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Lee Ellis Stanton

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THE ESTABLISHMENT, EXPANSION AND ECOSYSTEM EFFECTS OF
PHRAGMITES AUSTRALIS,
AN INVASIVE SPECIES IN COASTAL LOUISIANA

A Dissertation

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

in

The Department of Oceanography and Coastal Sciences

by
Lee Ellis Stanton
B.S., Livingston University, 1993
M.S., University of South Alabama, 1998
May 2005

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DEDICATION

This research is dedicated to the memory of

**Carrie Lynn Yoder
(1976-2003)**

In addition to being a bright and gifted doctoral candidate studying the ecology and conservation of coastal environments, Carrie had an amazing affect on all those she came in contact with. She was generous and her curiosity was insatiable. She was an explorer and experienced traveler. She had an amazing zest for life. I was fortunate that Carrie chose to make me an important part of her life- I discovered many things while I was with her, and in her passing, learned more about myself than I ever thought possible. I continue to learn about myself since her death, and know that my perspective of the world has been forever changed. It is to her spirit and memory that I dedicate this work.

*'Beautiful glooms, soft dusks in the noon-day fire,-
Wildwood privacies, closets of lone desire,
Chamber from chamber parted with wavering arras of
leaves,-
Cells for the passionate pleasure of prayer for the soul
that grieves,
Pure with a sense of the passing of saints through the
wood,
Cool for the dutiful weighing of ill with good;-

O braided dusks of the oak and woven shades of the
vine
While the riotous noon-day sun of June-day long
did shine
You held me fast in your heart and I held you fast in
mine;'*

Excerpt from:

The Marshes of Glynn

Written by Sidney Lanier in Baltimore, 1878. Hymns of the Marshes (1907).

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Before I began my work at LSU, I had always heard that the pursuit of a doctoral degree was a life changing journey. I found that to be true in more ways than I ever expected. The demands and deadlines mandated by post-graduate work alone are enough to make anyone question the decisions that led to that pursuit. When I was faced with a tragic event outside the realm of academia and beyond my control, my life changed more than I ever imagined it would. Support came from many different people from many different places. My immediate ‘family circle’ grew exponentially, and it was through this support, friendship and encouragement that enabled me to muster the courage, will and determination to get back in the saddle and see this degree through. I could never compile a complete list of each person that sent their thoughts and support to me, but I am eternally thankful for each one. I send a special thanks to Dave, Lynda

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ABSTRACT

As biological invasions have become a common phenomenon throughout the world, ecologists have intensified efforts to understand why natural communities are susceptible to invasion. Invading species can cause shifts in community structure that result in irreversible changes to ecosystem function. *Phragmites australis* has rapidly spread in North American coastal wetlands during the past 50 years and has become a dominant feature in Northern Gulf of Mexico brackish marshes. The rate at which *Phragmites* is spreading or the mechanisms controlling its establishment in these marshes is unknown. My research objectives were to: (1) determine the spatial and temporal patterns of *Phragmites* invasion and expansion; (2) evaluate how disturbance and nutrient enrichment controls brackish marsh invasibility and *Phragmites* establishment, and (3) identify the ecosystem impacts occurring within a brackish marsh during *Phragmites* invasion. I found substantial increases in the abundance and size of clones of *Phragmites* during the past 75 years. Annual increases of 11-23% occurred in area covered by clones, which had intrinsic rates of increase in size of 0.07 - 0.23 yr⁻¹. To test marsh invasibility, I manipulated both nutrient levels and disturbance regimes in conjunction with purposeful introductions of *Phragmites* seed and rhizome material. *Phragmites* demonstrated the potential for active growth and spread when rhizomes were introduced into brackish marsh. To examine the ecosystem impacts of *Phragmites* invasion, I located three isolated *Phragmites* invasions and identified four distinct community types along a transect from the center of each invasion to adjacent un-invaded marsh. My results demonstrate for the first time that *Phragmites* increases marsh surface elevation relative to un-invaded marsh. *Phragmites* invasion resulted greater aboveground biomass, increased organic matter accumulation and peat development and lower cellulose decomposition rates relative to un-invaded marsh.

The numbers and sizes of *Phragmites* invasions are increasing without apparent restriction in this Louisiana brackish marsh. These communities remain vulnerable to future *Phragmites* invasions if rhizomes are transported to new locations. Furthermore, *Phragmites* has an obvious affect as an ecosystem engineer and may allow invaded marshes to better tolerate increasing water levels due to sea-level rise/land subsidence than native short-stature graminoids.

CHAPTER 1

THE ESTABLISHMENT, EXPANSION AND ECOSYSTEM EFFECTS OF INVASIVE SPECIES

Introduction

Species introductions and invasions have fascinated both biologists and ecologists for over a century (Elton 1958, Baker 1965). More recently, however, these introductions and subsequent biological invasions have become recognized as posing a very serious threat to natural species biodiversity in natural areas on all continents, with the sole exception of Antarctica (Heywood 1989, Lonsdale 1999). The recent increase in species introductions have been exacerbated by more frequent human travel (Ewel 1986, Thompson et al. 1987), while anthropogenic and natural disturbances (Hobbs and Huenneke 1992, Burke and Grime 1996) and nutrient enrichment of natural areas (Halpern et al. 1997, Gordon 1998) have been hypothesized to increase the success of non-indigenous species. Furthermore, invading species have demonstrated the potential to significantly alter natural community structure and more importantly, natural ecosystem functions such as decomposition rates, nutrient transformations, fire cycles, and transpiration rates (Vitousek 1986, D'Antonio and Vitousek 1992, Cronk and Fuller 1995, Luken and Thieret 1997, Schmitz et al. 1997, Walker and Smith 1997, Gordon 1998). Few studies have examined the relationship between disturbance and nutrient enrichment on community invasibility and invader success. Furthermore, studies documenting ecosystem changes as a result of species invasion have not examined the rate of change over the course of the invasion. To better understand the processes promoting the successful establishment of invading species, studies are needed to examine the combined effects of disturbance and nutrient enrichment on community

invasibility. In addition, to understand the gradual physical and environmental changes caused by an invading species, ecosystem processes and functions must be examined over the course of the invasion. This is imperative to understanding the rates at which invasive species alter endemic ecosystem processes and functions after successful establishment.

The Process of Invasion

The process of invasion by non-indigenous species has become the subject of major ecological debate and experimentation in the last four decades (Elton 1958, Wilson 1961, MacArthur and Wilson 1967, Simberloff and Wilson 1969, Mooney and Drake 1986, Cronk and Fuller 1995, Williamson 1996, Simberloff et al. 1997). The process can be described through a generalized flow chart (Figure 1-1). Immigration of invading species occurs through the translocation of living material from one region to another (Cronk and Fuller 1995, Bazzaz 1996). Often these arrivals occur through natural events that typically occur within the evolutionary time frame and spatial scale of the species involved (e.g., seed dispersal in plants by wind and water currents, animal dispersal through adherence and ingestion). Long-distance dispersal events do take place, which establish species outside their normal range. However, they occur irregularly and are difficult to document or observe.

