and (3) if propagule predation does occur, does it have an influence on the observed species zonation? Since I have observed and sampled *A. germinans* propagules in the *Spartina* zone, propagule dispersal was not investigated.

METHODS

Study Site

I conducted experiments in a mangal/salt marsh community located on the edge of Bay Champagne on the southeastern coast of Louisiana at 29° 6' 35"N, 89° 11' 1"W, at the northern limit of the range of *Avicennia* in Louisiana (Figure 3.1). *Avicennia germinans* and *S. alterniflora* are the dominant plant species found in this community, with sparse occurrences of *Batis maritima*, *Distichlis spicata*, and *Salicornia* sp. *Avicennia germinans* is at its worldwide northern distributional limits here (Johnston 1983, Sherrod *et al.* 1986), with the largest individual plants reaching heights of approximately 2.5 m before being killed by periodic frost. Three plant zones can be delineated at the study site--an *Avicennia* -dominated zone starting at the edge of the bay and extending 20-60 m inland, a transition zone of mixed species composition (*Avicennia* and *Spartina*) further inland and ranging from 30-60 m wide, and a

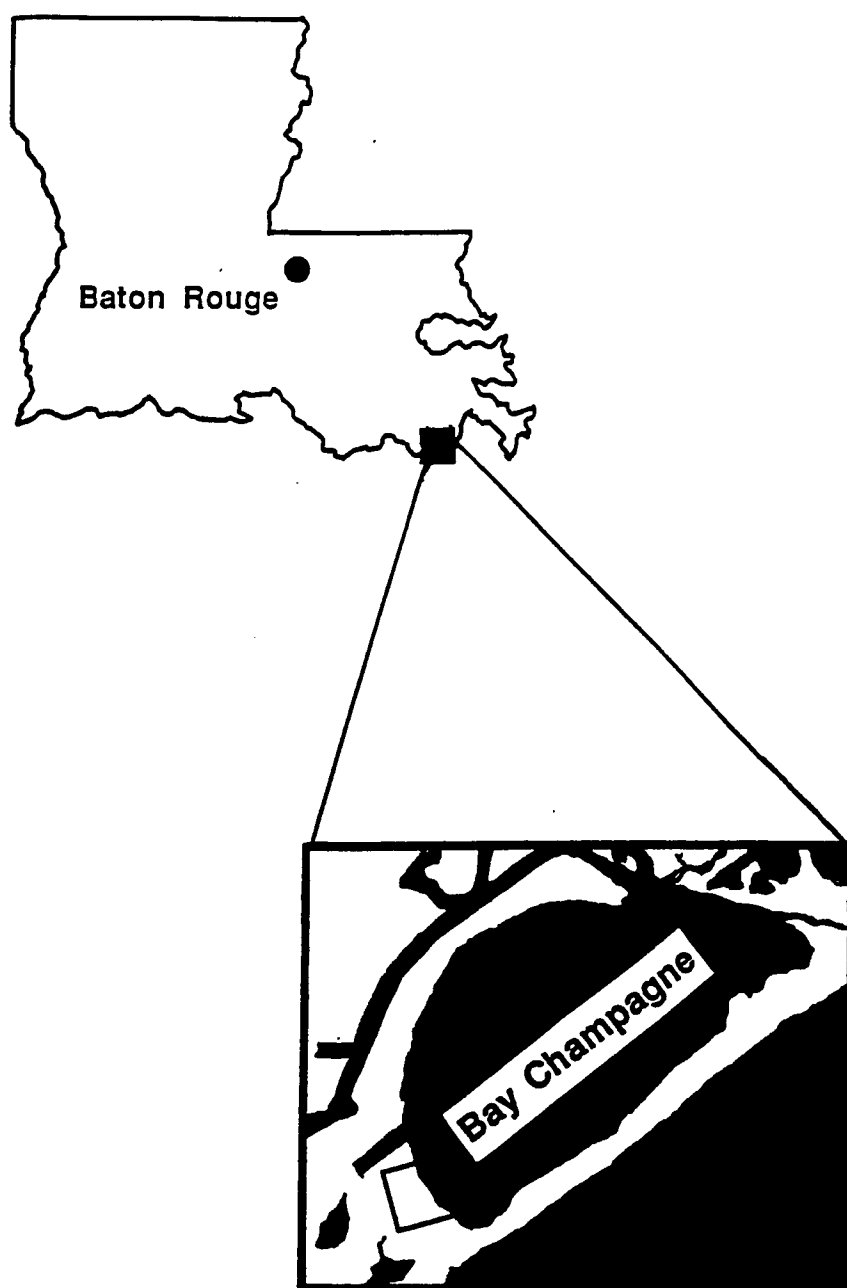


Figure 3.1. Location of the study site at Bay Champagne, Louisiana.

