

INTERSPECIFIC PLANT COMPETITION BETWEEN *ELEOCHARIS MONTEVIDENSIS*
AND *SCIRPUS VALIDUS* ALONG A SALINITY GRADIENT IN THE SAVANNAH
NATIONAL WILDLIFE REFUGE

By

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For my Mom, Dad, Grandparents, and Harpo

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TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS	4
LIST OF FIGURES	7
ABSTRACT	9
CHAPTER	
1 INTRODUCTION	11
Tidal Freshwater Marshes.....	11
The Savannah River and Marsh Ecosystem	15
Previous and Ongoing Studies of the Savannah River Marshes.....	17
Species Assemblages	20
Competition across Environmental Gradients.....	20
Species Zonation in Wetlands	22
Objective of the Experiment.....	28
2 MATERIALS AND METHODS	33
Study Sites	33
Species of Interest.....	34
<i>Eleocharis</i>	34
<i>Scirpus</i>	34
Methods	35
Site Selection.....	35
Initial Plot Creation and Donor Sites.....	35
Sampling.....	37
3 RESULTS	45
Salinity Data	45
Vegetation Data	45
<i>E. montevidensis</i> and <i>S. validus</i> Control Plots	46
<i>E. montevidensis</i> control plots.....	46
<i>S. validus</i> control plots	46
<i>E. montevidensis</i> Surrounded By <i>S. validus</i>	47
<i>S. validus</i> Surrounded By <i>E. montevidensis</i>	48
4 DISCUSSION.....	63
Salinity Gradient.....	63
Control Plots and Belowground Competition.....	64

<i>Eleocharis montevidensis</i> Surrounded by <i>Scirpus validus</i>	67
<i>Scirpus validus</i> Surrounded by <i>Eleocharis montevidensis</i>	68
Comparisons to Previous Competition Studies	69
Potential Mechanisms Contributing to <i>Eleocharis montevidensis</i> ' Competitive Success.....	71
Conclusions, Applications, Long-term Predictions, and Improvements	71
LIST OF REFERENCES	75
BIOGRAPHICAL SKETCH	81

LIST OF FIGURES

<u>Figure</u>	<u>page</u>
1-1 Marsh types present in a tidal river system, classified by interstitial salinity (Pearlstine et al., 1990) and surface salinity	31
1-2 Locations of areas used in previous vegetation studies along the lower Savannah River.....	32
2-1 Location of the study sites along the lower Savannah River.....	38
2-2 Monthly interstitial salinity at the tidal fresh and oligohaline sites from June 2004 to April 2005.....	39
2-3 Schematic drawing of experimental set up	40
2-4 Experimental unit consisting of <i>E. montevidensis</i> surrounded by <i>S. validus</i>	41
2-5 Experimental unit consisting of <i>S. validus</i> surrounded by <i>E. montevidensis</i>	42
2-6 Experimental unit consisting of <i>E. montevidensis</i> surrounded by <i>E. montevidensis</i>	43
2-7 Experimental unit consisting of <i>S. validus</i> surrounded by <i>S.validus</i>	44
3-1 Tidal Fresh Site: <i>E. montevidensis</i> surrounded by <i>E. montevidensis</i>	51
3-2 Oligohaline Site: <i>E. montevidensis</i> surrounded by <i>E. montevidensis</i>	52
3-3 Tidal Fresh Site: <i>S. validus</i> surrounded by <i>S. validus</i>	53
3-4 Oligohaline Site: <i>S. validus</i> surrounded by <i>S. validus</i>	54
3-5 Tidal Fresh Site: <i>E. montevidensis</i> surrounded by <i>S. validus</i>	55
3-6 Oligohaline Site: <i>E. montevidensis</i> surrounded by <i>S. validus</i>	56
3-7 Tidal Fresh Site: Relative percent change (RC) in number of stems over time in treatment <i>E. montevidensis</i> surrounded by <i>S. validus</i>	57
3-8 Oligohaline Site: Relative percent change (RC) over time in treatment <i>E. montevidensis</i> surrounded by <i>S. validus</i>	58
3-9 Tidal Fresh Site: <i>S. validus</i> surrounded by <i>E. montevidensis</i>	59
3-10 Oligohaline Site: <i>S. validus</i> surrounded by <i>E. montevidensis</i>	60
3-11 Tidal Freshwater Site: Relative percent change over time in treatment <i>S. validus</i> surrounded by <i>E. montevidensis</i>	61

3-12 Oligohaline Site: Relative percent change in number of stems over time in treatment
S. validus surrounded by *E. montevidensis*62

Abstract of Thesis Presented to the Graduate School
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Previous work within the Savannah National Wildlife Refuge (SNWR) has suggested that interspecific competition is an important factor in the species assemblages in the tidal marsh systems. However, this work was completed under different environmental conditions than were currently being experienced. Experiments to quantify competitive interactions within the marsh will lend insight to creating marsh succession models applicable to present conditions.

The competitive interactions of soft-stem bulrush (*Scirpus validus*) and sand spikerush (*Eleocharis montevidensis*) were studied under two different salinity levels in the field with a transplant experiment using non-destructive sampling methods. One salinity level was representative of freshwater conditions (under 0.5 ppt), while the other represented oligohaline conditions (between 0.5 and 5.0 ppt). Both species are prevalent within the refuge, but *S. validus* is the only species that is consistently present throughout the tidal salinity gradient from freshwater to mesohaline marshes and this gradient alone only partially explains the distributions. For this reason, I initiated a competition study to better explain the distribution of this generalist species, particularly in the upper reaches of the estuary dominated by both freshwater and oligohaline conditions.

At the initiation of the experiment, it was expected that *S. validus* would outcompete *E. montevidensis* in the oligohaline conditions because it is a generalist with a greater salinity tolerance. At the conclusion of the experiment, it was clear that belowground competition between the two species was occurring at both freshwater and oligohaline sites. *E. montevidensis* was able to invade *S. validus* plots more effectively and quickly than *S. validus* invaded *E. montevidensis* plots, regardless of salinity level. At the same time *E. montevidensis* was increasing in plots of *S. validus*, stems of *S. validus* were decreasing. *S. validus* was slower to invade *E. montevidensis* plots, and was found in lower density at the tidal freshwater site. The results suggest that *E. montevidensis* is able to tolerate oligohaline salinity conditions while remaining competitive at both salinities. It also suggests that under fresher conditions *E. montevidensis* may be capable of preventing invasion of *S. validus* for a longer period of time.

CHAPTER 1 INTRODUCTION

Tidal Freshwater Marshes

Tidal freshwater marshes are located upstream of tidal salt marshes and downstream of non-tidally influenced fresh water marshes. These marsh systems are typically defined based on surface water salinity (Cowardin et al. 1979) or interstitial salinity (Dusek 2003, Pearlstine et al. 1990) (Figure 1-1). Freshwater tidal marshes experience near freshwater conditions (average salinity of 0.5 ppt except in times of drought), with plant and animal communities dominated by freshwater species (Odum et al. 1984). Tidal freshwater marshes receive the same “tidal subsidy”—influxes of nutrients, carbon and dissolved oxygen—as coastal salt marshes, but without the accompanying salt stress (Mitsch and Gosselink 2000). This allows them to be extremely productive, and much more diverse than salt marshes.

The physical conditions required for tidal freshwater marsh development include adequate freshwater flow to maintain salinities less than one-half part per thousand, but insufficient flow to dampen upstream tidal movement (Mitsch and Gosselink 2000, Simpson et al. 1983). In the United States, these conditions occur primarily along the Atlantic and northern Gulf coasts, usually in association with large river systems, such as the Delaware, Hudson, Potomac, and St. Lawrence in North America (Odum 1988). Odum et al. (1984) estimated that Atlantic Coast tidal freshwater marshes cover about 164, 000 ha. Most are found along the Mid-Atlantic Coast, possibly with one-half in New Jersey. The Georgia and South Carolina Atlantic coast also contains a large amount of tidal freshwater marshes. Estimates made in the 1970s showed Georgia had approximately 19,040 hectares, while South Carolina had an estimated 26,115 hectares (Odum et al. 1984). The tidal freshwater marsh of the Savannah River at one time accounted for approximately 21% of the total freshwater tidal marsh found within both states and

25% of the total freshwater tidal marsh found along the east coast of the United States (Duncan et al. 2003; Pearlstine et al. 1993). These proportions have been significantly reduced in the recent past as a result of development in the Savannah Harbor (Pearlstine et al. 1993).

Today's coastal marshes were recently formed, lying in river beds that were created during the Pleistocene periods of lowered sea levels. As sea level rose after the last glaciation, coastal freshwater marshes expanded into drowned river systems filled with sediment (Mitsch and Gosselink 2000, Odum et al. 1984). Most of today's tidal freshwater marshes are less than 15,000 years old; however, this does not mean they did not exist in earlier geological periods. There is abundant evidence from coal deposits showing that early equivalents of present-day tidal freshwater marshes existed hundreds of millions of years ago (Odum et al. 1984).

Along the Atlantic Coast, 2 m semidiurnal tides and accompanying strong currents create an elevation gradient from tidal streams into adjoining marshes. The low marsh is typically geologically younger than the high marsh (Odum et al. 1984). Freshwater tidal marshes have been categorized into four major habitat zones based on hydrologic regimes: streams and tidally exposed stream banks that may or may not have vegetation; high marsh areas that are flooded twice daily for up to 4 hours by up to 30 cm of water; low marsh or ponded areas that are flooded for approximately 9 hours during each tidal cycle with up to 100 cm of water; and pond areas that are continuously flooded, but show regular flow reversal accompanied by changes in tidal direction (Whigham and Simpson 1976, Simpson et al. 1983). Virtually all freshwater tidal marshes contain the first two habitat zones, but the latter two are most often found in areas that have been diked or otherwise artificially manipulated (Simpson et al. 1983). These differences in flooding and elevation result in gradients of soil physical and chemical properties and plant zonation patterns consistent of freshwater tidal marshes (Mitsch and Gosselink 2000).

Community structure may also be influenced through interspecific competition, soil type, temperature, and herbivory (Odum et al. 1984).

Primarily very fine silts and clays make up the soils of freshwater tidal marshes, with a gradient of organic content ranging from 10-15% at the top of actively flooded levees to 30-45% in high marsh areas with minimal tidal activity (Whigham and Simpson 1975, Simpson et al. 1983). Sediment deposition rates in the high marsh areas appear to be low, but significant erosion and deposition occurs in stream channels, elevated levees, and lower, gently sloping stream banks (Simpson et al. 1983). Much of the sediment load is deposited onto the elevated levees of the marsh (Mitsch and Gosselink 2000).

Although no species of plant or animal is restricted solely to the tidal freshwater marsh, there is high diversity of both biota to be found. This is typified by high species diversity, and low dominance by any single species (Odum 1988). The plant community generally consists of broad-leaved emergent macrophytes, herbaceous annuals, annual and perennial sedges, rushes, and grasses, shrubform herbs, and a few hydrophytic shrubs and trees (Odum 1988).

The fish community of the tidal freshwater marsh is comprised of a complex and seasonally variable mixtures of freshwater forms tolerant to low salinity conditions, typical estuarine residents, anadromous fishes on spawning runs and their juveniles, juvenile marine fish using the area as a nursery ground, and adult marine fish that are seasonal transients (Odum et al. 1984). Many species of fish and crustacean venture into the tidal freshwater marsh, including menhaden (*Brevoortia tyrannus*), spotted seatrout (*Cynoscion nebulosus*), black drum (*Pogonias cromis*), snook (*Centropomus undecimalis*), brown and white shrimp (*Penaeus* spp.) and male blue crabs (*Callinectes sapidus*) (Mitsch and Gosselink 2000). Odum et al. (1987), in a comparison of fish types in freshwater tidal marsh using data from 13 sites from the Hudson

River, New York, and the Altamaha River, Georgia, found 60% were freshwater species, 20% were anadromous, 13% were estuarine, and 7% were marine species.

Mitsch and Gosselink (2000) have suggested that the largest and most diverse populations of birds may be supported by the tidal freshwater marsh of the wetland types. The structural diversity of the vegetation allows for many species of birds to intensely utilize the marsh. Odum et al. (1978) pointed out that it is clear that many species have preferences for different marsh types. For example, dabbling ducks, Canada geese, and whistling swans appear to prefer freshwater tidal marsh, while diving ducks, mergansers, snow geese, clapper rails, and sea ducks prefer salt marsh habitat.

In addition to providing feeding and nesting/nursery habitat to a large diversity of animals, tidal freshwater marshes also help process and buffer pollutants such as heavy metals and nutrients from upstream sources (Odum et al. 1984, Simpson et al. 1983, Whigham and Simpson 1978, Grant and Patrick 1970). Suspended sediments that would otherwise continue downstream into the estuary can become assimilated into the marsh itself. The tidal freshwater marsh can act as a filtration system, thus improving the quality of the water flowing downstream (Odum et al. 1984).

Tidal freshwater marshes are an exceedingly rare type of wetland at risk from human development and sea level rise associated with climate change. Many of these marshes are very close to major historic cities and have been experiencing alterations for hundreds of years. Poor farming methods, in addition to widespread forest clearing and land development, have created heavy sediment loads, increases in dissolved nutrients, and toxic heavy metals in the freshwaters entering the tidal freshwater marshes. Many of these marshes were converted to rice fields during the plantation era, while other alterations include interruption of freshwater input through

diking, dredging and filling, and eutrophication from sewage effluent (Odum et al. 1984). As is seen in the freshwater tidal marsh of the Savannah National Wildlife Refuge (SNWR), invasive plant species also pose a threat to these ecosystems (pers. obs.). It is critical to learn how to manage these unique wetlands so that they can continue to provide important ecosystem services, and understanding plant community assembly rules will help management and restoration efforts.

The Savannah River and Marsh Ecosystem

The headwaters of the Savannah River form in the mountains of North Carolina, South Carolina, and Georgia, flowing through four physiographic regions; the blue ridge mountains, the piedmont, and the upper and lower coastal plain before reaching the Atlantic Ocean approximately 500 kilometers later (Pearlstine et al. 1990, Dusek 2003). The Savannah River is formed by the confluence of the Tugaloo and Seneca Rivers, and has a basin area of approximately 26,000 km² (Collins et al. 2000). The historic cities of Savannah and Augusta, Georgia are located along the Savannah River. The Lower Savannah River is a deltaic system, branching into a series of distributary channels including: the Front, Back, Middle, and little Back Rivers. Approximately 65 kilometers before reaching the Atlantic, the Savannah River starts assuming a tidal signal, which is amplified to over 2 m further down river. This allows an estuarine salinity gradient to be detected over 40 kilometers up river (Latham 1990, Pearlstine 1990, Dusek 2003). The conditions permitting tidal freshwater and oligohaline marshes to form exist for only a few miles along the Savannah River, which underscores the importance of protecting these unique wetlands.

The development of the port has caused significant vegetation community change to the upstream SNWR marshes. At the time of the establishment of the SNWR, there were approximately 2,428 hectares of tidal freshwater marsh, and by 1997 due to cumulative impacts

of harbor deepening; the marsh system had declined to only 1,133 hectares. The most significant damage to the tidal marshes occurred from the construction of a tide gate and new channel (New Cut), which was created to encourage flushing in the Front River, and thus reduce the need for dredging in the Savannah Harbor (Eudaly 1999).

The tide gate was installed in 1977, altering the flow, direction, and velocity of the lower river, as well as affecting salinities throughout the SNWR. These changes in flow and salinity have been attributed to vegetation changes and loss of habitat value through conversion of tidal freshwater marsh to brackish marsh (Pearlstine et al. 1990). After these findings, the tide gate was removed in 1992, and salinities were reduced. A model based on the Pearlstine (1990) study predicted that the removal of the tide gate would allow freshwater marsh vegetation to recover, and this has happened to some extent although the effects may have been mitigated by a subsequent harbor deepening in 1994, from 11 meters to its current depth of 13 meters.

In 1999, the U.S. Congress authorized the deepening of the channel to a depth of 14.5 meters in the Water Resources Development Act. Similar to the tide gate, this deepening may have significant adverse effects to the freshwater and oligohaline marshes found within the SNWR, by again shifting the salinity gradient further upstream. This deepening is subject to a Tier II Environmental Impact Study and mitigation plan, part of which includes the development of a vegetative succession model. The U.S. Fish and Wildlife Service has estimated that if the deepening is not appropriately mitigated, the impact could result in degradation of up to 40% of the remaining freshwater tidal marsh (U.S. Fish and Wildlife Service. U.S. Fish and Wildlife Service Fact Sheet: Proposed Deepening of the Savannah Harbor. Retrieved October 13, 2010, from http://www.fws.gov/southeast/pubs/facts/sav_harbor.pdf)

Most of the previous studies conducted within the SNWR have been in response to changes in the system caused by port modifications, including the tide gate and continued dredging of the harbor. With continued involvement and study of the upstream marsh ecosystems, it may be possible to predict vegetation changes from proposed port modifications and the potential outcome from mitigation procedures. Understanding the biotic interactions of dominant plant species may be useful in predicting community changes within the SNWR based on abiotic changes in the system, such as salinity increases from downriver modifications.