Long-term climactic changes can also affect species distributions. The examination of historical pollen records demonstrate the long-term advance and retreat of forest species during glacial advance and retreat cycles (Rejmanek 1999), while fresh-water fish distributions in Canada have been predicted to change as a result of global warming (Minns and Moore 1995). Furthermore, global warming has been predicted to extend the northern boundaries of migrating birds (Repasky 1991). In addition, as global temperatures increase, shifts in species interactions

have been documented. Warmer temperatures have been correlated with a decline of net aerial primary productivity in C_4 grasses with increased abundance and production in exotic and native C_3 forbs (Alward et al. 1999).

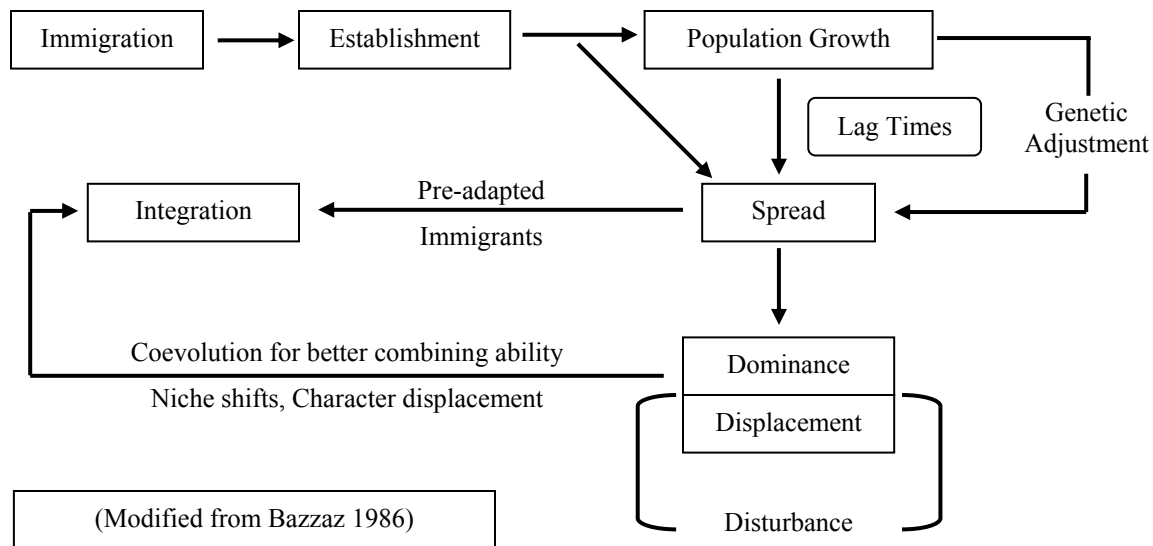


Figure 1-1. The process of invasion.

In contrast to natural dispersal and invasions, human aided dispersal events can occur over much larger (unnatural) evolutionary spatial and temporal scales (Baker 1986).

Anthropogenic activities can by-pass an organisms natural dispersal mechanisms, and result in the “inoculation” of new areas far removed from the organisms natural range and their natural control agents (Ewel 1986, Hengeveld 1989, Brothers 1992, Veit and Lewis 1996, Gordon 1998). Accidental dispersal of exotic species can occur through ship ballast water, impure crop seed, or in soils surrounding nursery stock, while deliberate dispersal can occur by the purposeful transport of forage, ornamental and medicinal plants, or species that perform a service (Baker 1986).

As such, introduced plants are given a “free ride” from the perspective of dispersal. Even if they have not evolved a long-distance dispersal mechanism, humans bypass this by transporting species long distances. Successful establishment is contingent on suitable habitat and if an adequate number of propagules have been deposited. Therefore, anthropogenic immigrations are likely to change the types of species that are most likely to invade. In addition, most of these establishments occur in the absence of the natural controls acting on species in their native habitat (Crawley 1986). Natural enemies can prevent invasion, or reduce rates of spread of invading species (Sheldon and Creed Jr. 1995). Furthermore, high competition intensities between native and introduced species may also decrease establishment success, and therefore reduce the invasibility of certain environments (Simberloff and Wilson 1969, Crawley 1986, Hengeveld 1989, Duncan 1997, Tilman 1997).

Human influence upon natural areas can indirectly favor the establishment of introduced species by reducing native species densities and altering natural environments (Brothers 1992). Prolonged human alteration in environments, such as lowering water tables through drainage or nutrient enrichment, can provide favorable habitats for non-indigenous species, and less favorable habitat for native species (Ewel 1986). Even if habitats are undisturbed and non-indigenous species are established in small isolated areas, a major disturbance (i.e., hurricanes, fire) could release expansion barriers and allow species to rapidly spread (McGinley and Tilman 1993, Horvitz et al. 1998).

Establishment Characteristics

Once introduced, the species become established within the site of initial introduction. Several factors influence the successful establishment of new species. To establish successfully, the species first must be pre-adapted for that environment (Ewel 1986), or be able to survive in a

wide range of habitats (a generalist species, sensu Wilson 1961). A major attribute of evolutionary success in a colonizing species is to survive in marginal habitats (Wilson 1961). During colonization and establishment of species in new areas, the prime habitat is often occupied by other species. Therefore, a species with a general adaptation will be favored over those that are more specific. An additional quality of being a successful generalist is the ability to replace competitors in areas of ecological overlap. The ability to survive and reproduce in marginal areas would allow growth of the population, and potentially to evolve adaptations that would favor introduced species over indigenous species.

Competition between native species and colonizers can affect colonizer success and establishment (Wilson 1961, Roughgarden et al. 1984, Crawley 1986, Duncan 1997, Halpern et al. 1997). In faunal colonization, interference competition often occurs, with the larger organisms usually displacing the smaller (Roughgarden et al. 1984). In plant communities, competition has been hypothesized to reduce the success of colonizing species (Baker 1986, Wiser et al. 1998). Often, increased species diversity is related to high levels of competition (Baker 1986, Tilman 1994, 1997). Experimental evidence has demonstrated, however, that this hypothesis does not always hold true (grasslands - Robinson et al. 1995; forests - Wiser et al. 1998). Both of these studies demonstrated that species rich plots with high rates of competition were more invulnerable than plots with low species diversity and low competition.

The Spread of Invasive Species: Pattern of Spread

Once established, small populations can either decline to extinction, or begin to spread. The pattern of spread is important, and allows some inference to the type of invasion occurring. The rate of spread will depend on several factors, which are termed post-establishment characteristics (Crawley 1986, Johnson and Carlton 1996). These variables can include certain

life history traits of the colonizing species, such as shade tolerance, vegetative growth form, and dispersal mechanisms, and be affected by allee and age dependent characteristic of the invader (Bazzaz 1986, Lewis and Kareiva 1993, Pyle 1995).