Spartina -dominated zone starting at the inland border of the transition zone and extending several hundred meters inland (Figure 3.2, Patterson and Mendelssohn 1991).

Propagule Establishment and Growth

I tested the ability of *A. germinans* propagules to establish in the *Spartina* zone through the use of enclosures. Enclosures were made by stapling 6 mm mesh galvanized steel hardware cloth to water-resistant wooden stakes. The enclosures, 0.6 m in height, circular, and encompassing an area of 0.1 m², were firmly pressed into the substrate so that the bottom of an enclosure extended about 1 cm into the substrate and prevented propagules from washing out from underneath the enclosures. The enclosure height of 0.6 m was about twice the height necessary to prevent propagules from floating out of the enclosures during a high tide. Propagules were collected from the parent trees in the *Avicennia* zone in November, which is at the beginning of propagule fall in Louisiana (personal observation), and 20 propagules were placed in each enclosure within 1 hour after collection. The propagules were not anchored to the substrate, as in some previous enclosure experiments (Rabinowitz 1978b, Jimenez and Sauter 1991), but were able to float within the enclosures. By allowing the propagules to float within the enclosures, it can be determined if the flooding regimes of the areas containing the enclosures are suitable for propagule establishment. If the propagules had been anchored to the substrate, establishment may have been forced in areas where excess flooding (depth and duration) would have prevented it.

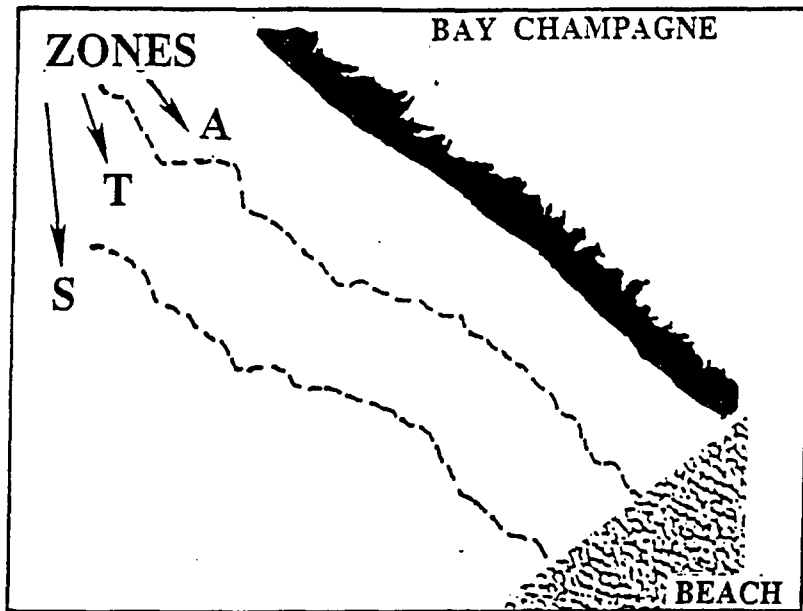


Figure 3.2 Location of plant species zones at the study site.

To determine flooding regimes in the enclosures, I took water level measurements in each enclosure during a high tide and related these measurements to simultaneous readings on a tide gauge 250 m from the study site, similar to methods used in studies of other Gulf Coast intertidal plant communities (Eleuterius and Eleuterius 1979).

The experiment was monitored from its beginning in November, 1988, until February, 1990.

Experimental Design/Analysis

Each enclosure was an experimental unit. The *Avicennia* and *Spartina* zones were the treatments, with 16 enclosures per zone in a completely randomized design. Percent survival was compared between zones after 4 months and 15 months (seedlings). Surviving propagules were defined as those which were green, not decomposing and without significant damage. Percentage of propagules rooted and standing were compared between zones after 4 months to determine if a difference in propagule establishment between zones was evident during that time period. Height growth differences of surviving seedlings were compared after 15 months. Percent survival and height growth were analyzed by analysis of covariance within a completely randomized design, with percent time flooded as the covariate. Also, percent time flooded was compared between zones in a separate analysis of variance. Residuals from the analyses of covariance were normally distributed (Proc Univariate, SAS 1985). Also, variances in all analyses were compared and found to be homogeneous. Therefore, data transformations were not necessary.

Propagule Predation

The propagule predation experiment was conducted from February 14 to March 5, 1990, at a time when all propagules had fallen from the parent trees but none had become rooted in the substrate, consistent with the finding by McMillan (1971) that *A. germinans* propagules are inhibited from rooting at temperatures lower than 15° C.

Experimental Design/Analysis

Experimental units were 12 m² plots. The treatments were the *Avicennia* and *Spartina* zones, with 10 randomly-located plots per zone, in a completely randomized design.