Previous and Ongoing Studies of the Savannah River Marshes

Previous studies have focused on documenting the vegetation response of the marshes to natural and man-made changes due to salinity, water level, and other environmental factors (Latham 1990, Pearlstine, et al. 1993, Dusek 2003). Seven sites were established for monitoring of water level, interstitial salinity, conductivity, and plant biomass (Dusek 2003). Four of these are sites that were previously been established along the salinity gradient of the Back River; two were set up in the intermediate zone of the Middle River, and an additional fresh site was later established off the Front River (Figure 1-2). The objective has been to create a model that can be used to determine community response to alterations in environmental conditions, particularly salinity. We are attempting to add to our knowledge base in order to produce a more precise predictive model. Utilizing a model like this may contribute to better conservation and management of these important marsh ecosystems and the many species of nekton, birds, and other animals that rely on them.

A study by Latham beginning in 1985 characterized the vegetation assemblages and distributions based on environmental parameters, morphology, competition, and disturbance throughout the tidal marshes of the Lower Savannah River. The study found that salinity was significant in separating major vegetation classes. A species of particular interest in the study

was *Scirpus validus*, or soft-stem bulrush, which is the only species found throughout the entire study area, ranging from mesohaline to freshwater tidal marsh. Latham studied several aspects pertaining to this species, namely the distribution patterns based on salinity and competitive ability (Latham 1990, Latham et al. 1993).

The distribution patterns of *S. validus* ranged from clumped in mesohaline marsh (5 - 18 ppt), uniform in strongly oligohaline marsh (2.5 - 5.0 ppt), and random throughout the freshwater (< 0.5 ppt) and mildly oligohaline marsh (0.5 - 2.5 ppt). The clumped and uniform distribution patterns in the mesohaline and oligohaline marsh indicates that competitive interactions were affecting the pattern. Further, greenhouse experiments that Latham conducted suggested that *S. validus* grew best in freshwater conditions. These conflicting results indicated that factors other than environmental conditions were affecting the distribution.

Part of the study Latham conducted entailed the transplant of sod-like blocks of marsh vegetation representative of freshwater (*E. montevidensis*), oligohaline (*S. validus*), and mesohaline (*Spartina alterniflora*) marsh between sites. Plots were surrounded by lawn edging to prevent belowground interference from outside the plot. The purpose was to determine how these plants grew outside of their dominant environment without the competition of other species. After 1 ½ years the above-ground vegetation was harvested, species identified, stems counted and biomass determined. It was found that the relative density and biomass of *E. montevidensis* decreased when transplanted to the mesohaline site, but not at the oligohaline site. Relative density and biomass of *S. validus* decreased at the freshwater site and mesohaline site. However, the results of her experiment were partly confounded by the fact that the lawn edging was not sufficient to prevent plants from invading the experimental plot.

In addition, Latham's study involved a removal experiment in which all species within a study plot were removed except *S. validus*. There were experimental plots set up within the fresh, oligohaline, and mesohaline tidal marsh. Inner plots representing the common vegetation of each marsh type had all species removed except *S. validus* and were surrounded by an outer plot in which only *S. validus* was removed. After approximately one year, all vegetation was harvested, sorted by species, and stems counted and weighed. The purpose of her experiment was to determine if *S. validus* would increase or decrease without neighbors, and what effect, if any, this species has on its neighbors.

The freshwater plot was the only one to show an increase in *S. validus*, although this was likely due to the fact that unlike plots at the other sites, they were not made exclusively of *S. validus*. Therefore more room was created when other species were removed. Inner plots were not completely filled with *S. validus*, but densities were approximately 10% greater and biomass 20% greater. The most common species found within these plots was *E. montevidensis*.

At the oligohaline site, *S. validus* decreased in density but not biomass. Some invasion of these plots occurred by *E. montevidensis* as well. Decreases in density and biomass of *S. validus* were greatest at the mesohaline site. The removal of neighbor species resulted in the invasion of available space by species other than *S. validus*, predominately *S. alternaflora*.

Removal of *S. validus* from outer plots did not result in any significant change in *S. validus* density or biomass in either the freshwater or oligohaline sites, but was significantly lower in the mesohaline site. The result was less *S. validus* and more *S. alternaflora*.

Latham concluded that the plant species found within the different marsh types were not a random conglomeration, but rather, one based on many different factors. These include varying

tolerances to the local environmental conditions such as salinity, and water-logged soils. A species' location within the marsh was also related to its competitive ability.

Species Assemblages

Species assemblages vary based on the type of ecosystem, the species in question, the site history, and other site-specific factors. Important mechanisms affecting species assemblages include competition, predation, facilitation, and mutualism. Generalist species are often found in more stressful environmental conditions, even though they may fare better in less harsh environments (Connell 1961). A study of the plant zonation of an Alaskan salt marsh (Snow and Vince 1984) was the first to suggest that the distribution of marsh plants was related to physical factors such as salinity and waterlogging in the harsher zone, while interspecific competition was an important factor in the less stressful zone.

Competition across Environmental Gradients

There are multiple theories on the role of interspecific competition in influencing species distribution along environmental gradients (Greiner La Peyre et al. 2001). For example, one theory predicts that as abiotic stress increases, the relative role of competition decreases (Grime 1973, Keddy 1990, Snow and Vince 1984). According to Grime's (1979) model, the distribution of plants in stressed environments is limited primarily by the tolerances of individual species to the conditions limiting productivity. He found this was the case in subalpine plant communities. Additionally, Del Moral et al. (1985) concluded from their research in a similar ecosystem that community structure in stressed habitats was the result of independent evolutionary responses to abiotic factors and not interspecific competition.

Others argue that as the environment can support fewer individuals in increasingly stressful abiotic conditions, competition will be most important (Wiens 1977, Sherwood and Risser 1979). Tilman's (1988) model predicted that plants limited by the same resource should

compete strongly in stressed or resource-poor environments. A third conflicting view argues that competition is important regardless of the environmental conditions (Newman 1973, Tilman 1982, Grubb 1985). Different definitions of the measurement of “competition” increase the confusion (Grace 1991). Grace was able to rectify many of the differences between the so-called competing theories between Tilman and Grime by pointing out that Grime defined competition in terms of capacity for resource capture while also stating that it is only one part of the mechanism a plant may utilize to suppress a neighbor. Grace describes Tilman’s focus on competitive success as the ability to draw resources to a low level and to tolerate the low levels of resources. Many of Tilman and Grime’s theories deal more specifically with the mechanisms of competition and are too complex to address or reconcile in this study (See Craine 2005).

Gradients in salt marshes (Snow and Vince 1984), grasslands (Gurevitch 1986) and freshwater shorelines (Grace and Wetzel 1981, 1998; Shipley et al. 1991; Keddy 1989) have all been used in removal experiments. Other environmental gradients that have been utilized include rocky shorelines (Connell 1961), soil depth in alvars (Belcher et al. 1995), soil nutrients in wetlands (Twolan-Strutt and Keddy 1996) and elevation on mountain sides (Wilson 1993). An experimental removal of macro-algae along an exposure gradient in the rocky intertidal zone showed that the effects of removal varied among sites (Dayton 1975). Transplant experiments using six shrub species in South Africa found evidence of negative effects on the performance of neighbors (Richards et al. 1997).

A removal experiment (Sammul et al. 2000) in eight different community types with a perennial grass (*Anthoxanthum odoratum*) found that the removal of other species resulted in increased growth of *A. odoratum* in all community types except one. The study also showed that competition intensity increased as community productivity increased.

Designs using natural gradients combine the thoroughness of planned and controlled manipulations with the generality of among-site comparisons. Keddy (2001) has stated that “this combination of natural gradients and experiments may be the most powerful tool available for probing the structure of ecological communities.”

Species Zonation in Wetlands

Descriptive studies themselves cannot generate information on levels of interspecific interaction; so manipulative field and laboratory experiments are required to determine the role that competition plays in creating vegetation zonation (Kenkel et al. 1991). Experiments have indicated that environmental variation, disturbance, and interspecific competition are all important factors in the formation of vegetation zones (Silander and Antonovics 1982, Snow and Vince 1984, Bertness and Ellison 1987). The role of competition is inferred from results indicating that species normally found at high salinity perform better in less saline areas when not subjected to interspecific competition. The advantage of experiments such as these is that they are performed under natural conditions. However, since gradients in the field are environmentally complex, it may be difficult to determine unequivocally which environmental factors are most important in controlling species distributions. Interpretations may be misleading if based on results from a single growing season (Kenkel et al. 1991).

Increased salinity can affect plant growth in several ways: imposition of water stress through increased osmotic potential for the rooting substrate; the accumulation in the soil of ions or other chemicals toxic to plants; and the accumulation of ions in plant tissue (Howard and Mendelsohn 1998). Studies with freshwater marsh plants have found that salinity tolerance depends on factors including the species, the duration of exposure to raised salinity, and the rate of salinity increase (Howard and Mendelsohn 1998, McKee and Mendelsohn 1989). The Howard and Mendelsohn study used four species common to oligohaline marshes in the Gulf of

Mexico (*Eleocharis palustris*, *Panicum hemitomon*, *Sagittaria lancifolia*, *Scirpus americanus*), and exposed each species to varying final salinity levels that were reached in different time periods. The study found that the final salinity level was more important than the rate of time it took to reach the final salinity. The researchers ranked the plants salinity tolerance from least tolerant to most tolerant as *P. hemitomon*, *S. lancifolia*, *E. palustris*, *S. americanus*. The results of the study accurately reflected the occurrence of the species in Gulf of Mexico coastal marshes.

In the lowest salinity level (6 ppt), *S. lancifolia* began experiencing leaf death after 4 weeks, but complete death occurred only at 12 ppt. *P. hemitomon* experienced the largest amount of leaf death, but the response took longer than *S. lancifolia*. Both *E. palustris* and *S. americanus* either continued to acquire biomass at a reduced rate or maintained biomass over time in both salinity treatments. A previous study in a greenhouse with *P. hemitomon*, *S. lancifolia*, and *Leersia oryzoides* found that both *P. hemitomon* and *L. oryzoides* were tolerant of salinities up to almost 10 ppt for at least one month, while *S. lancifolia* was affected by salinity as low as 4.8 ppt (McKee and Mendelsohn 1989).

A study of habitat partitioning and displacement in two species of cattails (*Typha latifolia* and *Typha angustifolia*) in freshwater marsh demonstrated the importance of competition in displacing plant species along an environmental gradient (Grace and Wetzel 1981). The two species naturally separate themselves along a water depth gradient, but when allowed to grow without competition; both species had maximum growth rates at the same depth. *T. angustifolia* was found to be the generalist of the two species; capable of growing in the shallow waters where *T. latifolia* was found. However, *T. latifolia* was the superior competitor, and had a narrower niche. In a follow-up study, Grace and Wetzel (1998) went back to the same pond to determine whether their results could be expanded to the long-term dynamics to this population.

They found that 15 years later, the competitive displacement between the *Typha* taxa remained stable over time. This is one of the few competition studies that went beyond two years of observation.

In an Alaskan salt marsh, Snow and Vince (1984) performed an experiment to examine the response of mature plants to different edaphic conditions including salinity, waterlogging and soil type. The dominant species from each of the five distinctive zones was reciprocally transplanted. The researchers determined that most often, the five species were able to survive and reproduce in other zones, and they showed similar growth preferences in that they all did best at two sites. This study was one of the first to use field experiments to test the hypothesis that abiotic factors were the sole limitation to species zonation.

A well-studied hypothesis is the zonation of species in environmentally stressful areas based on the species ability to tolerate conditions and the zonation of species in the more benign areas based on interspecific competition (Grime 1973, Keddy, 1990, Snow and Vince 1984). An experiment by Bertness et al. (1992) examined why *I. frutescens* naturally occurred only at the terrestrial border of marshes, but not within the flooded zones or the high marsh zones. The results indicated that flooding limited *I. frutescens* from areas of the marsh that experienced prolonged flooding, but that interspecific competition was responsible for preventing its establishment within areas more abiotically suited to it, such as the higher marsh. Previously, Bertness (1991) also showed interspecific competition was responsible for the zonation of the high marsh species *Spartina patens*, *Juncus gerardi*, and *Distichlis spicata* in dense vegetation.

Pennings and Callaway (1992) found that the abrupt zonation of *Salicornia virginica* and *Arthrocnemum subterminalis* was most dependent upon interspecific competition in the relatively benign middle marsh zones, where each species excluded each other from a portion of

the prime habitat. Experimental manipulations of salt marsh vegetation in the field have shown that competition between species can be important in determining natural patterns of zonation (Metcalf et al. 1986, Bertness 1991). The significance of biotic factors is also suggested by the fact that boundaries between marsh vegetation zones are often abrupt, whereas edaphic factors change gradually across the marsh. Also, in some cases the correlation between zonation patterns and edaphic factors is poor (Clarke and Hannon 1967, 1970, Watkinson 1985). A correlation between physical tolerances and plant zonation patterns does not necessarily imply a causal relationship; perturbation experiments are necessary to demonstrate the alleged importance or lack thereof of physical and biotic factors (Silander and Antonovics 1982).

In a series of experiments on an Ohio saltpan, Ungar et al. (1979) transplanted *Salicornia europaea* seedlings to areas representing five communities along a salinity gradient either with or without neighbors. At all sites transplants with no neighbors had considerably higher shoot dry weight production. The reduced growth at uncleared plots was indicative of the importance of interspecific competition in determining the level of plant production as well as species distribution along that particular salinity gradient.

Experiments by Crain, et al. (2004) with the transplant of *Spartina alterniflora* and *Spartina patens* (species typically found in salt marshes) into fresh marshes dominated by *Scirpus robustus* and *Typha angustifolia* resulted in complete suppression of *S. alterniflora* and *S. patens* after two growing seasons but with competitive release in the same zone grew as large or larger than in their natural zone. The mechanisms of competitive exclusion were not explored, but the high aboveground biomass achieved by both species suggests that both species have a light-capturing advantage.

Similar experiments (McIvor and Ungar 1978) with the species *Atriplex triangularis* Willd. had comparable results: the survival rate of transplanted seedlings was higher when they were without neighbors. The seedlings also had more vigorous growth. In a removal experiment within two wetland communities that varied by amount of standing crop, above and belowground competition intensity was examined (Twolan-Strutt and Keddy 1996). In this experiment, it was determined that competition intensity was greater in the high standing crop wetland, although there was no difference in below-ground competitive intensity.

A study by Emery et al. (2001) focused on how resource competition and physical stress interact to determine plant zonation patterns in a salt marsh. The study found that at naturally occurring species borders in two New England marshes, nutrient addition reversed competitive outcomes, with the stress-tolerant species being the best competitor in fertilized treatments. This implies that there is a nutrient-dependent competitive hierarchy in salt marshes in that region. Results of an additional removal experiment using reciprocal transplants with nutrient addition found that competition under normal marsh conditions is principally belowground, but is aboveground at high nutrient levels. Although nutrient additions may affect plant diversity in freshwater tidal marshes, there may be less of a connection between stress tolerant competitive dominance because freshwater tidal marshes generally are not low in nitrogen (Odum 1988, Bowden 1987)

Many coastal marsh zonation studies have been performed in northern climates, particularly in New England. The results of these studies indicating the mechanisms of vegetation zonation patterns have sometimes been generalized to coastal marshes in other geographic areas, but there is evidence that zonation factors may be dependent upon the geography (Pennings, et al. 2005). The Pennings, et al. study suggested that salinity stress is

more important in determining plant zonation in lower latitudes than in higher latitudes where flooding is hypothesized to be the major physical factor limiting plant distributions. In lower latitudes, hotter temperatures and evaporation can cause higher soil salinity than in the water, and these marshes have higher salinity soils than high-latitude marshes.

Studies in greenhouse conditions have shown the importance of competition in structuring plant communities. For example, a study with *Spartina patens*, *Sagittaria lancifolia*, and *Panicum hemitomon*, three common wetland species in the Southeastern United States, found that competition altered community composition equally over the salinity gradient (Greiner La Peyre et al. 2001). Plants were grown under four salinity treatments, in monocultures and in three species mixtures. The three plant species have very different salinity tolerances, but are found in overlapping zones across coastal marsh gradients. As salinity increased, dominance shifted toward the more salt tolerant species, *S. patens*. It was also found that each species had reduced growth compared to monoculture regardless of salinity level. The response of individual species to the salinity gradient was species specific, depending on the tolerance of the particular species. The results supported Grime's theory (1973, 1979) that as abiotic stress increases, competition becomes less of a limiting factor in regulating the abundance of species.