There are two basic patterns of spread that can occur once an introduced species becomes established. Populations can demonstrate a steady advance through an environment, such as a moving front. Mathematical models have been developed to predict the speed at which these invasions take place (Fischer 1937, Skellam 1951). The rate of advance is proportional to the square roots of the area occupied at each time, and is dependent on the intrinsic rate of natural increase for that species. The intrinsic rate of increase changes with fecundity, survivorship, developmental rate, and the number of generations produced per year (Crawley 1986). This method of population advance can be maintained by clonal-growth characteristics in plants.

The second pattern of spread occurs when invaders radiate from multiple, separated populations, or through the dispersal and repeated establishment from a founder population. A “filling in of the gaps” follows this between the new “satellite” populations and the founder population (Guzikowa and Maycock 1986, Kruckeberg 1986, Moody and Mack 1988, Lonsdale 1993, Husband and Barrett 1996, Weber 1998). This mode of population growth is directly related to the ability of the colonizing species to establish through the dispersal of viable seeds to surrounding areas, and germinating in a suitable habitat. This pattern of spread may be more likely to succeed in variable environments where dynamic changes or disturbances are produced.

Although populations of colonizing species are often characterized by exponential growth, there is often a lag time between the process of establishment and active spread. The process has been observed for many species, although little experimental work has been conducted to determine the causes (Bazzaz 1986, Ewel 1986). Several hypotheses exist, and

include: 1). Non-indigenous species may have been introduced into pristine conditions (i.e. less altered by man) and those environments are subsequently more invasion-resistant. Recent anthropogenic changes in habitat may have created environments more favorable to the introduced species, allowing distributions to expand; 2). Populations may have been expanding all along, but escaped notice until populations became a conspicuous component in the environment; 3). Introduced species may have been restricted to small populations in the natural habitat or on disturbed areas. These populations may persist over time, showering local areas with seed, and then emerging when a major disturbance occurs; 4). Populations occupying disturbed habitats may evolve adaptations over time, thus enabling more rapid colonization of adjacent habitat (Baker 1965).

The Spread of Invasive Species: Rate of Spread

The rate of spread is typically determined by the processes occurring at the leading fringe of the population (Williamson 1996). If spreading in a traveling wave, the processes may be either at the front edge (“pull”) or involve the entire front (“push”). In either case, this does not usually involve the population behind the front to any extent (Lewis and Kareiva 1993). Interestingly, if the rate of population growth is not maximal at the lowest population densities, for reasons of age structure or of Allee effects, then the rate of expansion will be slower (Lewis and Kareiva 1993, Veit and Lewis 1996). Age structures (individuals of different ages having different characteristics such as reproductive or growth rates) can have marked effect on population dynamics. Allee effects, or low density effects, include difficulties in finding a mate or successful pollination, greater risk of predation or herbivory, or inbreeding effects (Kot et al. 1996, Veit and Lewis 1996). If such effects are present, the population may fail to spread if the initial invasion has too few individuals or occupies too little space.

Interactions between invading and native species have been incorporated into the fabric of several models (Crawley 1986, Okubu et al. 1989, Higgins et al. 1996). Competition has been identified as a major determinate in the success or failure of invading species (Okubu et al. 1989, Duncan 1997). If competition is intense, the rate of spread for the invading species will likely be reduced (Duncan 1997), and in some cases stopped (Wilson 1961, Roughgarden et al. 1984). However, if the invader is a better competitor, the native species have been shown to yield (Roughgarden et al. 1984, Okubu et al. 1989).

Once invasive species become established, eradication or removal is often exceedingly difficult (Forcella 1985, Ewel 1986, Johnson and Carlton 1996). To stop invasive species spread, active campaigns against invasive species have been initiated (Williamson 1996) as well as the control of invasive species through the introduction of biological control agents (Daehler and Gordon 1997). It is rare that introduced species are eradicated completely, however examples of successful campaigns through intensive control and eradication efforts exist. (Williamson 1996). These programs however, also had detrimental effects on other species as well. The common thread between these campaigns is that efforts were initiated early in the establishment period of the invading species.

The uses of biological control on invasive species have also been conducted (Hoffman and Morgan 1991, Hight et al. 1995). However, the use of introduced organisms to control invasive species has been the subject of heated discussion and controversy (Simberloff and Stiling 1996, Daehler and Gordon 1997, Corrigan et al. 1998, Freckleton 2000, Fagan et al. 2002). Introductions have been made that not only slowed invasive spread, but shifted preferences to native species (Louda et al. 1997). Therefore, more pressure has been placed on experimental study and ecological ramifications of introduced biological control species.

Invasibility of Communities

Many generalizations pertaining to the susceptibility of communities to invasion by exotic plant species have been made (Elton 1958, Crawley 1986, Richardson and Bond 1991, Robinson et al. 1995, Wiser et al. 1998). Elton (1958) first proposed that communities having low species diversity are more susceptible to invasion from outside species due to low interspecific competition. Furthermore, Crawley (1987) hypothesized that in addition to lower interspecific competition, those communities with lower species diversity may contain more open niches, allowing invasive species demonstrating those characteristics to become successfully established. Several studies have supported this viewpoint by demonstrating a negative relationship between native and exotic species richness (Rejmanek 1989, Tilman 1997, Woods 1997). On the other hand, positive relationships between native and exotic species richness have been shown as well (Knops et al. 1995, Robinson et al. 1995, Wiser et al. 1998). Those communities exhibiting higher native species diversity may promote the establishment of exotic species in the same manner that led to initial high natural species diversity (Crawley 1987). In addition, naturally diverse communities may be lacking one or more dominant species, allowing a dominant or aggressive invader to successfully establish (Robinson et al. 1995), or a naturally diverse community with high spatial/temporal variability in both abiotic and biotic factors may promote the successful establishment of invading species (Tilman 1997, Wiser et al. 1998).

Invasibility, although affected by community structure, may also be influenced by the intensity and frequency of disturbance. The extent to which communities experience disturbances through grazing (Schierenbeck et al. 1994, Burke and Grime 1996) and

natural or anthropogenic habitat alteration (Higgins et al. 1996, Horvitz et al. 1998, Wiser et al. 1998) may change the rates at which invasion occur. Grazing may influence an invaders success directly through altering resource availability (Burke and Grime 1996), or indirectly by changing biotic interactions and subsequently community structure (Richardson and Bond 1991). Therefore the impacts that disturbances have on the invasibility of communities are often difficult to separate between those directly and indirectly affecting community structure.