Background density of naturally occurring propagules was determined in each plot. Subsequent analysis (ANOVA) revealed significant differences ($P=0.0023$), with mean background densities of 49.95 m⁻² and 0.43 m⁻² in the *Avicennia* and *Spartina* zones, respectively. The background density of the *Spartina* zone did not differ statistically from zero. To control for possible density-dependent effects, I manipulated the background densities of half of the plots in the experiment. Half of the *Avicennia* zone plots were randomly chosen and cleared of all propagules, to reduce their background density to zero. Propagules from each cleared *Avicennia* zone plot were transferred to a randomly-chosen *Spartina* zone plot, so that half the number of the *Spartina* zone plots inherited the background density of *Avicennia* zone plots immediately before the experiment began.

Avicennia propagules were collected at the study site on the beginning day of the experiment from areas outside the experimental plots and inspected to insure that they

were healthy and had no signs of predation or other damage. Propagules were tethered to bamboo stakes or other immovable objects, such as an adult *Avicennia* trunk, and located 0.5 m apart, with each plot containing 10 propagules. Also, as a control, two 0.5 m strings with nothing attached to the free end were placed in each plot, as in the experiment by Smith (1987a).

All plots were monitored after 4 days and 17 days for propagule predation and nonviable propagules, regardless of the cause of mortality. I chose 17 days as the time for the final monitoring because evidence from previous propagule predation experiments (Smith 1987b, Osborne and Smith 1990) suggests that almost all propagule predation occurs within 14 days of placing a propagule in an area. Predation was defined as any evidence of animal damage to a propagule, such as removal or scouring of plant tissue. A propagule was considered nonviable if more than 25 percent of a cotyledon or the radicle were eaten, decomposed or desiccated.

Percent predation and percent nonviable (mortality) were analyzed by analysis of covariance, with background density at day 17 as the covariate, similar to the analysis in a study by Smith (1987a). The nonviable category was further broken down into causes of mortality within a zone, and causes (as percent of total mortality) were analyzed by Fisher's Exact Test (Agresti 1990). Percent time flooded was determined in the same manner as in the enclosure experiment, and analyzed in a separate analysis of variance. As in the enclosure experiment, residuals from both analyses of covariance (percent predation and percent mortality) and the analysis of variance for percent time flooded were analyzed for normality. Residuals from all analyses were normally distributed and variances were homogeneous, consequently, data transformations were unnecessary.

RESULTS AND DISCUSSION

Propagule Establishment and Growth

There were no differences in percent survival between the *Avicennia* and *Spartina* zones after 4 months or 15 months (Figure 3.3), even though percent time flooded was significantly greater in the *Spartina* zone than in the *Avicennia* zone during the first 4 months (Figure 3.4) and the entire 15 months of the experiment (Figure 3.5). Also, there were no zone differences in percent of propagules rooted or standing after 4 months, indicating that the number of propagules establishing in each zone was equal over this time period (Figure 3.6). Although the percentage of time flooded in the *Spartina* zone was twice as high as in the *Avicennia* zone, the *Spartina* zone substrate was free of flooding (70% of the time during winter months, 61% of the time over a 15-month period) more often than it was flooded. According to other studies with *A. germinans* propagules (McMillan 1971, Rabinowitz 1978a), areas which are free of flooding 70% of the time during the months of propagule release should be suitable areas for establishment. As mentioned earlier, McMillan (1971) found that *A. germinans* propagules can establish in water up to 5 cm deep, but because there were no differences in the percentages of propagules establishing in the two zones, zone comparisons of flooding depths were unnecessary.

Mean seedling heights after 15 months were significantly greater ($P=0.0001$) in the *Spartina* zone (Figure 3.7), and remained significant after adjustment by the covariate ($P=0.03$). The height differences were probably caused by shading effects. Seedlings growing under a canopy of *Avicennia* trees were heavily shaded relative to those growing in the *Spartina* zone (personal observation) consistent with results of a