A similar study by Kenkel et al. (1991) with three grasses, *Poa pratensis*, *Hordeum jubatum*, and *Puccinellia nuttalliana*, was conducted under eight salinity levels. When grown in mixture, the three species had differing responses to the salinity level than when grown in monoculture. When grown in monoculture, all three species performed best at zero salinity. However, when grown in mixture, each species has a competitive advantage at different salinity levels. This shift in dominance across the salinity gradient appeared to be similar to the

vegetation assemblages found with these species in the field. The results suggest that there is an inverse relationship between competitive ability and salt tolerance.

Another type of plant interaction not often explored until recently is facilitation. Studies in salt marshes have found that although plant distribution is driven by competition, that secondary succession of disturbance generated bare space within the marsh is often driven by facilitation (Hacker and Bertness 1999). Bare space in the marsh created by floating vegetation deposits, also known as wrack, can become hypersaline due to increased evaporation from lack of shading. These bare spots precluded colonization of *Juncus gerardi* until *Spartina patens* and/or *Distichlis spicata* invaded patches and reduced the salinity. Interestingly, in another experiment with the same three species, Bertness (1991) found that *J. gerardi* dominated both *S. patens* and *D. spicata* in the absence of disturbance. Studies have shown that facilitation is of greater importance in harsher physical environments, while in more amenable environmental conditions; competition is the main driver of plant zonation (Crain 2008, Hacker and Bertness 1999, Hacker and Gaines 1997).

Objective of the Experiment

The competitive interactions of soft-stem bulrush (*Scirpus validus*) and sand spikerush (*Eleocharis montevidensis*) were studied under two different salinity levels in the field from May 2004 to May 2005 in the Savannah National Wildlife Refuge (SNWR). One salinity level was representative of freshwater conditions (under 0.5 ppt), while the other represented oligohaline conditions (between 0.5 and 5.0 ppt). Both species are prevalent within the refuge; but *S. validus* is the only species that is always present throughout the tidal salinity gradient from freshwater to mesohaline marshes, and this gradient alone only partially explains the distributions. For this reason, I initiated a competition study to better explain the distribution of this generalist species,

particularly in the upper reaches of the estuary dominated by both freshwater and oligohaline conditions.

My study will build on previous studies within the SNWR because it is a manipulative rather than an observational study. The other recent manipulative, reciprocal transplant study (Wetzel 2004) focused on the rate of plant community change along the salinity gradient. This study adds to that one by attempting to determine the tipping point between competitive ability and environmental conditions for the species *E. montevidensis* and *S. validus*. In contrast to Latham's (1990) previous manipulative competition study, it is focused only on competitive ability in two salinity levels between the species *S. validus* and *E. montevidensis*.

The previous competition study involved many more species, and was unable to effectively remove belowground competition with the barrier chosen. I used non-destructive sampling methods in my study, and was able to observe the same plants over time to determine the length of time before statistically significant changes occurred. The sampling also showed that the most significant factor in colonization for the two species of interest in the study plots was rhizomal growth, not growth from seedlings.

The question I sought to answer at the conclusion of my experiment was: how do the competitive interactions of *S. validus* and *E. montevidensis* change, if at all, based on freshwater or oligohaline conditions? Based on previous studies, at the initiation of my experiment, it was expected that *S. validus* would outcompete *E. montevidensis* in the oligohaline conditions because it is a generalist with a greater salinity tolerance. I predicted that in the oligohaline treatments, *S. validus* would maintain similar numbers from the baseline count in treatments in which competition between the two species was allowed. I also predicted that *S. validus* would be able to invade plots of *E. montevidensis* more quickly in the oligohaline. I predicted the

opposite result in the freshwater tidal site: that *E. montevidensis* would be a stronger competitor in freshwater conditions, and there would be a greater number of stems in treatments within that site.

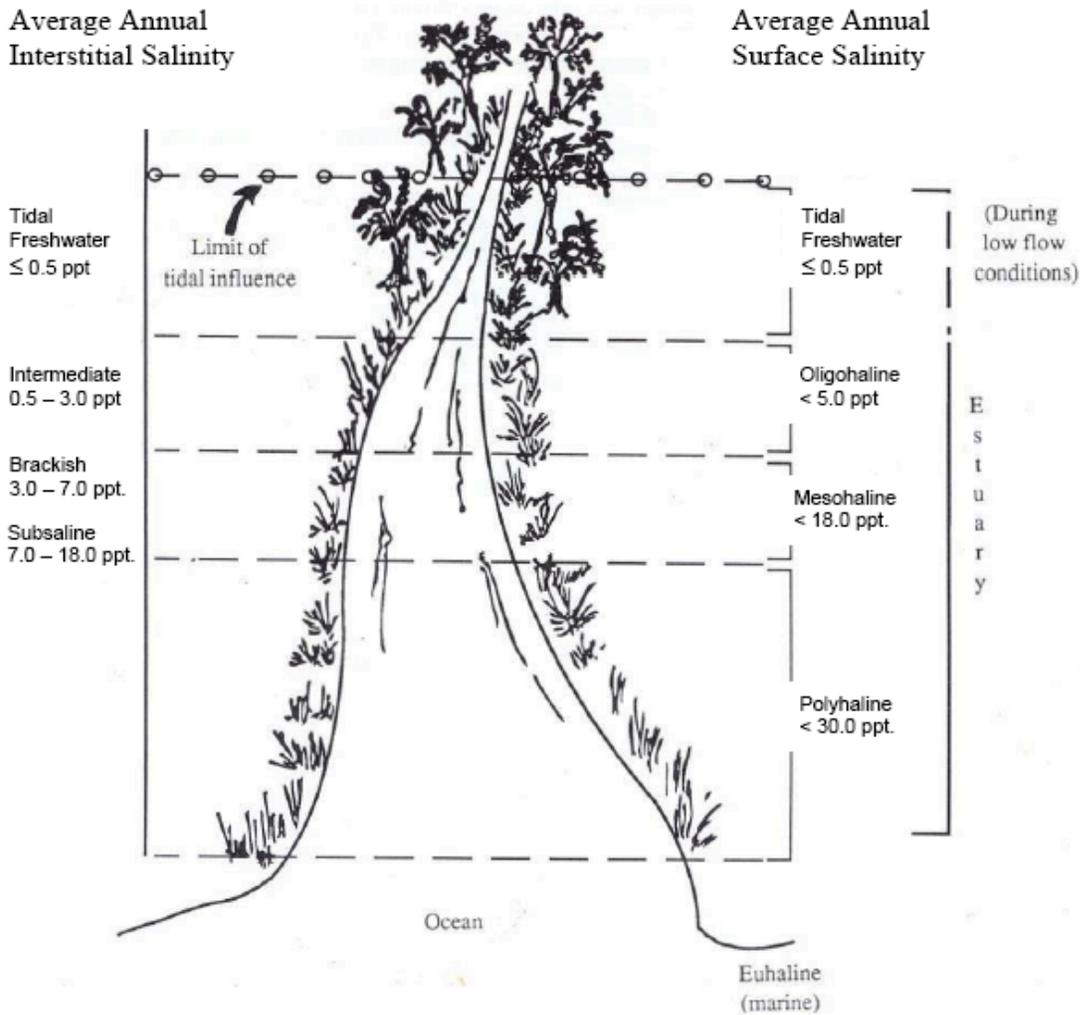


Figure 1-1. Marsh types present in a tidal river system, classified by interstitial salinity (Pearlstine et al., 1990) and surface salinity (Cowardin et al., 1979) (modified from Odum et al., 1984 by Dusek, 2003). [Reprinted with permission from Dusek, M. L. 2003. Multi-scale and spatial and temporal change in the tidal marshes of the Lower Savannah River Delta. Master's thesis (Page 8, Figure 1-1). University of Florida, Gainesville, Florida.]

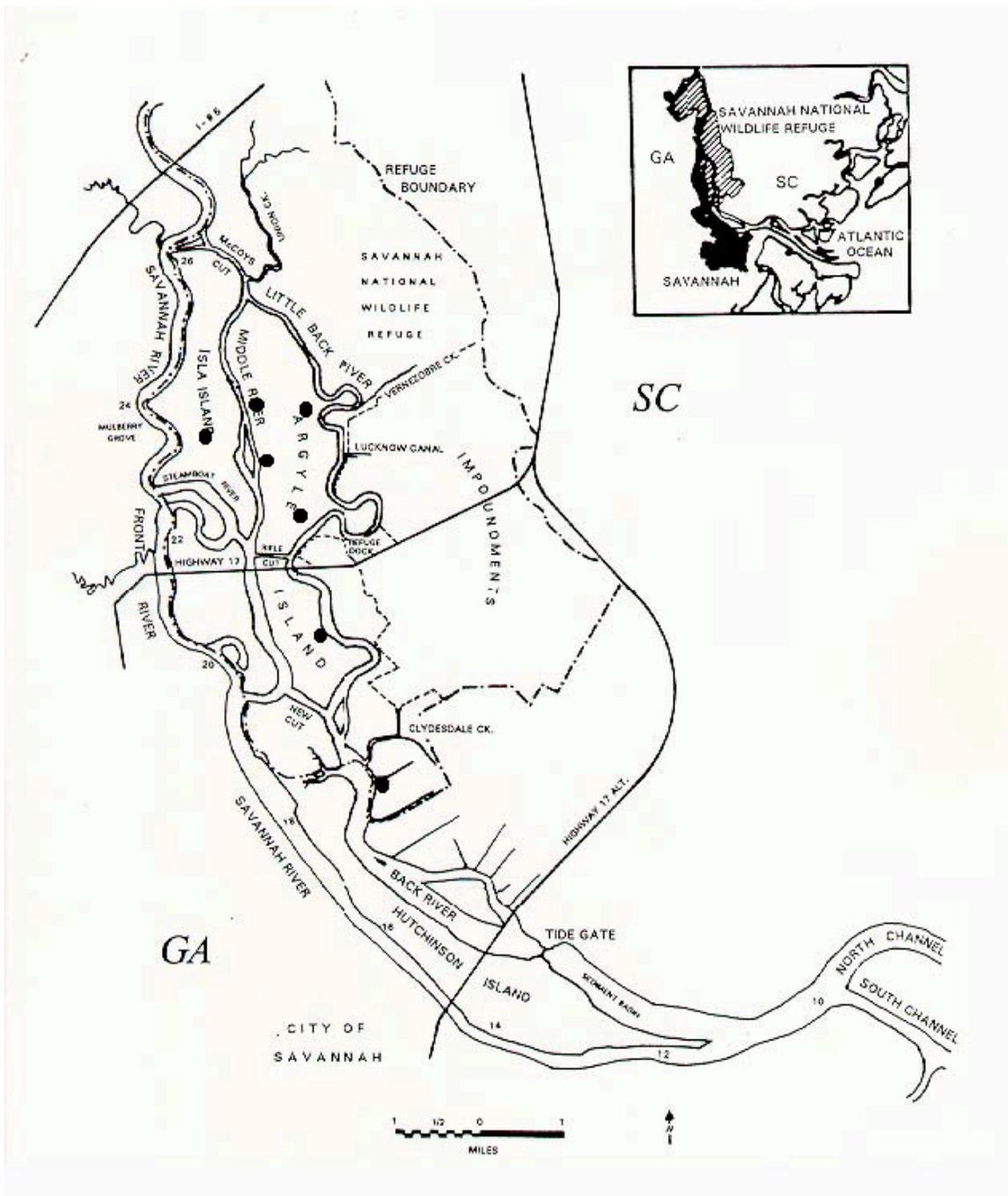


Figure 1-2. Locations of areas used in previous vegetation studies along the lower Savannah River. Black dots identify 7 sites utilized by Dusek (2003) and Latham (1990). [Reprinted with permission from Dusek, M. L. 2003. Multi-scale and spatial and temporal change in the tidal marshes of the Lower Savannah River Delta. Master's thesis (Page 14, Figure 2-1). University of Florida, Gainesville, Florida.]

CHAPTER 2 MATERIALS AND METHODS

Study Sites

The area of interest along the lower Savannah River was the subject of an on-going community analysis study beginning in the 1980s (Latham 1990, Dusek 2001). Two sites on the Back River were chosen to represent two differing salinity levels: tidal fresh and oligohaline conditions (Figure 2-1). Interstitial salinity at the tidal fresh site ranged from 0.2 to 0.8 ppt, while the oligohaline site ranged from 0.8 to 1.5 ppt (Figure 2-2). The tidal fresh site is located at the end of a small tidal creek that is perpendicular to the main river channel. The site is dominated by *Zizaniopsis milacea* and *Polygonum hydropiperoides* closest to the creek, and *Typha* spp., *Eleocharis* spp., *Aster elliotii*, *Scirpus validus*, and *Sagittaria* spp. are common farther from the creek. The substrate is quite unconsolidated, and becomes less consolidated the farther one proceeds from the creek into the high marsh. There are many areas of floating marsh (pers. obs.). Dusek (2001) found that the soil bulk density was 0.14 g/cm³, while the organic content was 49%.

Several miles downstream, the oligohaline site is a much more consolidated site, with no floating marsh (pers. obs.). The study area is located approximately halfway down a creek that runs perpendicular from the river channel. The soil bulk density as tested was 0.19 g/cm³ with an organic content of 39% (Dusek 2001). In the local area of interest, most of the species diversity is closest to the creek (pers. obs.). Common species include *Eleocharis* spp., *Aster* spp., *Ludwigia* spp., and *Bidens laevis*, while farther from the creek it is typical that only *Typha* spp., *Z. milacea* and *S. validus* are present (pers. obs.).

Species of Interest

Eleocharis

The genus *Eleocharis*, a member of the family Cyperaceae, commonly referred to as the sedge family, contains 90 genera and 4,000 species. *Eleocharis* are most commonly named spikerushes or club rushes (Horsburg 1995). The species resides in both aquatic and semi-aquatic habitats, and are found in salt marshes, bogs, ditchbanks and the shallow water regions along pond and lake margins (Odum et al. 1984, Horsburgh 1995). The genus *Eleocharis* characteristically has photosynthetic stems and therefore lacks leaves. Species of *Eleocharis* can be either annual or perennial (Tobe et al. 1998), and most have spikelets that are solitary and terminal (Ward and Leigh 1975). *Eleocharis* has been found to range from the tropics to the polar regions of both hemispheres (Horsburgh 1995).

Eleocharis montevidensis, also known as the sand spikerush, is a perennial species that has noticeable slender reddish rhizomes. The culm is wiry and up to 40 cm tall, with reddish leaf sheaths (Horsburgh 1995). The species is found in tidal and brackish waters, freshwater marshes, swamps and flatwoods depressions of the Coastal Plain region, extending from South Carolina to Florida, and west to California and Central and South America (Horsburgh 1995, Ward and Leigh 1975). The species spreads extensively by means of rootstocks (Ward and Leigh 1975) and forms dense mats (Horsburgh 1995).

Scirpus

Scirpus, found in the family Cyperaceae, and commonly referred to as bulrush, is a genus of approximately sedge with a cosmopolitan distribution, growing in wetlands and moist soils. Some species specialize in saline, marshy environments such as intertidal mudflats, while others are found in freshwater ponds or lakesides and riverbeds (Tobe et al. 1998). The plants are either annual or perennial, growing in tufts or large colonies. The stems are either sharply 3-angled or

slightly rounded and softly angled. The plants generally have grass-like leaves, but are reduced to bladeless sheaths in some species, and clusters of small spikelets that are often brown in color (Tobe et al. 1998).

Scirpus validus is a perennial species with a rapid rhizomatous growth form. The plant grows to approximately 2.5 m, with a rounded stem up to 1 in wide at the base, and gradually tapering upward. There are no leaf blades, only sheaths, and the inflorescences are found at the stem tip, with hanging clusters of spikelets. The species' range extends from Newfoundland to Alaska, south to Florida and California; Mexico; the West Indies, and South America (Beal 1986). It has a low tolerance to both shade and salinity. Studies have found that the plants phenotype responded to environmental factors, and suggested that there is a selection of genotypes along a salinity gradient (Beal 1986). A previous study posited that the assemblage of features in a population of plants was more related to local environmental factors than due to genetic differences (Arnold and Beal 1981).

Methods

Site Selection

Sites were chosen based on proximity to already-existing electronic salinity monitoring devices. These YSI 600 XLM Environmental Monitoring Systems were installed in stilling wells approximately 70 m along a 100 m transect perpendicular to tidal canals. The monitor recorded interstitial salinity every 15 minutes. At each site, four rows of each treatment were set up on both sides of the YSI meter (total of 8 replicates), starting approximately 32.5 m away, and then spaced every 10 m thereafter. Rows were separated by 5 m (Figure 2-3).