Ecological Impacts

Invasive species can have both direct and indirect effects on the populations of native species and the invaded ecosystem. Invaders can directly affect native species by reducing seedling germination and survival through litter deposition (Vitousek and Walker 1989, Walker and Vitousek 1991), reducing available light and moisture (D'Antonio and Vitousek 1992), or by altering disturbance regimes thereby decreasing establishment success of native species (Mack and D'Antonio 1998, D'Antonio et al. 2000). Invasive species can affect ecosystems indirectly by altering competitive processes and changing soil biogeochemistry, geomorphology and hydrology (Vitousek and Walker 1989, Gordon 1998, Mack and D'Antonio 1998). For instance, invasive *Acacia* species have been shown to alter levels of fixed nitrogen and carbon cycling through increases aboveground production and litterfall rates (Macdonald and Richardson 1986). Likewise, *Sapium sebiferum* (Chinese tallow) invasions in South Texas have been shown to increase soil nitrogen availability, and have been hypothesized to facilitate conversion of natural open prairie to wooded areas (Cameron and Spencer 1989). As invading species move across community boundaries, changes in ecosystem function and

diversity should be expected (Simberloff 1981, Vitousek 1986, 1990, Vitousek et al. 1996, Parker et al. 1999). When examining the effects of invaders on native species, it is difficult to determine if invaders are out competing natives or altering ecosystem properties and disturbance regimes, thus preventing native species from maintaining viable populations.

Conceptual Model of Ecosystem Effects

As natural areas are invaded by non-indigenous species, changes become readily apparent in vegetative community structure and species diversity. Less apparent, however, are the ecosystem effects of invading species on physical and environmental factors such as biogeochemical processes (e.g., nutrient pools, carbon cycling), geomorphology (e.g., peat accumulation, soil composition changes, surface elevation change) and hydrology (e.g., water table levels). Furthermore, the rates at which these changes in function take place relative to invasion remain largely unexamined in invasive species literature. Processes operating on the ecosystem level develop over time. Thus, it would be intuitive to think that gradual changes take place over the course of an invasion (Figure 1-2).

Research Rationale

The study of biological invasions has recently become an issue of great concern for many ecologists (Vitousek 1990, Gordon 1998, Mack and D'Antonio 1998, Lonsdale 1999, Schweitzer and Larson 1999, Smith and Knapp 1999, Tilman 1999). Noticeably lacking, however, are experimental studies integrating the rate of spread of invaders, community invasibility and successful invader establishment characteristics, and furthermore, examining the changes occurring in ecosystem functions over time to a biological invasion (Carroll and Dingle 1996, Parker et al. 1999, Smith and Knapp 1999). With this research, I test and integrate hypotheses

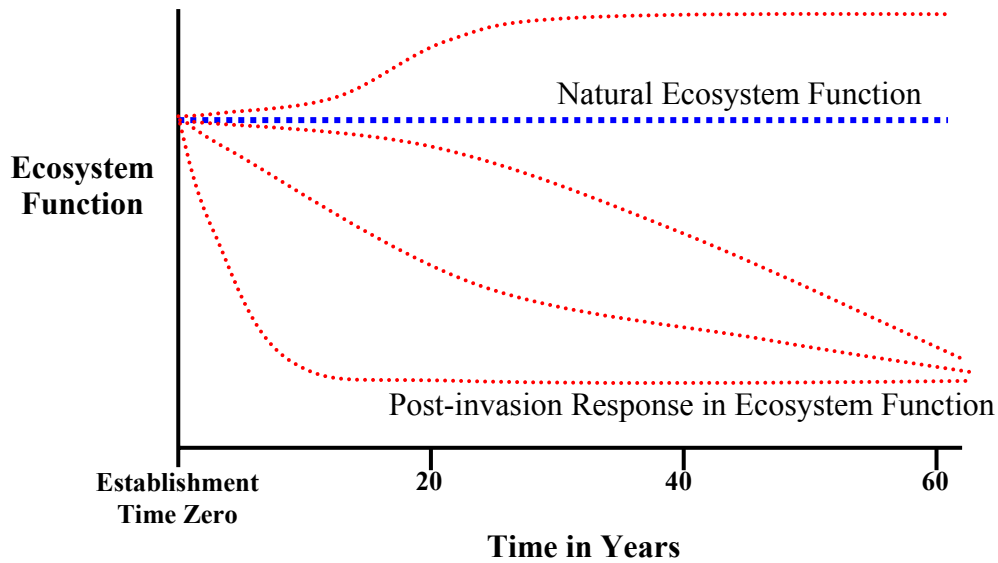


Figure 1-2. Change in ecosystem function over time as a result of invasion.

concerning: 1) the rates and patterns of invasive species spread; 2) the effects of disturbance and nutrient enrichment on community invasibility and establishment success of an invading species; and 3) the consequence of invasive age on the structural, environmental and biogeochemical processes that occur within natural vegetation.

The Model Species: *Phragmites australis*

Although many examples of invasive plant species exist in North America (e.g., *Imperata cylindrica* (cogon grass- Southeast US), *Pueraria lobata* (kudzu- Southeast US), *Lythrum salicaria* (purple loosestrife- Northeast US), *Spartina anglica* (cordgrass- West Coast, US), *Carpobrotus edulis* (ice plant- West Coast, US), etc.), considerable attention has recently been placed on *Phragmites australis* (Cav.) Trin. ex Steudel, the common reed (hereafter referred to as *Phragmites*).

Phragmites is an emergent clonal grass, with tall culms (> 3 m) emerging from perennial underground rhizomes (Ekstam 1995). It is considered the most widely distributed angiosperm in the world (Bird 1962), and is a native component of North American wetlands (Orson et al. 1987, Cross and Fleming 1989). *Phragmites* often grows in monotypic stands, especially in disturbed or impounded areas, and stands are typically composed of 80-100 aerial shoots per square meter (Haslam 1972). Establishment of *Phragmites* most typically occurs through transport of vegetative material. Although germination from seed does occur, it is not common (Cross and Fleming 1989). Seeds must be kept moist in order for germination to occur, and must remain wet until the seedling become successfully established. Stems produce tassels in late summer, but may begin to flower as early as mid-July. In most stands, approximately half of the stems will produce flowers, which subsequently die. These stems can remain standing for up to 4 years (Haslam 1972). Seeds generally ripen in late September, and are dehiscent as inflorescences dry throughout the winter.

Rhizomes are responsible for maintaining the stand, and is where carbohydrate nutrient reserves and hormones are stored (Ekstam 1995). Rhizomes grow most rapidly from late summer to early winter, and can grow as deep as 1 m (Burdick et al. 2001). Underground buds are formed in the fall, and typically remain dormant through the winter (Haslam 1969). Buds formed early are much larger than those formed later in the season due to the large amount of nutrient reserves available in the early portion of the season. In addition, *Phragmites* can mobilize rhizome carbohydrate reserves quickly, and can produce culms as tall as 1 m within two weeks after disturbance events remove aboveground vegetation (L. Stanton, pers. obs.).