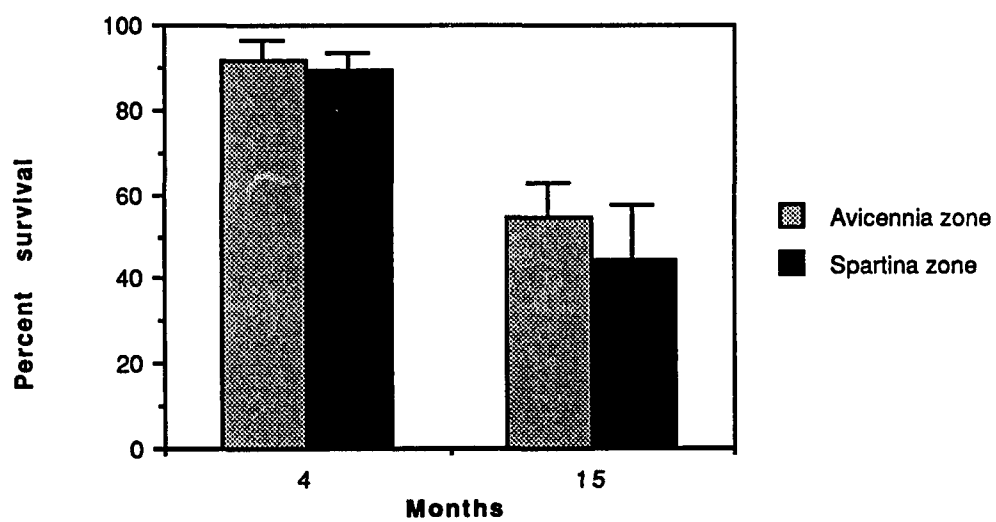


Figure 3.3. Percent survival of propagules in enclosures.

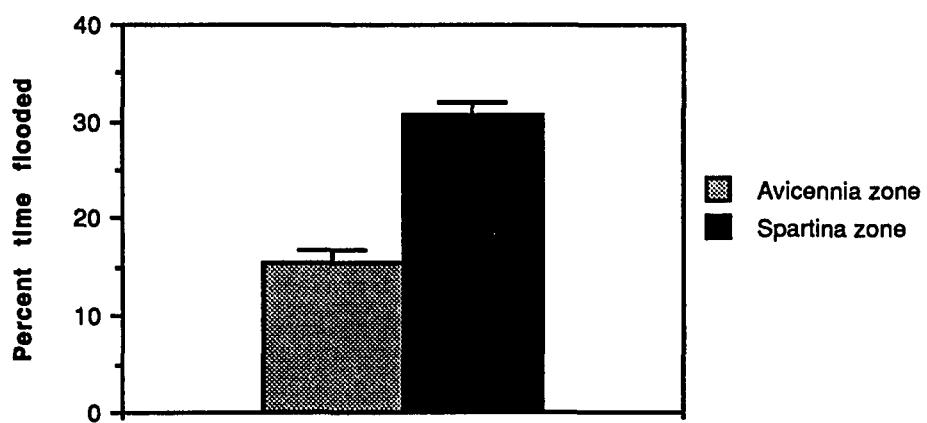


Figure 3.4. Percent time flooded during the first 4 months of the enclosure experiment.

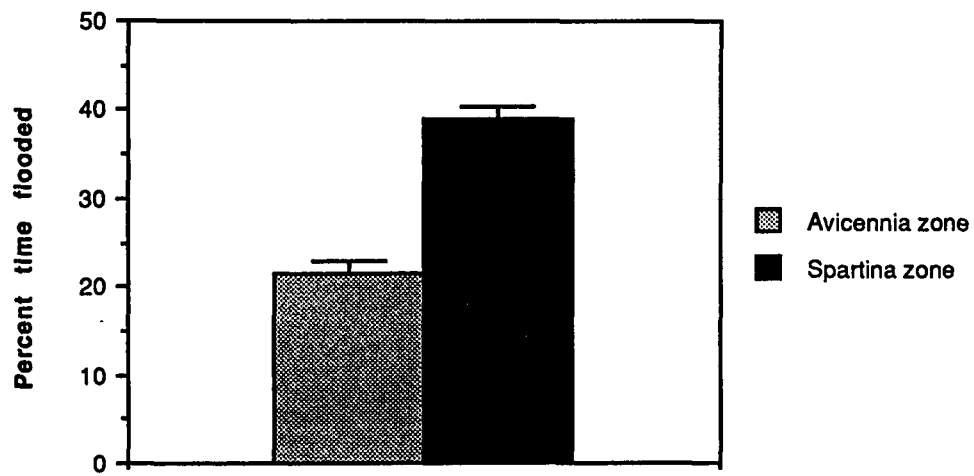


Figure 3.5. Percent time flooded for the duration (15 months) of the enclosure experiment.