Initial Plot Creation and Donor Sites

Due to the decision to specifically study *E. montevidensis* and *S. validus* it was necessary to locate areas where these species were prevalent. Beginning in November 2004, a search of the

frequently sampled areas in the Savannah National Wildlife Refuge (SNWR) was performed to find ideal donor sites. This was actually much more difficult to locate than it was at first perceived to be. The ideal areas would consist of only one or the other species. Because these are field conditions, it was challenging to conform to this high standard. Another factor increasing the difficulty was the season, because at this time most of the plants were already senesced, making it difficult to determine if there were other species that would grow back in the spring.

A donor site for *S. validus* was readily found at the oligohaline site, which was almost completely monospecific. The only other species present in small amounts in this area was *Sagittaria* species (either *S. lancifolia* or *S. latifolia*). Locating an area that was nearly monospecific *E. montevidensis* proved to be much more difficult. This species tends to grow in the company of many other species of plants, and it is common to find over 20 species within only 0.25 m² where this species is present (pers. obs.). A donor site was selected that was farther upstream than the recipient sites, as higher densities of *E. montevidensis* are found in fresher areas. At the time of the transplant, there was very little growth of species other than *E. montevidensis*, however, as the growing season progressed, more species became apparent.

In January 2004, sod-like blocks of 0.125 m x 0.125 m plots, approximately 15 cm deep were collected from donor sites and transplanted to recipient marsh sites. These blocks were used to create four types of larger experimental units (0.375 m x 0.625 m): *E. montevidensis* surrounded by *Scirpus validus*; *Scirpus validus* surrounded by *E. montevidensis*; *E. montevidensis* surrounded by *E. montevidensis*; and *Scirpus validus* surrounded by *Scirpus validus* (Figures 2-4, 2-5, 2-6, and 2-7). Each (8 replicates) had two interior blocks (0.125 m x 0.125 m), one with a buried PVC liner to approximately 30 cm deep to inhibit belowground

competition and one without. The experimental units were protected from invasion by surrounding vegetation by a thick plastic liner buried to a depth of at least 15 cm.

Sampling

After the initial transplant was completed, stems were counted and identified bi-monthly beginning in May 2004 for the growing season. The initial sample was to provide a baseline stem count for the species as the transplants acclimated. Subsequent samples were taken in July and September 2004, and a final sample in May 2005. The two interior blocks of each experimental unit were divided into quarters, leaving a sampling area of 0.0625 m x 0.0625 m for ease of sampling. Each quarter was assigned a number between 1 and 4 (moving clockwise from the top left of the square) and then a number was randomly chosen to sample. After the sampling area was selected, all species were identified, and stems were counted for every plant within this area. If a species other than the two species studied were found that had the potential to become so large it would take over the sampling area (e.g. *Zizaniopsis*, *Typha*, etc.), the stem was cut and removed at the time of sampling.

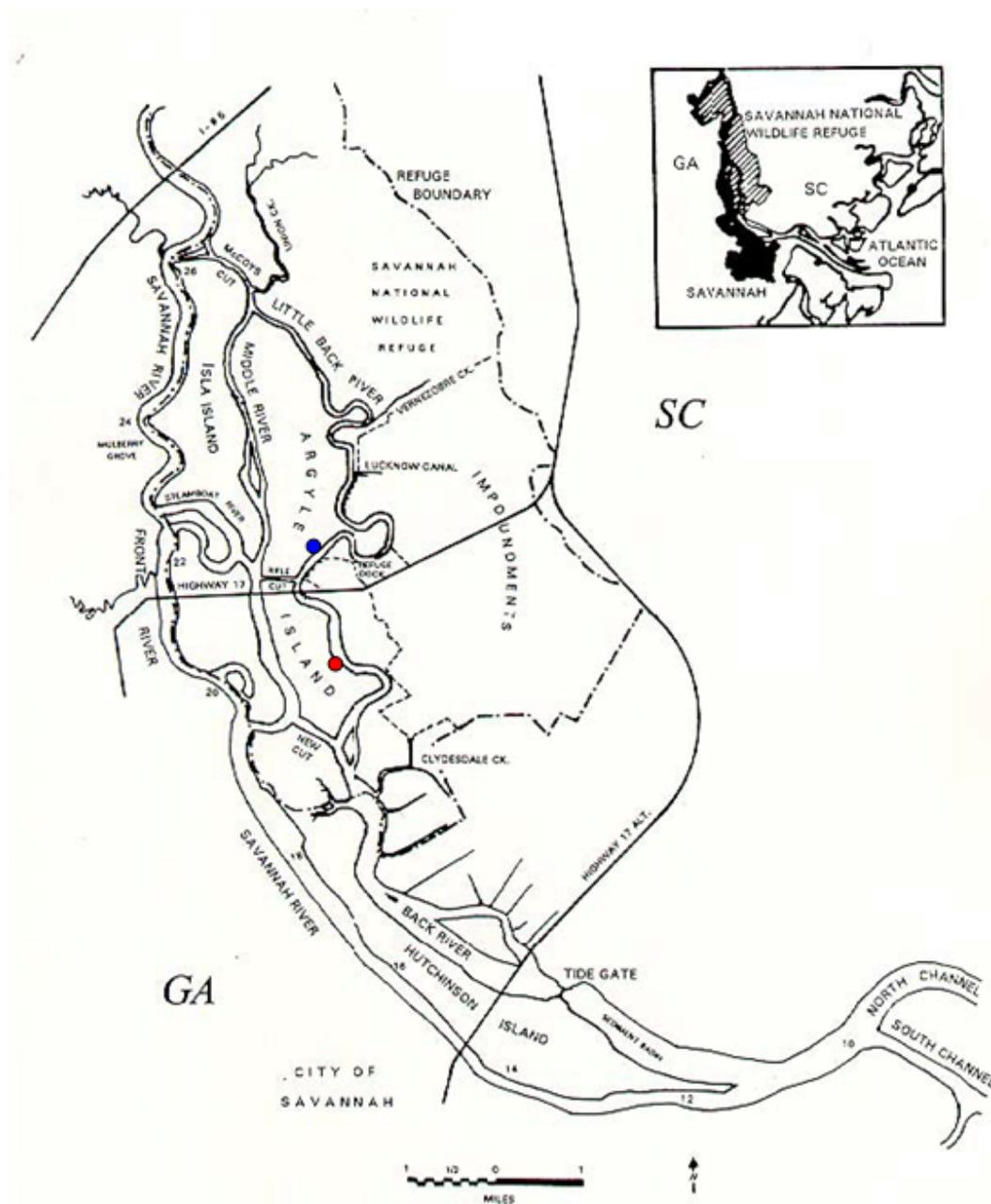


Figure 2-1. Location of the study sites along the lower Savannah River. The blue dot indicates the tidal fresh site, and the red dot indicates the oligohaline site. [Reprinted with permission from Dusek, M. L. 2003. Multi-scale and spatial and temporal change in the tidal marshes of the Lower Savannah River Delta. Master's thesis (Page 14, Figure 2-1). University of Florida, Gainesville, Florida.]

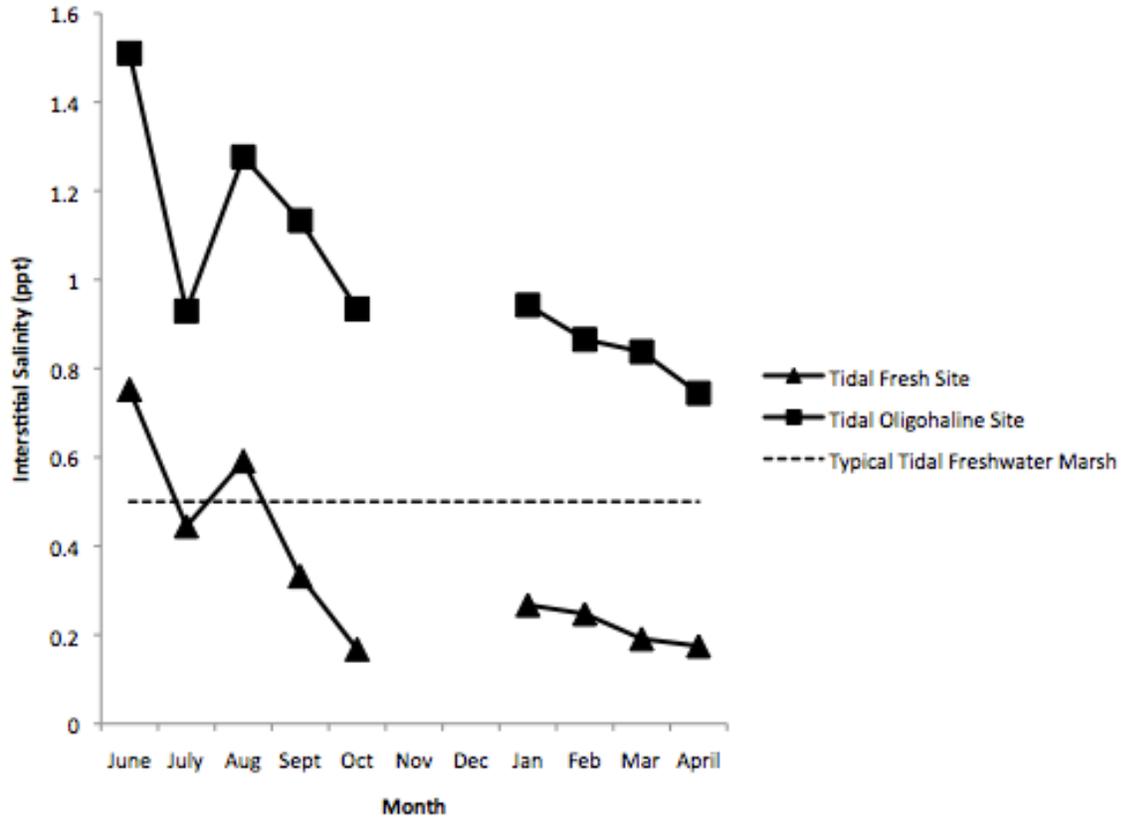


Figure 2-2. Monthly interstitial salinity at the tidal fresh and oligohaline sites from June 2004 to April 2005.

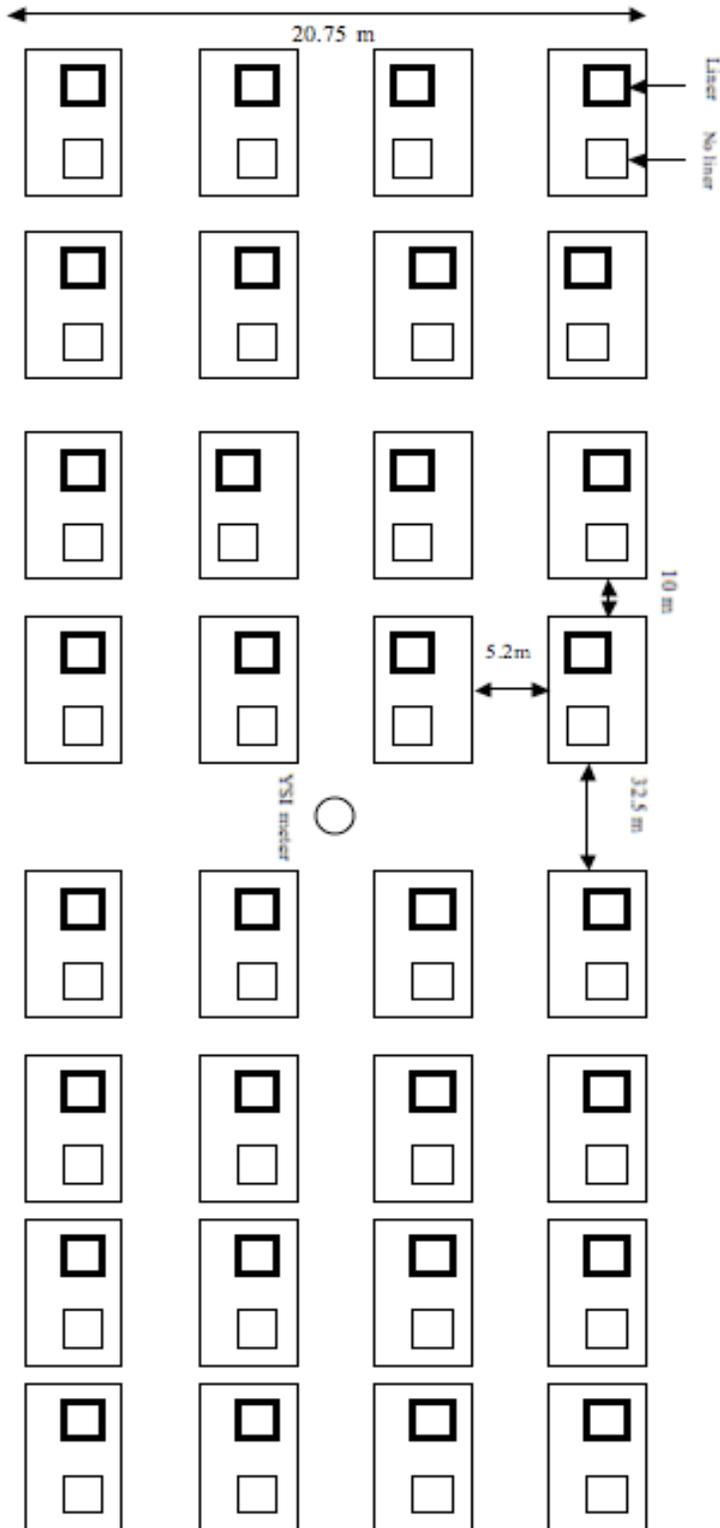
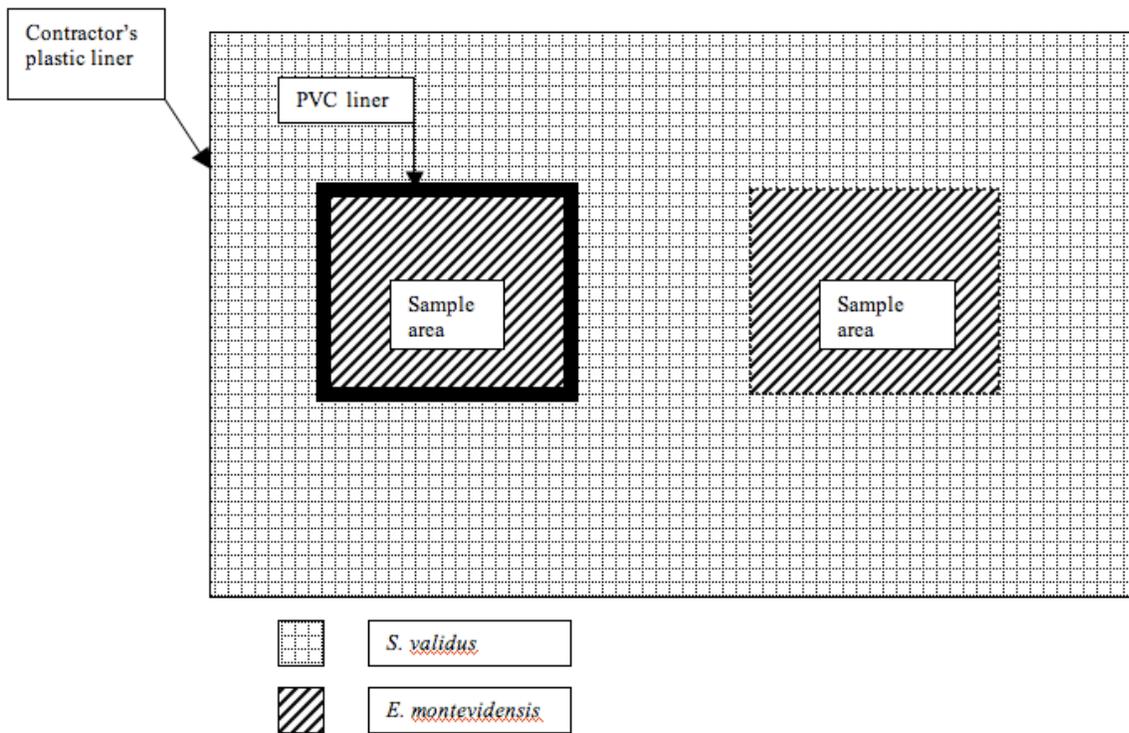


Figure 2-3. Schematic drawing of experimental set up. Blocks contained either *E. montevicensis* surrounded by *S. validus*, *S. validus* surrounded by *E. montevicensis*, or a control plot consisting of the same species. The design was the same at each site. Drawing is not to scale