Problems Associated With *Phragmites*

Phragmites historically has been considered a minor component of tidal wetland plant communities in North America (Orson et al. 1987). Within the past 50 years, however, this cosmopolitan wetland species has aggressively expanded its distribution throughout many freshwater, tidal brackish and salt marsh communities in the United States, forming large monospecific stands (Phillips 1987, Buck 1995, Chambers et al. 1999). Although this spread has been especially apparent in salt marshes in the Mid-Atlantic States (see Chambers et al. 1999), populations are rapidly expanding in coastal marshes in the Northern Gulf of Mexico. It is clear that *Phragmites* is invading areas where it previously did not occur, yet the factors contributing to the initiation and subsequent spread of *Phragmites* are not well known.

Phragmites is native to Louisiana (Montz 1977, White 1983), occurring over large areas in the Mississippi River Delta and Chenier Plains of southwestern Louisiana. This species has been observed to be invading coastal habitats in Louisiana (Tom Hess, LDWF, Rockefeller Refuge, pers. com.); it frequently occurs along both canals and the edges of natural marshes in salt, brackish and freshwater areas. Additionally, *Phragmites* is invading the interior of natural marshes, forming large populations that replace the indigenous vegetation (Cronk and Fuller 1995). Because populations (sensu Harper 1977, Cronk and Fuller 1995) of this species form large circular stands with culms of 3-4 m that are much taller than the short indigenous grasses (*Spartina patens* and *Distichlis spicata*), invasions are particularly noticeable, even from a considerable distance. These stands form *Phragmites* “islands”, varying in size and age, surrounded by an expanse of the indigenous *S. patens*/*D. spicata* short grass habitat. No research to date has quantified the distribution, rate of expansion, and effects on ecosystem processes of *Phragmites* invasions in Louisiana.

The causes of the recent expansion of *Phragmites* in North America vary. One theory attributes its spread to changes in the abiotic and biotic environment related to human disturbance of water flows and heavy development pressure in coastal areas (Chambers et al. 1999). These disturbances, exacerbated by natural sea level rise and land subsidence, could potentially act together to cause large shifts in vegetative community structure in coastal wetlands (Rooth and Stevenson 2000). Similarly, it has been suggested that increasing nutrient levels in coastal waters caused by agricultural runoff, urban runoff, and the loss of wetland area may also contribute to increased *Phragmites* growth and hasten subsequent spread (Clevering 1998, 1999, Romero et al. 1999, Ostendorp et al. 2001). Furthermore, an aggressive invasive genotype originating from Europe has been identified through both field samples and herbarium collections (Saltonstall 2002), and is reported to be responsible for much of the observed spread along the eastern seaboard of the United States. Other than being identified at the mouth of the Mississippi River, it is not known to what extent this genotype has invaded the gulf coast (Saltonstall 2003).

The Cascading Ecosystem Effects of *Phragmites*

The colonization of *Phragmites* can have significant effects on both the structure and the function of the ecosystem. Typically, there is a decline in plant species diversity (Chambers et al. 1999). The resultant monospecific stands of *Phragmites* have considerable potential for altering natural ecosystem processes, such as nutrient cycling (Dinka and Szeglet 1999, Ostendorp et al. 2001, Windham and Ehrenfeld 2003, Windham and Meyerson 2003), decomposition rates (Mendelssohn et al. 1999, Windham 2001, Van Der Putten 2003), sedimentation rates (Rooth and Stevenson 2000, Rooth et al. 2003), and soil biogeochemical

cycles (Portnoy 1999). However, examining how ecosystem processes change relative to the age of the population has been given little scrutiny.

Research Questions and Objectives

This research addresses two overriding questions related to plant invasions: (1) what controls the invasibility of brackish marsh and the successful establishment and expansion of an invasive plant? (2) How does the age of the invasive plant community affect physical, environmental and biogeochemical processes? The following objectives address these questions.

1. Determine if and how the spatial distribution of invasive species populations and their time of establishment aid in assessing mechanisms of invasion and success.
2. Evaluate the effects of disturbance and nutrient enrichment on the invasibility of brackish marsh and the successful establishment of an invasive plant.
3. Quantify the effects of species invasion and population age on the structure and ecosystem function of the natural un-invaded plant community.

To address these objectives, I conducted three studies in brackish marsh in Southwestern Louisiana where *Phragmites* invasion is occurring. To evaluate the rate and pattern of *Phragmites* spread (Chapter 2), I examined and compared historic aerial photography using Geographic Information Systems (GIS). To test brackish marsh invasibility and the successful establishment of *Phragmites*, I manipulated both nutrient levels and disturbance regimes in conjunction with purposeful *Phragmites* introductions (Chapter 3). And lastly, I examined the ecosystem impacts of *Phragmites* invasion within three isolated communities of *Phragmites* and identified four distinct community types along a transect from the center of each *Phragmites*

community to the adjacent un-invaded marsh (Chapter 4). I measured variables specific to soil composition, decomposition, peat development, marsh surface elevation and biomass production over the course of a 40 year *Phragmites* invasion.

My results indicate that the numbers and sizes of *Phragmites* communities are increasing without apparent restriction in this Louisiana brackish marsh and are likely to replace this native community. Although seedling emergence was not observed throughout this study, this community remains vulnerable to future *Phragmites* invasion if rhizomes are transported to new locations. Furthermore, *Phragmites* had an obvious effect as an ecosystem engineer. Marsh surface elevation in *Phragmites* increased relative to un-invaded marsh by greater organic matter accumulation, peat development and lower cellulose decomposition rates. These effects may allow *Phragmites* dominated marshes to better tolerate increasing water levels due to sea-level rise/land subsidence than native short-stature graminoids.

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CHAPTER 2

POST-INVASION DYNAMICS OF *PHRAGMITES AUSTRALIS*, THE COMMON REED

Introduction

Most native species are not considered invasive in their home region. There are, however, cases of native species that invade relatively undisturbed habitats, to the detriment of other native species (Baker 1996; Brewer 2002). Such invasions by species within their native regions are poorly understood (MacArthur and Wilson 1967; Simberloff and Wilson 1969; Baker 1996).