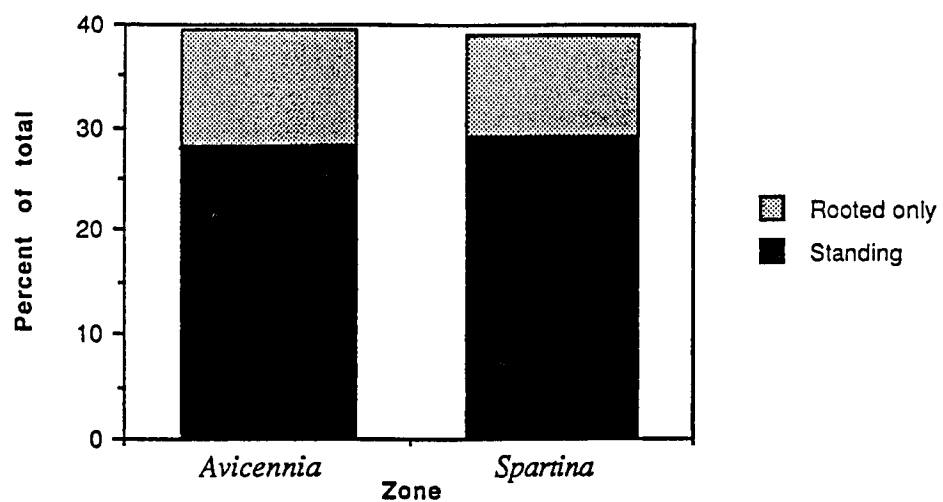


Figure 3.6. Percent of total propagules rooted and standing in enclosures after 4 months. Standard errors are: *Avicennia* zone rooted 1.70, *Spartina* zone rooted 1.73, *Avicennia* zone standing 1.83, *Spartina* zone standing 1.86.

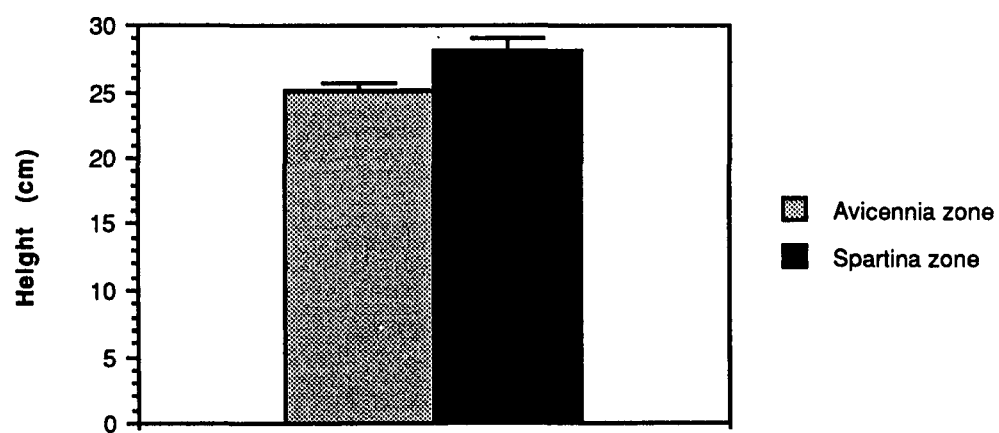


Figure 3.7. Seedling heights in enclosures after 15 months.

similar experiment with *A. marina* propagules (Smith 1987b) in which the propagules grew taller in light gaps. However, other environmental differences between zones may have contributed to the observed height differences.

Although the enclosures were not originally designed to exclude predators as in Smith's (1987b) study in Australia, I did not observe any evidence of propagule predation within the enclosures, such as partially consumed cotyledons or snail scouring trails, and therefore assumed that the enclosures inhibited the activities of potential predators at this study site.

Anderson (1989) stated that seed predation is only important to recruitment in plant communities if it significantly reduces the number of plants establishing in safe sites, defining a safe site as one in which a plant's seeds could normally establish if not consumed by a predator. The results of the enclosure experiment have shown that even though percent time flooded was twice as high in the *Spartina* zone as in the *Avicennia* zone during the first 4 months and the entire 15-month period of the experiment, numbers of propagules surviving and establishing and subsequent seedling height growth were not diminished when *Avicennia* propagules were held in the *Spartina* zone by enclosures. However, it is uncertain whether propagules could remain viable in the *Spartina* zone long enough to establish if predation pressure was high. Therefore, propagule predation in this mangrove/salt marsh ecotone could possibly influence recruitment and plant species zonation if it is possible for propagules to remain in the *Spartina* zone long enough to establish and was considered in addition to tidal and environmental factors.

Propagule Predation

After 4 days predation and mortality were negligible (data not shown). After 17 days there were highly significant differences in propagule predation ($P=0.0001$), with rates of 40 percent in the *Spartina* zone and 5 percent in the *Avicennia* zone (Figure 3.8). Percent predation in the *Avicennia* zone did not differ from zero. Final background density differences between zones were marginally significant ($P=0.077$), with levels of 18.45 m^{-2} and 2.77 m^{-2} , in the *Avicennia* and *Spartina* zones, respectively, but did not effect the results of the analyses of covariance for percent predation and percent mortality. The types of propagule damage due to predation were from snails (*Littorina irrorata*) and crabs (probably *Sesarma cinereum*). There was no evidence of larval insect predation, as found in another study (Robertson, *et al.* 1990). It is possible that insects with a larval stage dependent on mangrove propagules are not found at this site because of the effects of periodic freezing events. When sub-freezing temperatures kill the *Avicennia* trees, there are several years without propagules (Sherrod and McMillan 1985, personal observation).