A

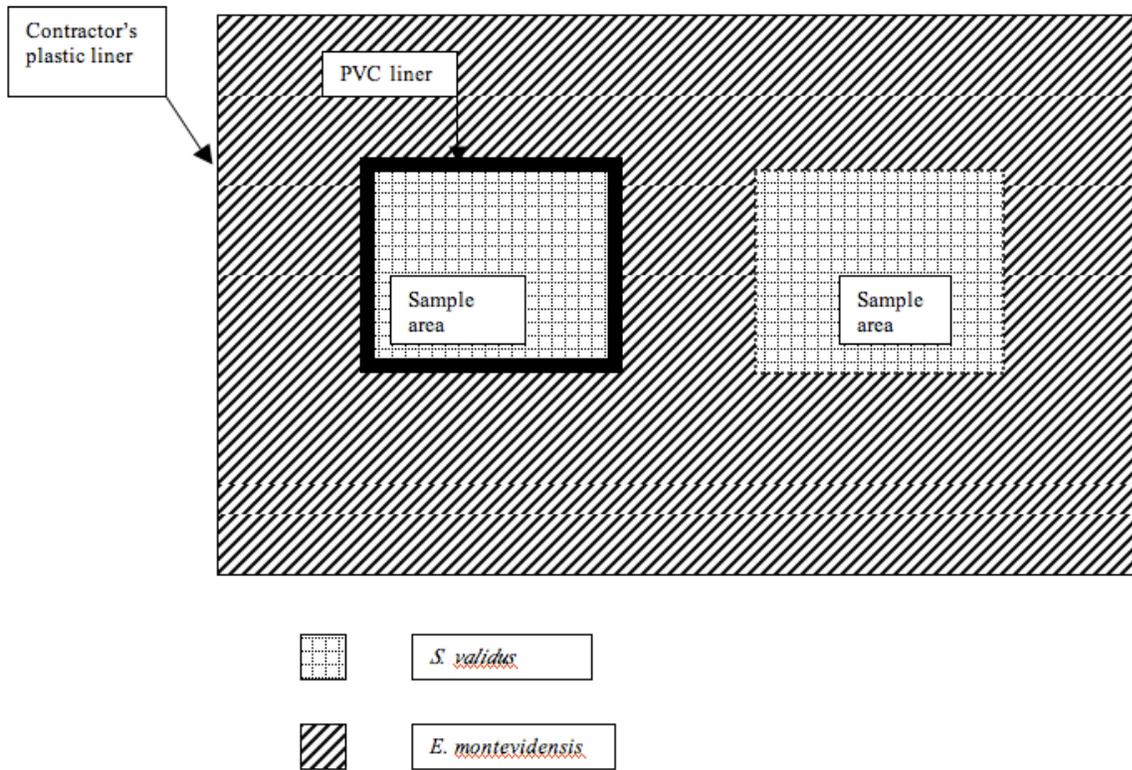


B

Figure 2-4. Experimental unit consisting of *E. montevidensis* surrounded by *S. validus*. A. Photograph taken at the oligohaline site in May 2004. B. Schematic representation of experimental unit.



A



B

Figure 2-5. Experimental unit consisting of *S. validus* surrounded by *E. montevidensis*. A. Photograph taken at the tidal fresh site in May 2004. B. Schematic representation of experimental unit.

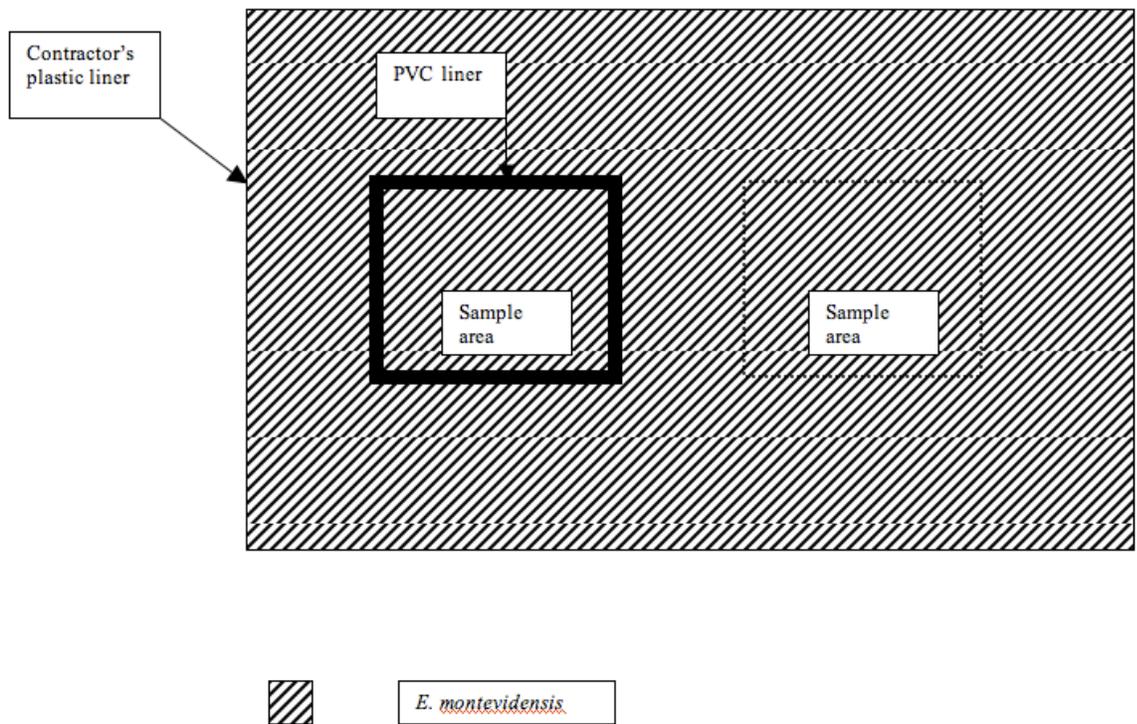
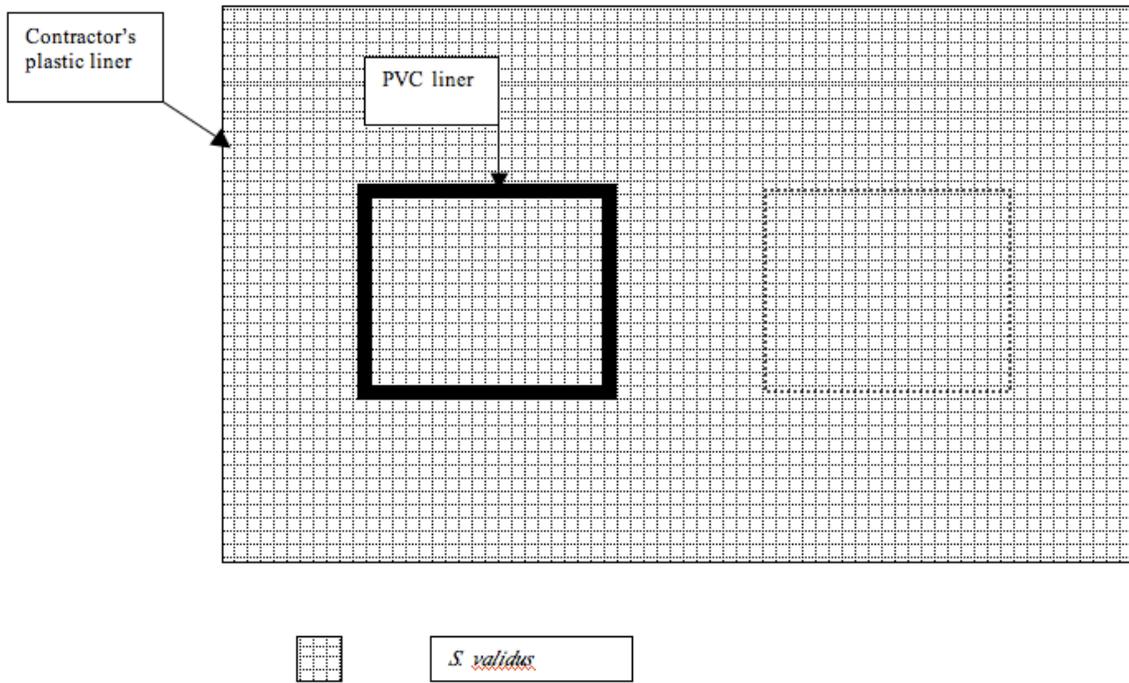


Figure 2-6. Experimental unit consisting of *E. montevidensis* surrounded by *E. montevidensis*.
 A. Photograph taken at the tidal fresh site in May 2004. B. Schematic representation of experimental unit.



A



B

Figure 2-7. Experimental unit consisting of *S. validus* surrounded by *S. validus*. A. Photograph taken at the tidal fresh site in May 2004. B. Schematic representation of experimental unit.

CHAPTER 3 RESULTS

Salinity Data

Monthly salinity measurements were analyzed using a repeated one-way analysis of variance (ANOVA) (SPSS 11.0, Chicago, IL, 2002). Salinities between sites were first compared by month from June 2004 – September 2004, and December 2004 – March 2005 (See Figure 2-2), and determined to be significantly different during each month ($p < 0.0000$ for each date). Due to a malfunction of the XLM 600 Environmental Monitoring Systems at both sites, salinity for the months of November and December 2004 was not available and therefore not used in the analysis. Salinity at the tidal fresh site averaged 0.35 ppt, while the average salinity at oligohaline site was 1.02 ppt, a significant difference ($p < 0.00$). Throughout the entire study period, the salinity at the tidal fresh site remained lower than at the oligohaline site.

Vegetation Data

Vegetation data were analyzed using general linear modeling (GLM) to test for competitive effects, salinity effects, as well as differences over time using SAS statistical package (SAS Version 8, Cary, NC, 2000). Data for the treatments *E. montevidensis* surrounded by *S. validus* and *S. validus* surrounded by *E. montevidensis* were analyzed using logistic regression with presence/absence data due to the large number of zeros present, which complicated many other test results.

Finally, relative percent change (RC) in average number of stems for the two non-control treatments was calculated. Relative percent change was calculated using the formula

$$\text{Relative percent change} = \frac{(\text{New Value} + 1) - (\text{Reference Value} + 1)}{(\text{Reference Value} + 1)} \times 100$$

In the RC calculations, the reference value used was the average stem count from the first sample date (May 2004). However, in some cases the first reference value was zero, which makes the RC calculation impossible. In order to standardize the RC calculation, one stem was added to every monthly average count.

***E. montevidensis* and *S. validus* Control Plots**

The PVC liner was used as a means of preventing belowground competition, and it was necessary to determine if the use of the liner would have any other unforeseen effects, such as causing disproportionate numbers of stems in either of the treatments. Therefore, controls consisting of *E. montevidensis* surrounded by *E. montevidensis* and *S. validus* surrounded by *S. validus*, both with and without liners, were used to avoid cross species interactions.

***E. montevidensis* control plots**

General linear modeling was performed to test for time and salinity effects in *E. montevidensis* stem counts in the *E. montevidensis* control plots. For all four sampling dates, there were no significant differences due to the use of the liner. However, during all but the first sampling period, there were significant differences due to salinity. During the remaining sample dates, the stem counts were significantly greater at the oligohaline site. Peak stem counts occurred in July at the oligohaline site, and were especially pronounced, while average stem counts remained more stable at the tidal fresh site (Figures 3-1 and 3-2). When comparing average stem counts between salinities, the average stem count was always greater at the oligohaline site.

***S. validus* control plots**

Again using general linear modeling, no significant differences were found in *S. validus* control plots between treatments with or without a liner at either salinity level. Although the *S. validus* stem counts were not significantly different, in all but two occurrences (tidal fresh site,

May 2004 and oligohaline site, September 2004) there were higher average stem counts of *S. validus* in treatments with the liner compared to those without (Figures 3-3 and 3-4). The lowest average stem counts occurred in September 2004 at both salinities. Average stem counts also tended to be higher at the oligohaline site.

E. montevidensis* Surrounded By *S. validus

At both salinity levels, no significant difference in *E. montevidensis* stem counts between treatments with and without competitive exclusion was found using general linear modeling, which corresponds to the results with the *E. montevidensis* control. Salinity was found to be insignificant except for July 2004. Stem counts were much higher at the oligohaline site than the tidal fresh site during that month. Average stem counts appeared to follow the same seasonal patterns for both sites, with a pronounced peak in July 2004 at the oligohaline site (Figure 3-5), and a much flatter seasonal change at the tidal fresh site (Figure 3-6).

The average number of *S. validus* stems differed based on whether competition was allowed between species, which was expected. Over time, *S. validus* began appearing in very small numbers in treatments where belowground competition was allowed, while it was effectively excluded from treatments with liners. Using GLM, significant differences were found in September 2004 in treatments with and without competition, as well as significant salinity differences, with significantly more stems found in the oligohaline site. Also, in May 2005, there was a significant difference in treatments with and without competition. Logistic regression showed that there was both a significant effect between treatments with and without competition on the number of *S. validus* stems ($p = 0.0003$), and an effect from the salinity ($p = 0.0194$). According to the model, it was 5.7 times more likely to find *S. validus* stems in treatments allowing interspecific competition, and 0.345 times more likely to find it in the oligohaline site.

Relative percent change (RC) calculations performed for the tidal freshwater site showed increases in average stem counts of *E. montevidensis* during each sample, in both plots with and without interspecific competition allowed (Figure 3-7). In plots with no interspecific competition, the increases were greater and ranged from a 41% increase in July 2004 and a total of 22% increase after a year. The plot that allowed interspecific competition increased approximately 13% after one year. *S. validus* had positive relative percent change only in plots of *E. montevidensis* with competition allowed. By the final sample period it increased approximately 357%.

At the oligohaline site in the plot allowing competition, there was a relative increase of 175% of average number of *E. montevidensis* stems in the July 2004 sample, which continued to decrease until the stem count was approximately the same as the first sample (Figure 3-8). In the plot without competition, there was a smaller RC during the July 2004 sample, which decreased to approximately the same count as May 2004. *S. validus* counts in plots with competition had a relative increase of 100% in the September 2004 sample, and 390% by the final sample.

S. validus* Surrounded By *E. montevidensis

Significant differences were found using GLM in number of *S. validus* stems in the September 2004 and May 2005 samples at both sites with and without competition. Significantly greater numbers of *S. validus* stems were found within the plot that did not allow interspecific competition. In every occasion except one (May 2004, tidal freshwater site), the average number of *S. validus* stems was higher within treatments with no interspecific competition (Figures 3-9 and 3-10). This pattern also corresponds to the control plot averages, however this was only an observed trend in average number of stems, and not a statistically significant difference. Additionally, there were salinity effects in the September 2004 sample.

During this sample date, there were significantly greater numbers of stems in the tidal fresh site. All other differences in *S. validus* stems were insignificant.

Stem counts of *E. montevidensis* at both sites began increasing in treatments with interspecific competition allowed in July 2004 (Figures 3-9 and 3-10). Differences in stem counts with and without interspecific competition were significant in July 2004, September 2004, and May 2005. In both sites, as stem counts of *E. montevidensis* increased over time, there was a similar decrease in stems of *S. validus*. There were no significant differences based on salinity.

Logistic regression utilizing presence/absence data for the *E. montevidensis* stem counts showed that the liner was effective in preventing interspecific belowground competition. Rhizomes were unable to penetrate the liner ($p = 0.0001$), and no significant salinity effect was found. The regression showed that it was 83.11 times more likely to find *E. montevidensis* in the treatment with interspecific competition allowed than in the treatment without.

Relative percent change calculations (RC) within the tidal fresh site confirm the increase of *E. montevidensis* stems with the corresponding decrease of *S. validus* stems within the plot with competition allowed (Figure 3-11). By the end of the study, *S. validus* stems had decreased almost 40%, while stems of *E. montevidensis* had increased over 1400%. Stems of *S. validus* in plots without interspecific competitive interactions actually increased 16% by the end of the study.

In the oligohaline site, *E. montevidensis* increased 2400% by the conclusion of the study (Figure 3-12). Stems of *S. validus* decreased in plots with competition 60% by the final sample date, and 7% in plots without competition allowed. The correlation is not quite as clear at the oligohaline site as the tidal fresh site between increase of *E. montevidensis* and decrease of *S. validus* because average stem counts of *S. validus* decreased in plots without competition

allowed also, although *S. validus* did experience a greater negative RC in that site over the sample period.