The dynamics of invasions by both native and exotic species appear similar. The invasion process typically begins with initial immigration by one to several individuals. Although immigration of plants may be restricted by dispersal (e.g., Tilman 1997), anthropogenic introductions bypass this block, perhaps for both native and exotic invasions. Over time, colonizers appear to become adapted for the new environment or persist until environmental conditions become favorable (Horvitz et al. 1998). Like exotic species, native invading species may occupy specific habitats when invading a new area. There they may persist until environmental conditions become more favorable, if there is a large-scale natural or anthropogenic disturbance that releases competitive restraints, or if selection removes less-fit life history traits (Orians 1984; Hobbs and Huenneke 1992; Carroll and Dingle 1996; Luken and Thieret 1997; Alward et al. 1999). Ultimately, these invasive species initiate unchecked growth and rapidly spread at some point in the invasion process. The invasion often goes unnoticed until the population has expanded beyond control, thus documentation of the initial invasion process is often incomplete (Moody and Mack 1988). Moreover, environmental conditions and ecological processes contributing to unchecked growth have only rarely been described,

especially for invading native species (Guzikowa and Maycock 1986; Baker 1996; Weber 1998; Brewer 2002).

One native species of particular concern is the common reed, *Phragmites australis* (Cav.) Trin. Ex Steud., which has spread rapidly in North America during the past 50 years. Although a native species occurring both in coastal fringing and inland fresh water marshes throughout North America (O'Neil 1949; Nichols 1959b; Montz 1977a; b; Neiring and Warren 1980; Orson 1987; Winogron and Kiviat 1997; Galatowitsch et al. 1999; Clevering and van der Toorn 2000; Rice et al. 2000), *Phragmites australis* (hereafter referred to as *Phragmites*) has invaded freshwater, coastal brackish and salt marshes of the mid-Atlantic region of the United States, often forming large monospecific stands (Chambers et al. 1999; Meyerson et al. 2000). Likewise, *Phragmites* has become invasive in brackish and salt marshes in coastal Louisiana (Hess Jr. personal communication). Not only has it frequently invaded the edges of bayous and canals, but *Phragmites* is also invading undisturbed interior areas of natural salt and brackish marshes (Stanton personal observation). It's 3-4m culms are much taller than the short (typically < 1 m tall) vegetation in coastal marshes (Cheplick 1998), and forms large circular stands (which we refer to as clones or colonies without implying genetic homogeneity) that easily replace the natural vegetation (Cronk and Fuller 1995; Chambers et al. 1999; Galatowitsch et al. 1999).

The invasion of *Phragmites* provides an opportunity to examine native species invasions in relatively undisturbed coastal environments. Its distinct growth form and signature on aerial photography is easily identified. We address two questions in this study: What is the rate of spread by *Phragmites* stands in coastal marshes? Do expansion rates differ with age or environment? We used post-invasion expansion rates to predict possible immigration periods for present-day *Phragmites* stands as well as future expansion and spread. We used the expansion of

invading *Phragmites* stands over the last 60 years to project future clonal spread in a brackish marsh in Southwestern Louisiana.

Methods

Study Site

Rockefeller Wildlife Refuge (29°55' N and 92°30' W) is located within the southeastern portion of the Chenier Plain Region (Cameron Parish, LA; Figure 2-1). It is bordered on the south by the Gulf of Mexico, on the north by the Grand Chenier Ridge complex, and contains about 32,000 hectares. It was purchased by the Rockefeller foundation in 1914, and subsequently deeded to the state of Louisiana in 1920 under the mandate to “preserve, maintain, and improve the refuge lands in perpetuity”. The majority of the refuge is actively managed through water control structures designed to maximize food for waterfowl (Wicker et al. 1983).

Phragmites has historically been present in the refuge, but only in fresh and oligohaline marsh communities (O'Neil 1949; Nichols 1959b). In the 1940's and 50's, before marsh management, *Phragmites* distributions did not extend into brackish and saline marsh habitats from surveys of the area (O'Neil 1949; Nichols 1959b). *Phragmites* has spread quickly, occurring on canal banks in salt marsh areas and as discreet circular stands in relatively undisturbed brackish marsh.

In this study we focused on a 1000-hectare portion of brackish marsh on the western border of the refuge. The majority of this area, which is bounded to the south by the Gulf of Mexico, has remained unmanaged since the inception of the refuge. It is comprised of *Spartina patens* and *Distichlis spicata*, with sparse inclusions of *Schoenoplectus robustus* and *Juncus roemerianus*. *Spartina alterniflora* is also present, but is restricted to areas adjacent to water