Percentages of propagules nonviable in each zone after 17 days were similar: 28 percent in the *Spartina* zone and 27 percent in the *Avicennia* zone (Figure 3.9). However, the causes of mortality were different between zones, with 4 possible observed causes: desiccation, predation, decomposition, or a combination of predation and decomposition (where there was evidence of both decomposition and predation on a propagule which had been determined nonviable, but it was impossible to determine whether one factor or both caused the propagule to become nonviable).

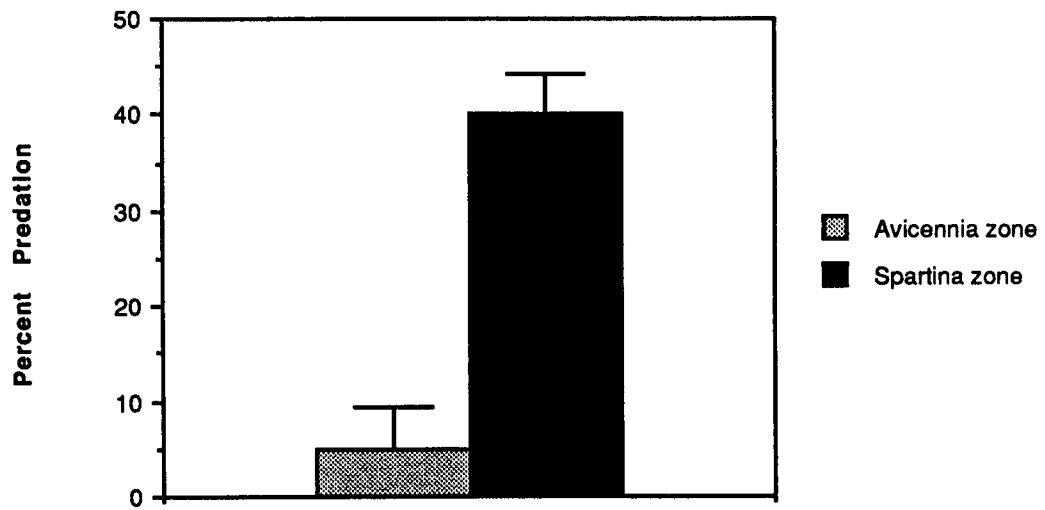


Figure 3.8. Percent propagule predation after 17 days.

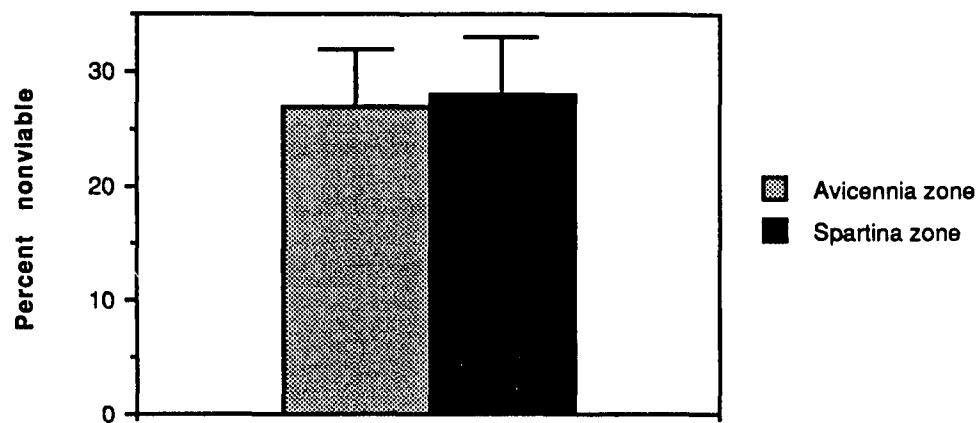


Figure 3.9. Percent of total propagules nonviable after 17 days.

If predation was not the primary cause of mortality in the combination category, it probably accelerated mortality.

In the *Avicennia* zone the predominant cause of mortality was desiccation (Table 3.1), with decomposition and predation secondary in importance. In the *Avicennia* zone decomposition and predation were equally important statistically, with percent nonviable due to predation not different than zero.

In the *Spartina* zone none of the propagules were nonviable due to desiccation, probably because percent time flooded was significantly greater in the *Spartina* zone (38.2%) than in the *Avicennia* zone (23.2%) during this experiment ($P=0.0001$). Therefore, predation, decomposition, or a combination of predation and decomposition accounted for all propagule mortality in the *Spartina* zone, and these 3 causes were equally important statistically (Table 3.1). Since 40 percent of all propagules had been attacked in the *Spartina* zone after 17 days (Figure 3.8), but only 28 percent of all propagules had been rendered nonviable (Figure 3.9), it should be noted that many of the propagules which had been attacked by predators (approximately 50%) were still viable. However, it can be assumed that any removal of propagule tissue or wounding by predators would significantly reduce the chances of a propagule to establish. In addition, although the total percentage of propagules nonviable did not differ between zones, predation would have a greater impact on *Avicennia* recruitment in the *Spartina* zone because natural propagule background densities were significantly lower in that zone (0.43 m^{-2} in the *Spartina* zone and 49.95 m^{-2} in the *Avicennia* zone).