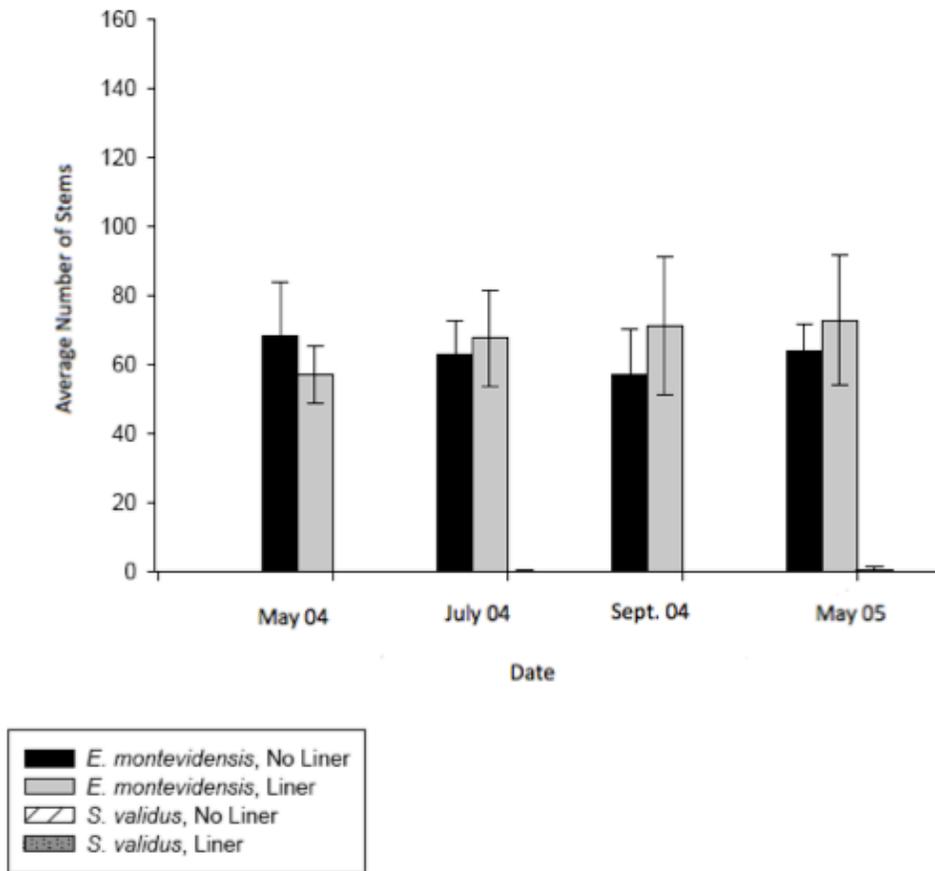


Figure 3-1. Tidal Fresh Site: *E. montevidensis* surrounded by *E. montevidensis*.

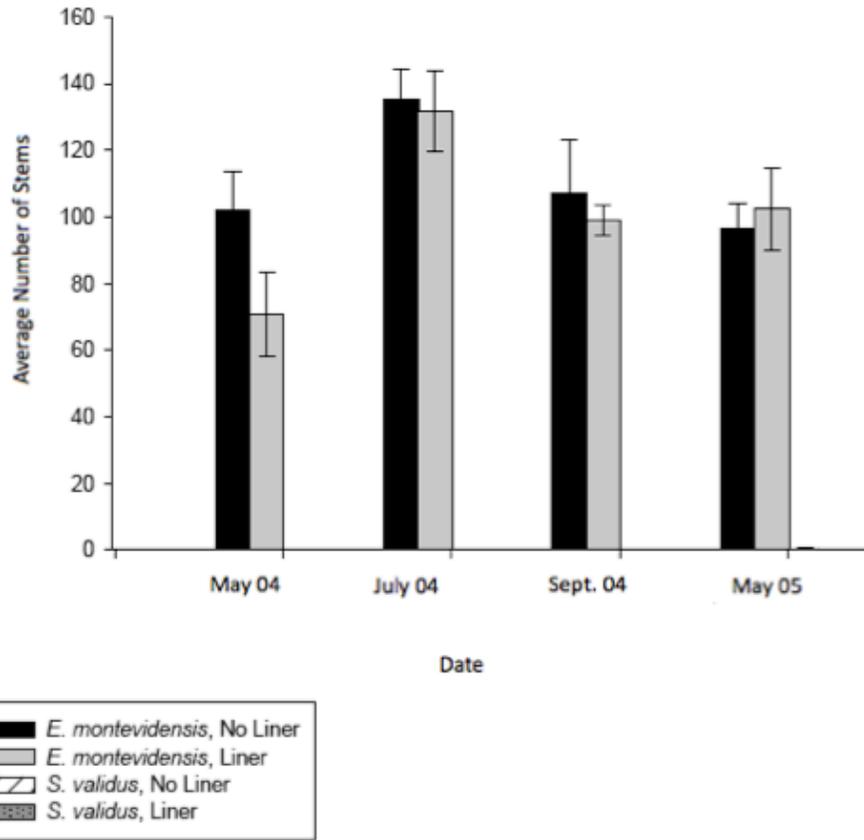


Figure 3-2. Oligohaline Site: *E. montevidensis* surrounded by *E. montevidensis*.

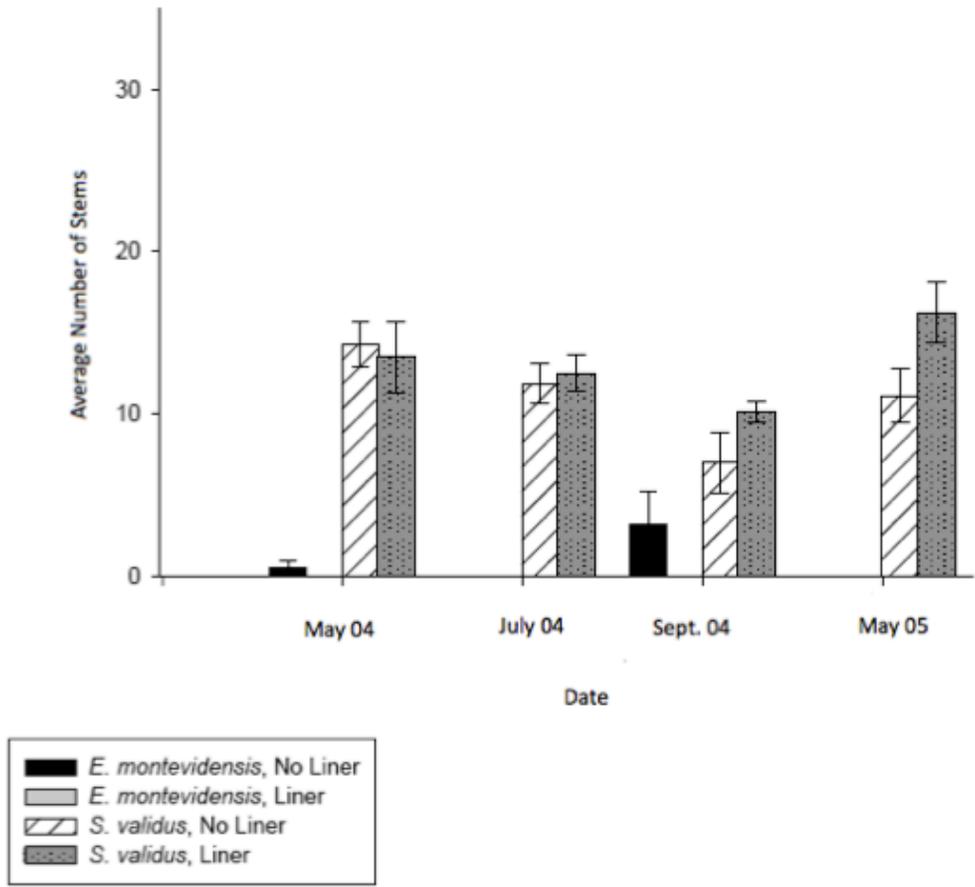


Figure 3-3. Tidal Fresh Site: *S. validus* surrounded by *S. validus*.

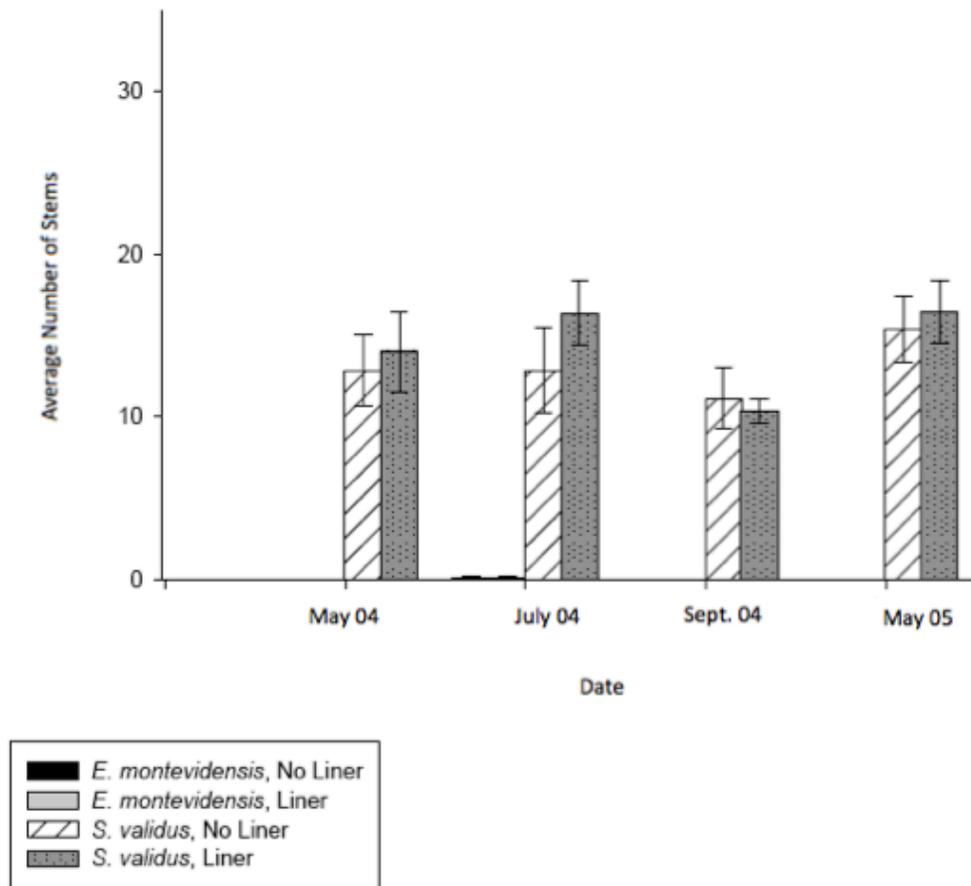


Figure 3-4. Oligohaline Site: *S. validus* surrounded by *S. validus*.

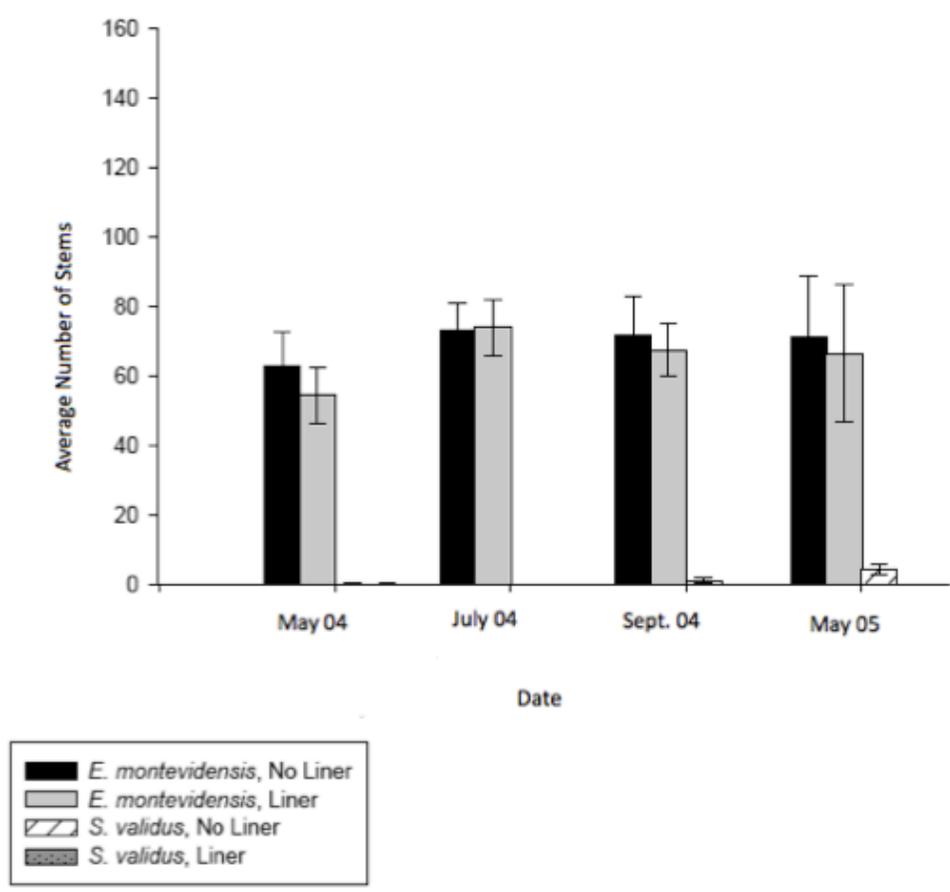


Figure 3-5. Tidal Fresh Site: *E. montevidensis* surrounded by *S. validus*.

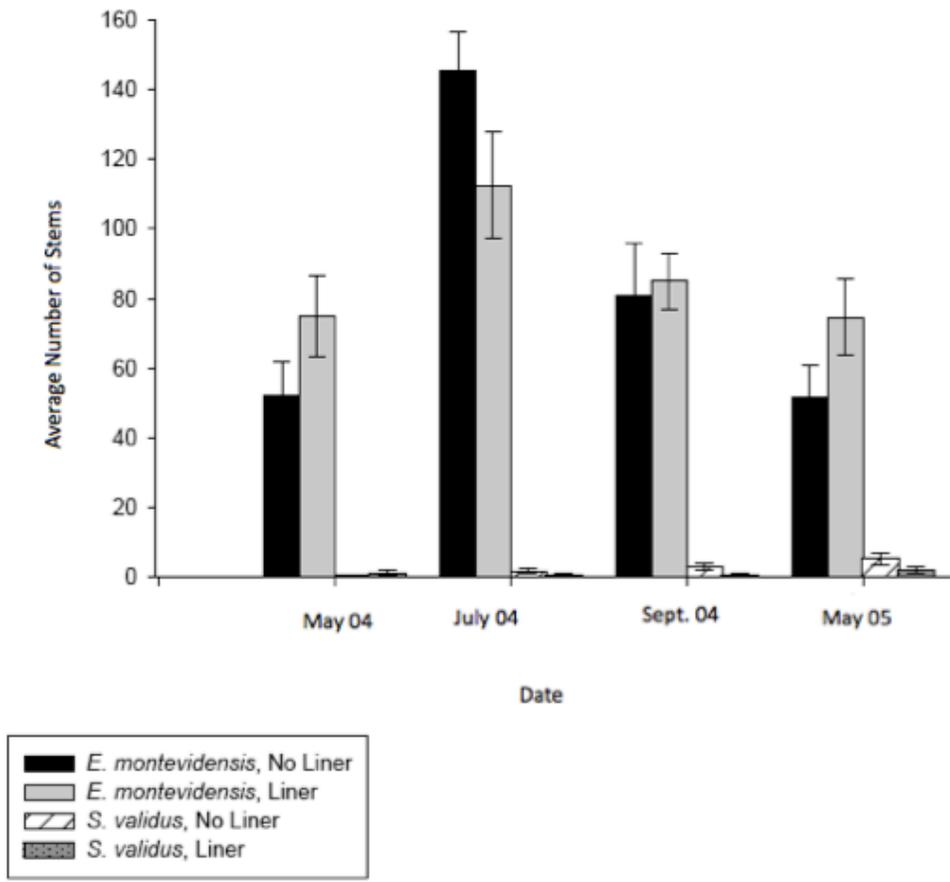


Figure 3-6. Oligohaline Site: *E. montevidensis* surrounded by *S. validus*.