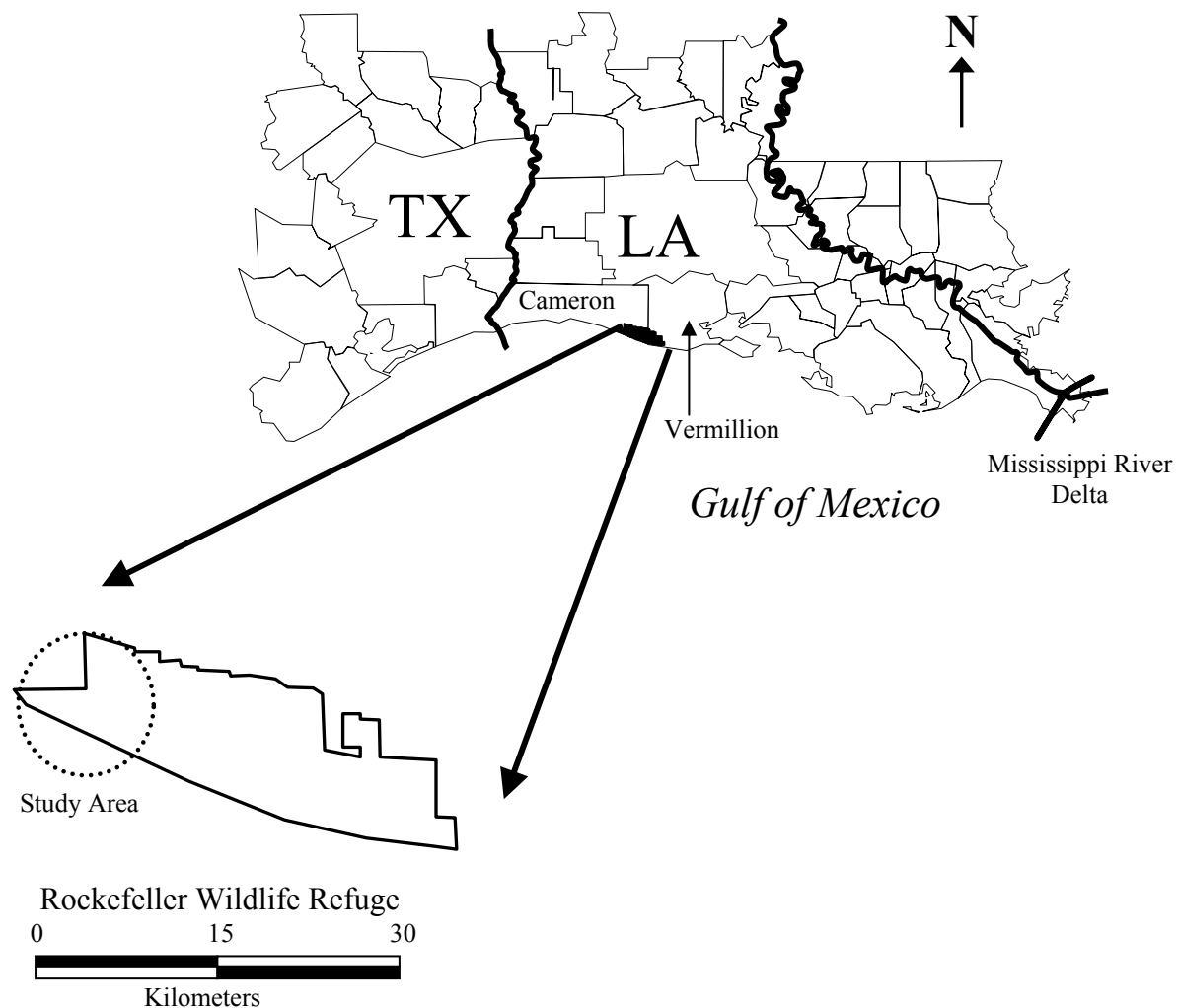


Figure 2-1. Location of Rockefeller Wildlife Refuge, Louisiana. The refuge lies in southwestern Louisiana on the border between Cameron and Vermillion Parishes. The northern boundary of the refuge is the Grand Chenier Ridge complex, a natural ridge formed by erosional processes and then stranded inland after accretion events.

(Nichols 1959b). Discrete stands of *Phragmites* are present within both managed and unmanaged areas.

Phragmites Expansion

To determine the extent of the *Phragmites* invasion, clones in the study area were mapped using GPS (March, 1999). Each GPS measurement was differentially corrected and had an accuracy to within 1 meter. Ground-truthed *Phragmites* clones in the marsh were compared to signatures observed on color-infrared 1998 aerial photography (National Aerial Photography Program) using surveys conducted from both airplanes and airboats. The Arc View geographic information system (ERDAS, version 8.4) was employed to create a base map of the study area in 1998 from Digital Orthophoto-Quarter Quadrangles. The spread of *Phragmites* was estimated based on numbers and size of clones located in the field and on aerial photographs.

Black and white aerial photographs and high altitude color-infrared photographs were obtained for eight different times: 1933, 1955, 1968, 1978, 1982, 1985, 1995 and 1998 (Table 2-1). Nine-inch contact transparencies of the original photographs were digitized using a high-resolution digital scanner (600 dpi). Each frame was then mosaiced and rectified to the base map using Imagine (ERDAS, version 8.4). Clones of *Phragmites* in the marsh tend to form large circular areas and have a distinctive brown to pinkish signature that is discernible from other marsh vegetation (Figure 2-2). In addition, the height differentiation between *Phragmites* and the shorter graminoids allowed clones to be differentiated using stereoscopic pairs of aerial photography. The comparison of field observations with signatures obtained from aerial photography enabled us to identify the smallest stands that were readily detectable in the photographs. Several smaller clones did not exhibit stem densities great enough to be detected on aerial photography, although stands were identified in the field. Thus, some low-density

Table 2-1. The year, scale (inches), type and source of aerial photography used in this study.

Year	Scale	Type	Source
1933	1:18,000	Black and White	Tobin Research
1955	1:24,000	Black and White	Tobin Research
1968	1:40,000	Black and White	Tobin Research
1978	1:40,000	Black and White	Agricultural Stabilization and Conservation Service
1982	1:24,000	Color Infra-red	Agricultural Stabilization and Conservation Service
1985	1:65,000	Color Infra-red	USGS/NAPP
1995	1:32,500	Color Infra-red	USGS/NAPP
1998	1:40,000	Color Infra-red	USGS/NAPP

colonies may persist undetected on aerial photography until stem densities increase. Dense stands of *Phragmites* with diameters greater than approximately 5 m were readily measurable in the aerial photographs; thus we limited our measurements of rates of spread to established stands of at least a diameter of 5 m.

We estimated the area of each clone from the aerial photography. Polygons were constructed around each *Phragmites* colony using Arc View (ERDAS, Version 8.4) and the digital 1998 color-infrared photographic images. Each clone was then followed backward in time through each photo set to the smallest sizes at which each stand was measurable using stereoscopic pairs. These data were used to estimate rates of increase in the sizes of clones, as well as changes in the number of clones within the marsh. Only those clones that could be measured on the 1998 photography were included in this study.

Expansion Analysis Methodology

Although studies describing clonal expansion rates using simple deterministic growth models have appeared in the literature (Rice et al. 2000; Warren et al. 2001), stochastic models