Table 3.1. Causes of propagule mortality within zones. All values represent percentages of the total nonviable propagules within each zone. Effects with the same letter are not significantly different.

<u>Cause</u>	<u>Avicennia zone</u>	<u>Spartina zone</u>
Predation	14.29 b,c	39.29 a
Decomposition	21.43 b	32.14 a
Desiccation	64.29 a	0.00 b
Pred.+ Decomp.	0.00 c	28.57 a

CONCLUSIONS

From previous observations I know that *A. germinans* propagules are dispersed into the *Spartina* zone at the study site. The purpose of the enclosure experiment was to hold propagules in place, not allowing them to be moved away by the tides but allowing them to float within the enclosures. The results showed that the flooding regime alone did not prevent establishment of *A. germinans* propagules in the *Spartina* zone, because survival and establishment were equal between the *Avicennia* and *Spartina* zones over a 15-month period. It is possible that in the absence of the enclosures the tides would have moved the propagules in the *Spartina* zone away before they could establish. However, because propagule dispersal is dynamic relative to the tides, it is also likely that propagules could be continually re-introduced into the *Spartina* zone from the *Avicennia* zone as long as they were available. The results of the enclosure experiment, in which the numbers of propagules rooted and standing did not differ between zones, did not indicate that more propagules established in the *Avicennia* zone.

Propagule predation probably also influences zonation at this site. According to Anderson (1989), seed predation can be important to recruitment in plant populations if there are "safe sites" available to the plants which have not been colonized. Results of the enclosure experiment would indicate that the *Spartina* zone could be a safe site for *A. germinans* propagules to establish unless they are moved away by the tides to sites where establishment would be impossible.

Predation was significantly higher in areas where *A. germinans* is not found, and not effected by background density, consistent with other studies on propagule predation and mangrove zonation (Smith 1987a, Smith *et al.* 1989). Duration of

inundation apparently did not have a negative effect on predation, as in another study (Osborne and Smith 1990) because predation was higher in the more-inundated *Spartina* zone.

The most likely reasons that *A. germinans* is not found in the *Spartina* zone are a combination of the following factors: (1) at any given time from November through February (post propagule dispersal) the density of *A. germinans* propagules in the *Spartina* zone is low, (2) because the *Spartina* zone experiences a greater percent of time flooded, propagules which are dispersed to the *Spartina* zone have a greater chance of being washed away by tides and/or prevented from stranding than propagules in the *Avicennia* zone and (3) because propagule predation is relatively high in the *Spartina* zone, the few propagules which could remain on the *Spartina* zone substrate long enough to establish are probably eaten or substantially damaged by predators so that they are less likely to survive.

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OVERALL CONCLUSIONS

In many studies on plant species zonation in intertidal communities, soil physicochemical characteristics have differed across vegetative zones, which has led to hypotheses purporting that plant species zonation is dictated by site-specific environmental factors. In an intertidal plant community on the southeastern coast of Louisiana, where *Avicennia germinans* intergrades with *Spartina alterniflora*, I found that soil physicochemical characteristics of the *Avicennia* zone were markedly different from those of the transition and *Spartina* zones (Chapter 1). The *Avicennia* zone was significantly higher in elevation, had higher soil bulk density, higher redox potential (Eh) at several times during the year, indicating more oxidized conditions, and higher interstitial water salinity and concentrations of ions associated with seawater (Ca, Mg, K). Interstitial water sulfide levels were relatively high in the transition and *Spartina* zones during most of the year, but remained undetectable in the *Avicennia* zone during the entire year.

The lower elevation of the *Spartina* zone suggested that it would be flooded a greater percentage of the time, and that *Avicennia* may be absent from the *Spartina* zone because of its lower elevation and hence more inundated, high sulfide environment, so I tested the ability of *A. germinans* seedlings to grow under permanently flooded conditions. The hypothesis that *A. germinans* seedlings can not survive under permanently flooded conditions was rejected with the results of a greenhouse experiment (Chapter 2) in which *A. germinans* grew under permanently flooded conditions for 13 months. However, when *Avicennia* was grown under these same conditions in the presence of *S. alterniflora*, the growth of *A. germinans* was inhibited. Thus, it appears that although *Avicennia* can grow under permanently flooded conditions, its growth is reduced where it co-occurs with *Spartina*. However, greenhouse experiments can never completely simulate field conditions,

e. g., although sulfide levels were high in the more inundated *Spartina* zone in the field, sulfide concentrations in the greenhouse experiment never became elevated.