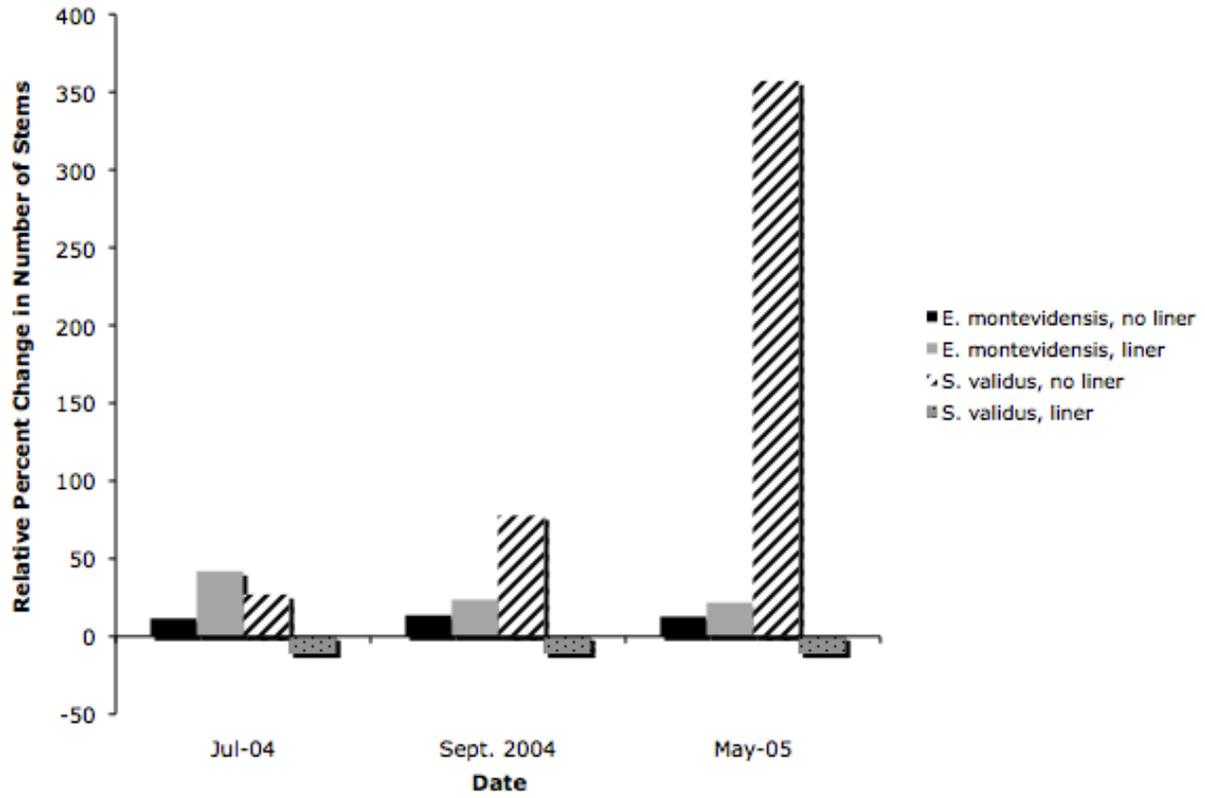


Figure 3-7. Tidal Fresh Site: Relative percent change (RC) in number of stems over time in treatment *E. montevidensis* surrounded by *S. validus*.

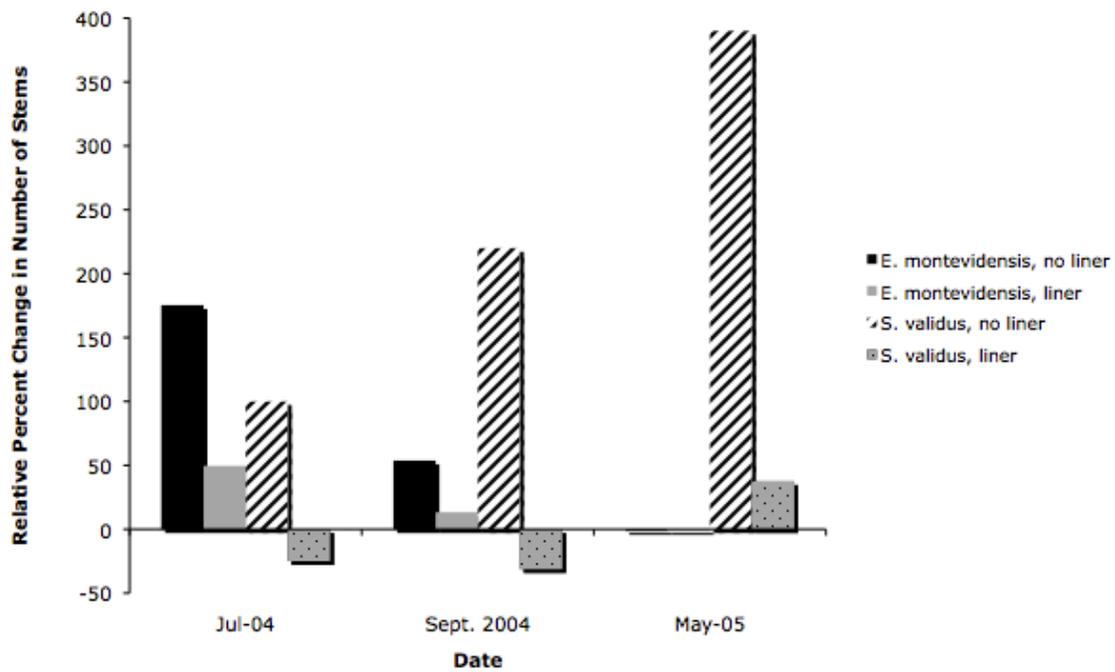


Figure 3-8. Oligohaline Site: Relative percent change (RC) over time in treatment *E. montevidensis* surrounded by *S. validus*.

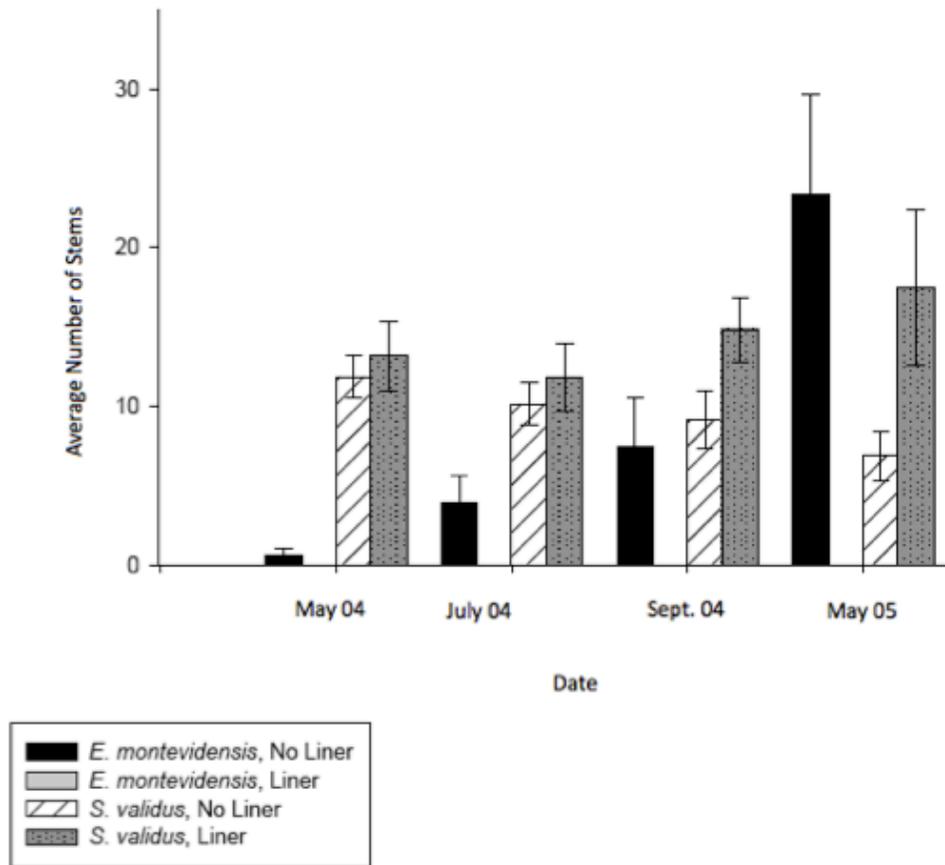


Figure 3-9. Tidal Fresh Site: *S. validus* surrounded by *E. montevidensis*.

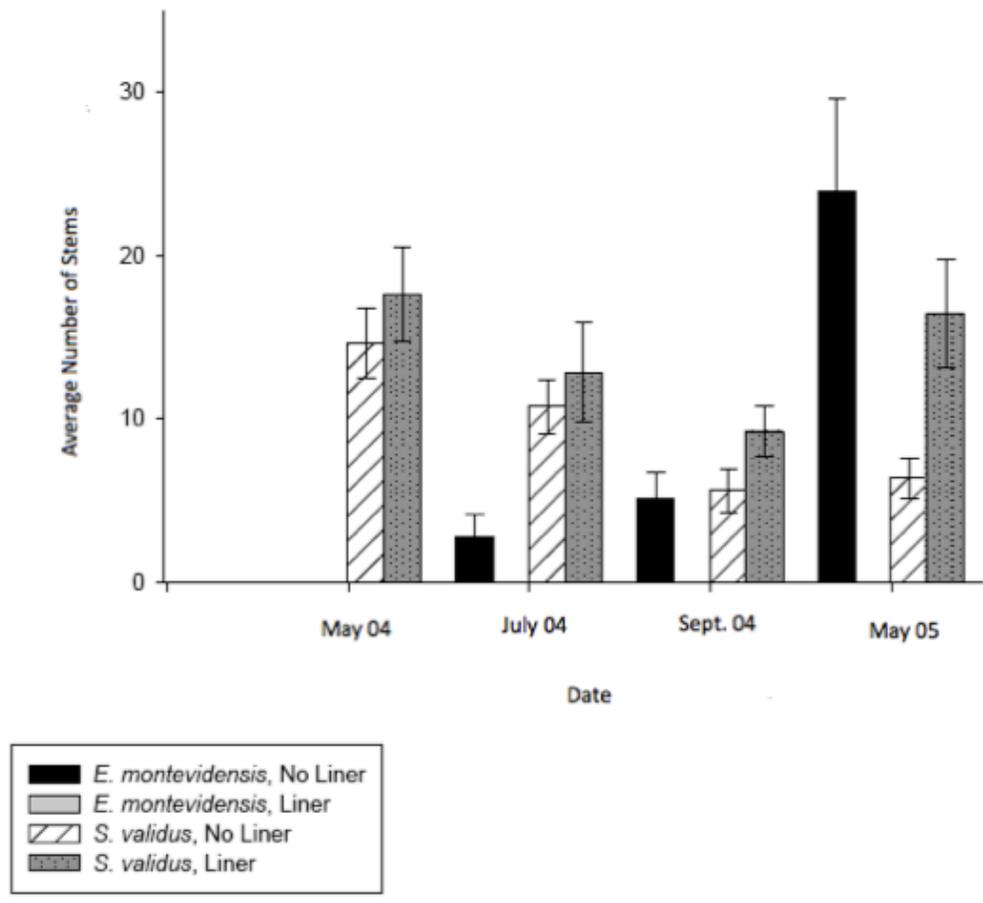


Figure 3-10. Oligohaline Site: *S. validus* surrounded by *E. montevidensis*.

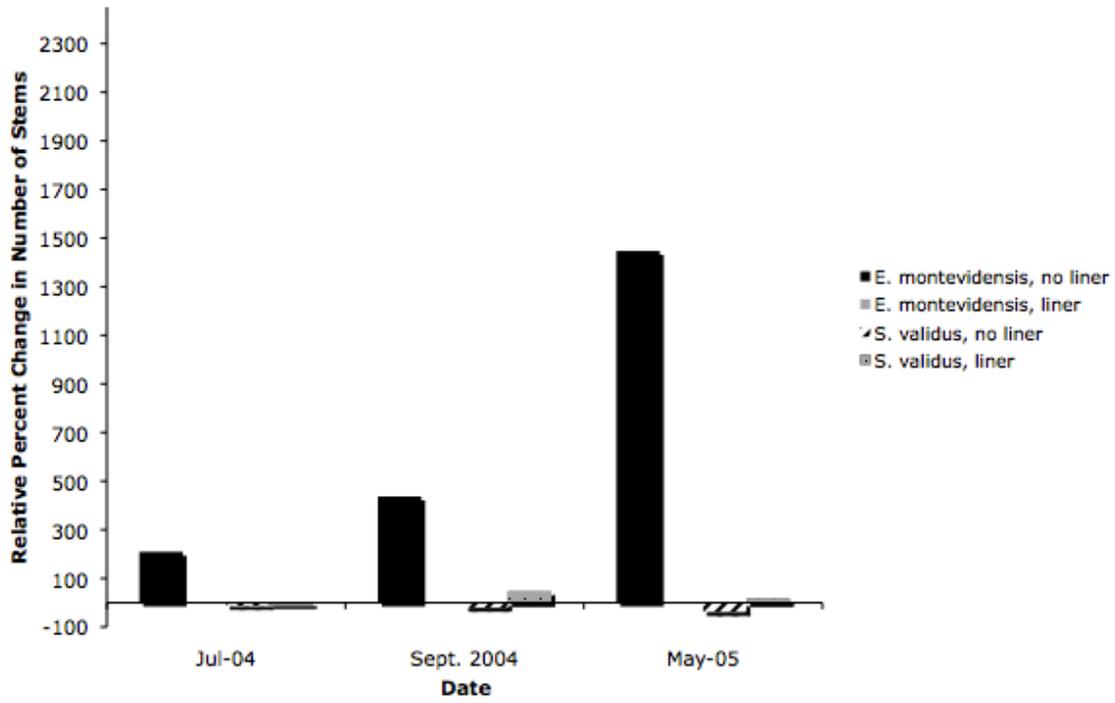


Figure 3-11. Tidal Freshwater Site: Relative percent change over time in treatment *S. validus* surrounded by *E. montevidensis*.

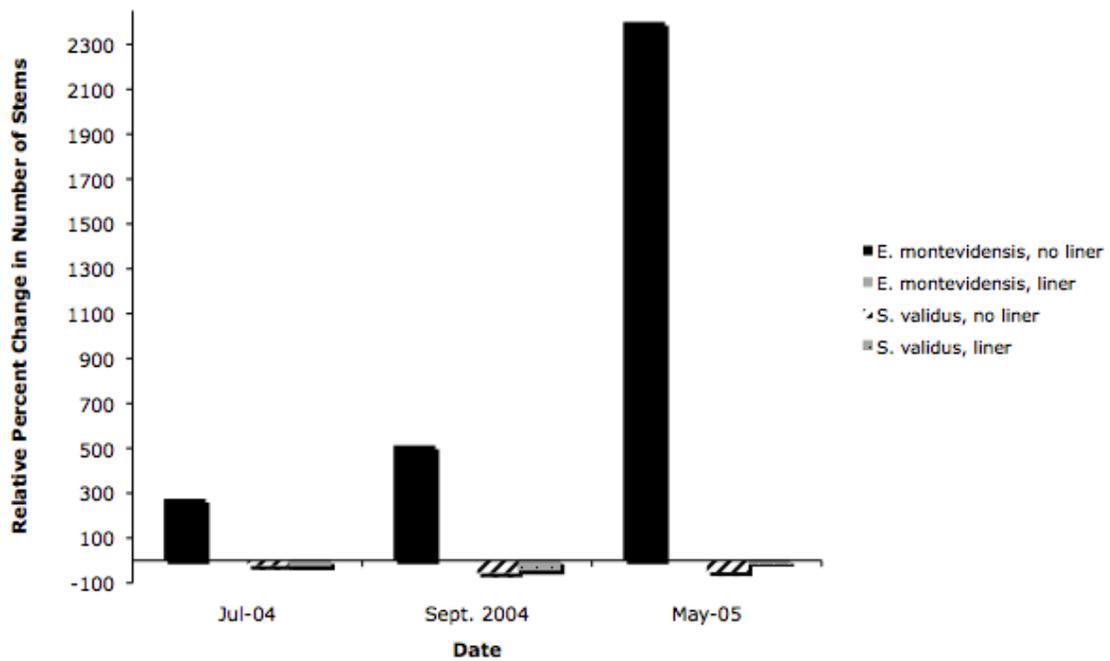


Figure 3-12. Oligohaline Site: Relative percent change in number of stems over time in treatment *S. validus* surrounded by *E. montevidensis*.

CHAPTER 4 DISCUSSION

Salinity Gradient

The salinity gradient at the time of the study (January 2004—May 2005) was one in which there was very little difference in salinity between the two study sites. Drought conditions had ended by 2004 and river flow had reached normal levels, resulting in fairly low salinity throughout the study area. Prior to 2003, there was a much more apparent salinity gradient; representative of the drought conditions and the tide gate era, and the salinity was much higher at both study sites. Therefore, this study measures competition between the two species during a more typical hydrologic regime and salinity conditions.

For all dates with salinity data during the study, the oligohaline site maintained an average interstitial salinity of over 0.5 ppt, and was significantly greater than the tidal fresh site. The salinity of both sites paralleled one another, decreasing and increasing simultaneously (See Figure 2-2). However, two-thirds of the months had an average interstitial salinity of less than 1.0 ppt. Although this is greater than the salinity level that defines an oligohaline marsh (0.5 ppt) (See Figure 1-1), it is still a relatively low salinity, and unlikely was significantly stressful to the species targeted in the study based on the study results. Previous studies with freshwater marsh species and increased salinity support this assumption, because although the target species were not studied, both the genera *Eleocharis* and *Scirpus* were studied in greenhouse conditions, and did not experience mortality even at salinity levels of 12 ppt, and either continued to increase in biomass or stayed the same (Howard and Mendelssohn 1998). The similarity in salinities, though found to be significantly different, in addition to the low salinity at both sites, give subtle results concerning salinity effects upon the species' competitive abilities.