I next compared the ability of *A. germinans* to grow in the different zones of the community (Chapter 2), and since the transition and *Spartina* zones were similar across most physicochemical variables studied in Chapter 1, it was not necessary to use the transition zone as a treatment. As expected, I found that the *Spartina* zone was flooded a greater percentage of the time than the *Avicennia* zone by taking water level measurements during a high tide and relating these measurements to simultaneous tide gauge readings on a nearby gauge (Chapter 2). A field transplant experiment was conducted to compare survival and growth of *A. germinans* seedlings in 3 areas at the study site: (1) the *Avicennia* zone, where it exhibits maximum height and density (2) the higher-elevation areas of the *Spartina* zone, where small isolated individuals of *A. germinans* are occasionally found and (3) the lower areas of the *Spartina* zone, where I have never observed *A. germinans* (Chapter 2). I found marginally significant ($P=0.069$) survival differences between the lower part of the *Spartina* zone and the other 2 treatments, with the least survival in the *Spartina* low zone, but the survival rate of 44 percent in that area was ecologically significant, since *A. germinans* is not naturally found there. Although the long-term survival of *Avicennia* seedlings in the *Spartina* zone was not investigated, it seemed likely that some components of propagule dispersal and establishment were probably the most important influences on *A. germinans* distribution at the site, because survival of *A. germinans* seedlings in the *Spartina* zone over one growing season was higher than what would have been expected if *A. germinans* was being excluded from the *Spartina* zone by competition or physical or chemical conditions beyond its physiological limits.

I have observed *A. germinans* propagules in the *Spartina* zone during the period of propagule fall at the study site (November-January), but have never observed high densities of propagules there. Therefore, absence of *Avicennia* from the *Spartina*

zone is not caused by a lack of ability of the *Avicennia* propagules to disperse into that zone.

When *A. germinans* propagules were held in 0.1 m² enclosures, they had equal survival and establishment rates in the *Avicennia* and *Spartina* zones (Chapter 3), and height growth of propagules over one growing season was greater in the *Spartina* zone. Propagule predation was significantly higher in the *Spartina* zone (40%) than in the *Avicennia* zone (5%), which would be expected if predation had an influence on species zonation (Chapter 3).

In summary, although many zone differences were found in soil physicochemical characteristics (Chapter 1), *A. germinans* seedlings and propagules (in enclosures) were able to survive and grow in all vegetated areas of the study site (Chapters 2,3). The most important factors controlling the distribution of *A. germinans* in this mangal/salt marsh community are probably related to the fate of its propagules at the study site. Although propagules are dispersed from the parent trees in the *Avicennia* zone to the *Spartina* zone for several months during propagule fall, propagule densities in the *Spartina* zone are not high at any one time. The *Spartina* zone is at a lower elevation (Chapter 1) and thus experiences more flooding than the *Avicennia* zone (Chapters 2,3), so that propagules which are dispersed to the *Spartina* zone have a greater chance of being washed away by tides than propagules in the *Avicennia* zone. Since propagule predation is significantly higher in the *Spartina* zone than in the *Avicennia* zone (Chapter 3), the few propagules which could remain on the *Spartina* zone substrate long enough to establish are probably completely consumed or damaged enough by predators to render them nonviable before they can establish.

The long-term survival of *A. germinans* in Louisiana is doubtful. At the present time, this species is only found in isolated areas on the southernmost parts of the coast and on some barrier islands, and these areas are continuing to erode and subside. *Avicennia germinans* depends on the survival and establishment of its propagules to

re-colonize its present areas of distribution in Louisiana after a severe freeze, and the decreasing elevations and eventual loss of these areas over time due to erosion, subsidence and global sea level rise will decrease the chances that *A. germinans* can re-establish after freezing events.

VITA

Charles Stuart Patterson was born on January 21, 1956, in Vicksburg, Mississippi. His parents had a great appreciation for nature, and it was instilled in him at an early age. From childhood through high school he spent time raising fish in aquaria, learning about trees in the woods, and catching all forms of aquatic creatures living in a creek near his house. As an undergraduate at the University of Southern Mississippi he decided to major in biology, and after enduring a couple of years of dissections and taxonomy, became excited about many aspects of ecology. After receiving a Bachelor's degree in biology, he tried other endeavors, such as dental school (1.5 years) and drilling water wells (2 years), but realized all the time that he really wanted to be an ecologist. When the above-mentioned distractions had run their course, he went to LSU, with the help of an Alumni Federation Fellowship, to pursue a Ph. D. in Marine Sciences. His Ph. D. research was on mangrove ecology in coastal Louisiana, a field in which he had no previous knowledge before entering LSU but which he found to be interesting.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

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Major Field: Marine Sciences

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