When comparing stem counts of the same species in the same treatment between sites, both species generally had higher stem counts in the oligohaline site. This is inconsistent with expectations that both species would achieve greater numbers in the less stressful freshwater conditions. However, it is possible that the salinity differences simply were not sufficient to affect either species, and other environmental factors were at play such as differing levels or length of flooding. Another possible contributing factor is the nature of the substrate: the tidal freshwater site was unconsolidated, and perhaps because of the floating conditions, the sod blocks were unable to take root as easily, and experienced increased or decreased levels of flooding due to the inability to take root. Additionally, this site had a population of wild boars that would occasionally traverse through the area, causing some degree of damage to the experimental units.

Control Plots and Belowground Competition

In contrast to some other transplant experiments that have been completed in the Savannah marsh (See Wetzel et al. 2004, and Latham 1990), the purpose of my experiment was to test competitive effects between only two species in varying salinity. Therefore, it was imperative to prevent plants outside the experimental unit from interacting with the plants within the experimental unit. The use of contractor's plastic was successful, as it was buried at least 0.15 meters underground, but was flexible enough to allow water movement over the marsh. Previous experiments used only lawn edging, which was buried to only a few centimeters deep (See Latham 1990), and this would have allowed root interactions as the root mat extended much farther into the ground (pers. obs). Plants were also able to move aboveground across the lawn edging (pers. obs.).

The purpose of the interior PVC liner was to prevent belowground competition between the inner and outer blocks of the experimental unit. Although both species produce seeds, the

primary method of reproduction used is rhizomal propagation. The PVC liner successfully excluded movement into or out of treatments by plants through rhizomal growth, as was shown by the results. However, it would not necessarily have stopped seeds from dropping or floating into the inner plot surrounded by the liner because tides at both sites were higher than the PVC liner (pers. obs.). Seed recruitment during the study did not appear to have a significant effect based on the difference in results between stem counts between plots with and without a PVC liner. The PVC liner did not have any unintended statistical effects on the number of stems of either species. However, an observed effect of the liner was a longer retention time of water during high tides within the treatments with liners (pers. obs.).

It is also important to note that all significant results of this study occurred within treatments with no liner, suggesting that belowground competition between species is the most important form of competition in these sites and aboveground competition has minimal to no effect on the interactions between the two species. Since the aboveground growth of neighboring plants was not trimmed during my experiment, aboveground competition would have continued. This is consistent with many other competition studies that find higher biomass and growth rates in treatments with either no neighbors or with the neighbor's root systems separated (Wilson and Tilman 1991, Putz 1992, Shipley et al. 1991, Goldsmith 1973).

The Emery et al. (2001) experiment found that in salt marshes competition was reversed from below to aboveground with nutrient additions and allowed the stress-tolerator species to become more competitive. However, my experiment was performed under ambient marsh conditions (with no addition of nutrients), so one can only speculate as to effects from added nutrients. Although added nutrients in the Emery, et al. (2001) study affected belowground competition, my experiment was performed in fresher marshes that are typically not limited by

nutrients (Odum 1988, Bowden 1987). If there were a switch to aboveground competition, *S. validus* seems an ideal competitor due to its above ground biomass accumulation and stem height compared to *E. montevidensis* (See Crain, et. al. 2004, the light-capturing ability of *T. angustifolia* and *S. robustus*).

Wilson and Tilman (1991) also found no significant difference between removal of aboveground competition and no removal of competition in three grass species in a Minnesota old field under low nutrient conditions. Plants grown with no neighbors grew significantly larger than those grown with neighbors under both high and low nutrient conditions. In an experiment on slash pine growth on a cutover site in Florida, Putz (1992) found that slash pine seedlings benefited from reduction in root competition but not from decreased above ground competition. Over the two-year experiment, seedlings doubled the aboveground growth from reduction of belowground competition using trenching. Trenching also resulted in increased foliar nitrogen and phosphorus concentrations and higher soil moisture. My experiment did not use trenching or removal with bare ground so was less likely to have effects from the treatment.

Though my experiment dealt with stem counts and presence/absence data of species rather than biomass, one can infer a similar conclusion: belowground competition is a significant factor in zonation of *E. montevidensis* and *S. validus* in the locations they were studied. This is apparent from the significant changes in species invasion (increase in number of stems or presence) into treatments with interspecific competition allowed, while in other similar experiments this is represented by increased biomass in plots where species were grown without other species. The advantage to the method used in my experiment is that there are stem counts taken throughout the growing season so it is clear when significant changes occurred and seasonal trends are easily visible.

Eleocharis montevidensis* Surrounded by *Scirpus validus

It took approximately nine months to observe *S. validus* invasion into plots of *E. montevidensis* in treatments with interspecific competition allowed in the oligohaline site. The tidal fresh site experienced a significant change only after a full year of observation, and there were fewer stems on average of *S. validus* at this site when compared to the oligohaline site. At the initiation of my experiment, it was hypothesized that *S. validus* would be more competitive at a higher salinity, and there is evidence for this based on the results, at least based on the speed of invasion of *S. validus* into *E. montevidensis*.

Of interest in *E. montevidensis* stem counts was that the stem counts in the control and the *E. montevidensis* surrounded by *S. validus* plots followed different patterns based on site (Figures 3-1, 3-2, 3-5, 3-6). *E. montevidensis* stem counts in the tidal fresh site were generally flat over the length of my experiment, but in the oligohaline site, there were distinct seasonal fluctuations with peaks in stem counts in July 2004. There was also a trend of a greater numbers of stems (even though not always statistically significant) of both species in the oligohaline site, regardless of the treatment or use of the liner. These results support the assumption that there were differences between sites, perhaps beyond the salinity differences that were noted and planned for during the study.

Still, it is important to note that while not statistically significant, there were generally a greater number of stems found for both species in the oligohaline site, no matter what the species was surrounded by, and regardless of use of the liner.

A reciprocal transplant study utilizing the same study areas found an increase in stems of all species when planted in tidal fresh (<0.5 to 1.7 ppt) and oligohaline sites (0 to 2.7 ppt), and a decrease in stems at a fresh site farther upstream not used in the present study (<0.5 to 1.7 ppt) (Wetzel et al. 2004). However, because the salinity at both fresh sites was very low, this

indicates that species already present upstream could more easily out compete *S. validus*. The Wetzel et al. (2004) study included many more species than were involved in this study, but the results still appear to be similar.

Scirpus validus* Surrounded by *Eleocharis montevidensis

Stem counts of *S. validus* within the plots of *S. validus* surrounded by *E. montevidensis* showed a significant difference between treatments with and without competition excluded on the last two sampling dates, with a significantly greater number of stems found in treatments without interspecific competition. Although there was not a significant difference in the *S. validus* control plots based on use of the liner, the trend of more stems within the liner was apparent. This makes it unclear as to whether the *S. validus* was able to achieve greater numbers within the liner due to removal of interspecific competition, for example, invading *E. montevidensis* suppressing *S. validus* growth, or if intraspecific competition or an environmental factor such as a slight hydrologic difference affected the counts.

After the initial sampling date, all remaining samples in which interspecific competition was allowed had significant numbers of *E. montevidensis* that increased substantially each time. Based on Figures 3-8 and 3-9, it is apparent that over time as stem counts of *E. montevidensis* increased steeply in plots with interspecific competition, stem counts of *S. validus* actually decreased almost linearly. There were also greater numbers of *S. validus* stems within the liner during each sampling date regardless of site.

By the end of the study, the *E. montevidensis* stems still had not penetrated to the interior of the plots. I predict that over time, if the salinity remained low, that this would occur, and stem counts and distribution of *S. validus* would continue to decrease and resemble the random distribution found in the freshwater tidal marsh. The salinity range present in this study had no significant effect on *E. montevidensis*' ability to invade *S. validus*. The salinity at the oligohaline

site was not above the threshold level of tolerance for *E. montevidensis*, as it remained just as competitive at both sites, and the average number of stems was about the same.

Comparisons to Previous Competition Studies

Many plant competition studies have found along a stress gradient, interspecific competition determines plant zonation in the less stressful part of the gradient, and that species tolerance to environmental conditions became more important in the more stressful end of the gradient (Grime 1973, Snow and Vince 1984, Gurevitch 1986, Grace and Wetzel 1981, Shipley et al. 1991, Keddy 1989, Bertness 1991, 1999, Bertness et. al 1992, Hacker and Bertness 1999). Snow and Vince (1984), studied competition along a salinity gradient, and concluded that salinity was an important limiting factor in salt marshes. Experiments in high and low marsh with differential flooding found that interspecific competition was responsible for plant zonation patterns in the less stressful high marsh (Bertness and Ellison 1987, Bertness 1999, and Hacker and Bertness 1999).

Though a complete salinity gradient was not utilized in the current study (the more stressful end of the gradient was excluded), the results with *E. montevidensis* and *S. validus* correspond to these previous experiments with findings that interspecific competition was significant in zonation in the less stressful part of the gradient. It was clear throughout my experiment that competition was a factor in both the oligohaline and tidal fresh sites. Based on previous studies with both species within the Savannah National Wildlife Refuge (SNWR), it was also apparent that had the experiment been performed at very high salinities, *E. montevidensis* would not have survived.

Water depth was not studied or accounted for in my experiment but plots within the same site were set up in the same general vicinity of the marsh to avoid these issues. Also, because both species are found coexisting throughout the Savannah National Wildlife Refuge this was

not anticipated to be a confounding factor affecting one species over another. In a competition study among three marsh plants, Shipley, et al. (1991) planted shoots of each species (*Carex cinita*, *Acorus calamus* and *Typha angustifolia*) in cleared and uncleared areas along a water depth gradient. The study found no significant differences in growth along the water depth gradient but biomass in cleared areas was approximately one-third greater than in uncleared areas. However, Grace and Wetzel (1981), Bertness et al. (1992) and Sher and Marshall (2003) found differing competitive abilities of plant species along a water depth gradient. Varying results are expected as water depth is another form of environmental stress, and not all plants can tolerate flooded conditions.

Many of the experiments also showed that when conditions within the high marsh became hypersaline due to vegetative die-off and subsequent heightened evaporation, that only the most salt tolerant species were able to invade the patch, followed by less salt tolerant species once salinity was lowered (Bertness and Ellison 1987, Bertness 1999, and Hacker and Bertness 1999). Facilitation in the most stressful conditions was followed by competition between species once conditions were once again less stressful.

These results do not contradict the previous or current studies, but rather compliment them. In this case, environmental stress prevented all but the most stress tolerant species from colonizing bare spots until shading allowed marsh conditions to again resemble the surrounding vegetated marsh, and led to competition again being a determining factor in species composition. In fact, Latham's study of the plant interactions in the SNWR found that in areas of disturbance caused by feral hogs, *S. validus* grew back rather than *Z. miliacea*. It is possible this is a form of facilitation, and over time *S. validus* may have been outcompeted after making the conditions of the bare patch more inhabitable for less tolerant plants. However, if salinity were raised for long

periods of time, this could result in vegetative community shifts toward more salt resistant species within the tidal gradient.

Potential Mechanisms Contributing to *Eleocharis montevidensis*' Competitive Success

The experiments I performed for my study only addressed whether belowground competition was occurring, not the mechanisms causing *E. montevidensis*' competitive superiority over *S. validus*. *E. montevidensis* is a smaller species in both above and belowground biomass, and it is surprising that numbers of *S. validus* decreased so significantly over time as *E. montevidensis* increased. In a study on dwarf spikerush (*Eleocharis coloradoensis*), the authors noted that some of its competitive advantages include the ability to live submerged in water or in very wet soil, a rapid rate of vegetative growth and expansion into unoccupied sites through rhizomes, rapid flowering and seed production when exposed to air, and profuse production of underground tubers (Frank and Dechoretz 1980). The authors showed that dwarf spikerush was an alleopath with the two species they experimented with. Yeo and Thurston (1984) also concluded that dwarf spikerush was an alleopath. However, experiments with *Eleocharis smallii* were unable to isolate an alleopathic chemical to explain the competitive exclusion of *Zizania palustris* L (Quayyum et al. 1999).

To my knowledge there is no literature on the alleopathic qualities of *E. montevidensis*. My study did not test for such qualities, but it is possible that one of the mechanisms for competitive superiority over *S. validus* is alleopathic chemicals. This is only one explanation but merits further research in discovering how this small plant is so successful over larger species.

Conclusions, Applications, Long-term Predictions, and Improvements

At both sites during the study period, *E. montevidensis* was able to successfully compete with *S. validus* and invade the plots where interspecific competition was allowed. Conversely, *S.*

validus was also able to enter plots with *E. montevidensis*, but to a much lesser extent, and later in the study. *S. validus* also appeared to be moderately more competitive at the oligohaline site, as it was slightly more likely to find in *E. montevidensis* plots in the oligohaline site. This is interesting, because there was no inverse significant effect on *E. montevidensis* numbers or presence in *S. validus* plots.

If salinity remains stable on the Savannah River, I predict that over time one will observe an increase in *E. montevidensis* in both study sites. The oligohaline site already contains large numbers of *E. montevidensis* nearest to the tidal creek; there is no reason to believe that it will not continue to expand outward. Some plots were located in areas of the site where no *E. montevidensis* was found, and this did not appear to affect the establishment or mortality of *E. montevidensis* within the plot. These results show it was not environmental conditions preventing establishment throughout the site, it is more likely a matter of slow expansion from where the species was currently located. This shift toward freshwater species would be expected to be very slow; as salt tolerant species must be competitively excluded (See Wetzel et al. 2004). The Wetzel et al. study showed community change to be the slowest when plants were moved from higher salinity locations to a lower salinity, and change was still occurring after more than 30 months of study.

On the other hand, if salinity levels do not remain stable and the system experiences another upward shift in salinity, *E. montevidensis* will be reduced in the areas of increased salinity. According to Wetzel et al., up to 71% of tidal freshwater plant species present were lost when salinity increased by over 5 ppt. Changes occurred quickly, with freshwater transplants resembling the brackish community in as little as 6 – 10 months. Community

change will occur more quickly when species die back from environmental change rather than from successional change caused by factors such as competition (Wetzel et al. 2004).

One of the drawbacks of this study was the narrow salinity regime that was used. It was unexpected that the salinity differences would be so small, and a better site choice may have been to use the freshwater site and a location farther downstream to accentuate salinity differences. This would have been a better test of *E. montevidensis*' ability to compete successfully with *S. validus* under more saline conditions. Another difficulty with the study was using a non-destructive sampling method. This was good for observing change over time in more controlled conditions, and the ability to sample the same areas multiple times, but did not yield values other than stem counts. It is difficult to make comparisons of number of stems of different species, especially if the species have dissimilar sizes. Harvesting aboveground biomass at the conclusion of my study would have allowed the data to be relativized. Finally, it would have been useful to continue monitoring the sites for a multiple-year period since community changes have been shown to be slow, particularly in low salinity sites.

Tidal marshes provide significant ecological and economic benefits, including storm buffering, nursery grounds for species of crustacean and fish, and biochemical filtering (Crain 2008, Odum et al. 1984). Coastal marshes have been and continue to be substantially impacted by humans, and restoring coastal marshes has become more important. The ecology of marsh systems is dynamic, with many variables affecting the salinity of the tidal marsh. These include both local and watershed rainfall totals, and alterations both up and downstream. One of the largest unknown variables affecting plant zonation in the marshes of the Savannah National Wildlife Refuge marsh system continues to be the downstream port, and the modifications involved with maintaining it. Understanding plant assembly rules along salinity gradients is

essential to making restoration and mitigation efforts successful and managing marsh systems that have abiotic changes due to human impacts such as freshwater diversion, climate change, and dredging and port modifications (Crain 2008). For example, in the SNWR, if salinities remained low within areas of the refuge that had previously been more species diverse, it is possible that the introduction of *E. montevidensis* plants could increase the rate of community change and recovery in a restoration scenario.

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BIOGRAPHICAL SKETCH

Kristianna Lindgren was born in Reston, Virginia, where she grew up hiking and camping in the Smokey Mountains with her parents. This contributed to a lifelong love and appreciation for nature and led to her decision to pursue an education focused on the environment. She moved to Florida with her family and later received a Bachelor of Science with a major in environmental science from the University of Florida in 2001. She began her master's research studying wetland ecology at the University of Florida and was later accepted to the University of Florida law school where she focused on environmental law. She will graduate December 2010 with Juris Doctor and Master of Science degrees.

In her spare time, Kristianna enjoys spending time outdoors hiking with her dogs, camping, and scuba diving. She also competes with her two horses in show jumping.