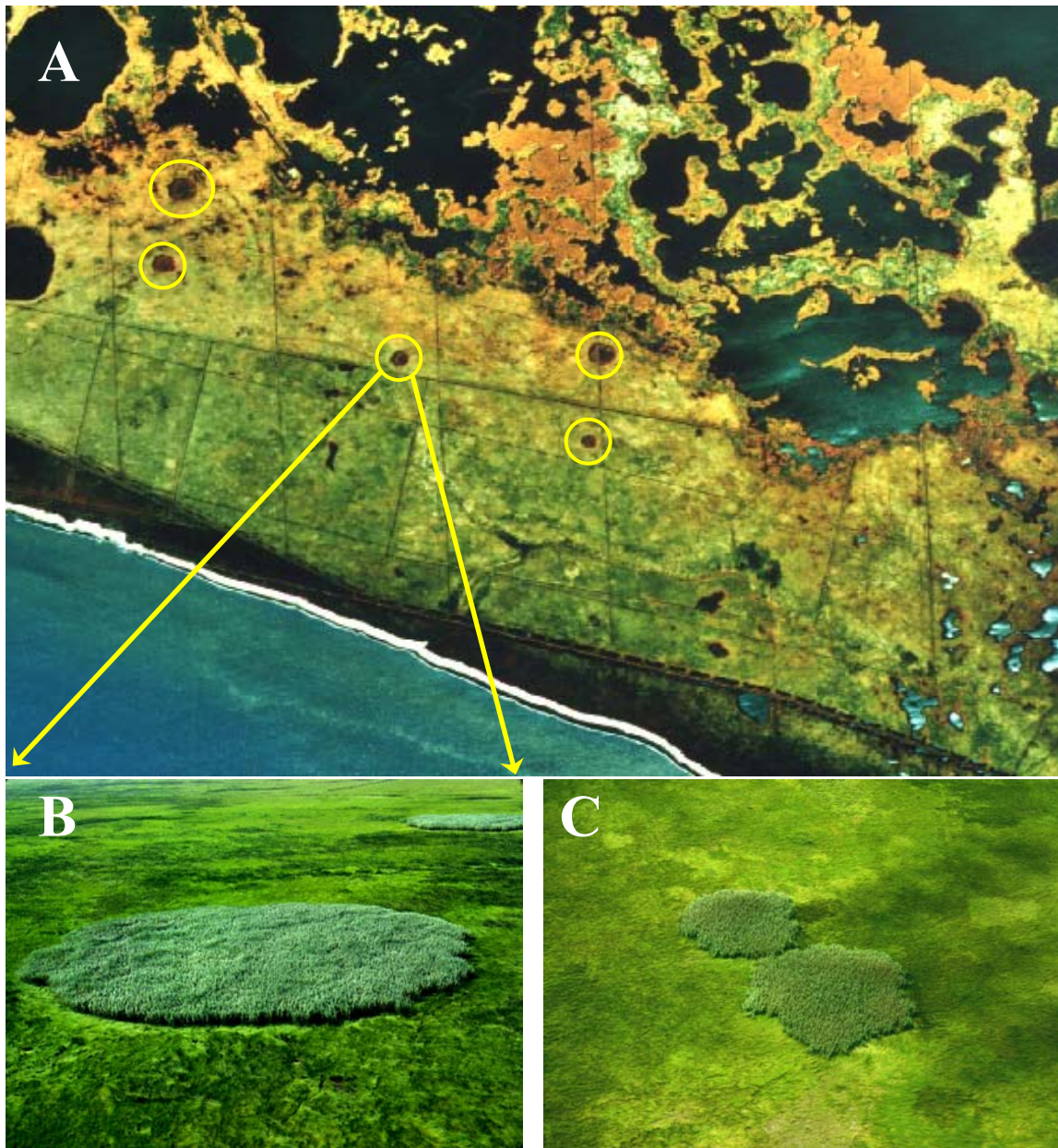


Figure 2-2. Circular *Phragmites* clones are evident from aerial photography (Photograph A) taken May 1999 (scale = 1:40,000). Lower altitude photography demonstrates the striking differences between *Phragmites* and the natural *Spartina patens*/*Distichlis spicata* community. Also evident in the lower altitude photography are other *Phragmites* stands (background right in Photograph B). *Phragmites* appears to be actively spreading in Photograph C (note ramet extensions spreading outward from the main population). The clone size in Photograph B is estimated at 80 m in diameter, while the size of the clones in Photograph C are smaller, measuring approximately 35 m in diameter.

should provide greater predictive power in examining past changes in expansion rates as well as providing future estimates. Three methods were used to assess *Phragmites* expansion rates in this study: 1) a non-linear approach, 2) a linear approach where effects were assumed fixed, and 3) a linear approach where *Phragmites* clones were assumed to be members of a random population. The non-linear equation is based on the Malthusian exponential growth model where growth rates are expressed as the intrinsic rate of increase (r). In contrast, a linear analysis using log-transformed data gives statistical latitude in assigning effects as either fixed or random. The fixed effect model yields growth estimates and standard errors for each individual colony, whereas the random effect model considers the observed colonies to be a random sample from a potential population of clones and thus gives one expansion estimate and standard error.

Non-linear Growth Model

The expansion of *Phragmites* was estimated using a nonlinear growth model to estimate an “intrinsic” rate of increase in clone size. We used the exponential growth model:

$$(1). \quad N_0 = N_t e^{rt}$$

Where N_0 represents the area at time 0, N_t is the area at time t since initial observation, r reflects the intrinsic rate of increase in area of the clone. To estimate the intrinsic rate of increase, all area and time data were included for each stand. Nonlinear estimation gave an estimated r and an associated standard error for each clone (SAS PROC NLIN, 1999).

Linear Expansion Models: Fixed Effects Analysis

Alternatively, a linear model may be considered using $\log(\text{area})$ as the response. In contrast to the nonlinear model discussed above (where initial areas are a fixed multiplicative constant), the linear model calculates a y-intercept for each colony (or colony effects). An analysis of covariance model yielded a significant time by colony interaction ($p < 0.0001$) and

suggested different linear regression lines for each colony. Estimated intercepts and slopes for these fixed effect models were determined using PROC GLM in SAS (SAS Institute, Inc. 1999).

Linear Expansion Models: Random Effects Analysis

The use of a random effects ANCOVA increased the scope of the analysis. The observed clones were considered to be a random sample from a potential population of clones. The observed expansion rates (slopes) and initial areas (intercepts) were treated as measurements from a population of possible parameters. The intercepts β_{oi} were assumed to be normally distributed with mean μ_{β_0} and variance $\sigma^2_{\beta_0}$, the slopes were assumed to be normally distributed with mean μ_{β_1} and variance $\sigma^2_{\beta_1}$, and the errors were assumed to be normal with mean 0 and variance σ^2 . The random intercept allowed for variability in the colony's initial area (taken to be at time = 0); thus, the starting area of each colony could be different. The randomness assumed in initial starting area may be interpreted as variability in time from true colony establishment to actual observation on the photography, or it may represent randomness in the quality of the initial photograph, while the variability in expansion rates among colonies is likely due to differences in environmental conditions and genet growth rates.

Colony Expansion Contrasts

Once the intrinsic rates of expansion (non-linear estimate) and fixed effects expansion rates (linear estimate) were determined for each *Phragmites* colony, data were analyzed using a Student T-test. Colonies were divided into groups based on first appearance in each year set of photography (1968, 1978 and 1982). These colonies were then compared to determine if significant differences in rate of spread arose based on time of first observation, or alternately, based on the age of the colony. In addition, colonies were separated and compared based on

growing environment (growing in unmanaged and those growing in water management areas) and if adjacent to open water areas.

Results

Phragmites Colony Abundance and Size

Twenty-eight distinct *Phragmites* clones were identified and delineated within the study location through initial ground-truthing. Twenty of these were of sufficient size and density to be positively identified on the 1998 photography (Table 2-2). Only clones visible on more than 2 dates were included in the analysis; thus, 2 clones first observed on the 1995 aerial photographs were excluded. Of the 18 remaining clones, clones 8 and 10 were a result of the merging of 3 smaller clones first observed on the 1995 photography (Table 2-2). To remain consistent within the models, the areas of the separate clones prior to coalescence were included in the analysis (four data points in each case), but combined areas after merging were omitted. Thus, a total of 22 clones were included in the analysis (Table 2-2). Initial clone sizes, measured from photography, ranged from 6 to 204 m², and measurements in 1998 ranged from 174 to 11,471 m² (Table 2-2).

Phragmites was first observed in the 1968 aerial photographs. These clones have steadily increased in number since that time (Figure 2-3). No evidence of *Phragmites* was found on either the 1933 or the 1955 black and white photographs. The 1933 and 1955 photographs were taken at a much lower altitude relative to other photography used in this study and had high contrast and resolution, thus it is unlikely that any existing *Phragmites* clones at least 5 m in diameter would have been overlooked (Table 2-1). Thirteen clones were first observed in 1968, and two new clones appeared in 1978. Six clones were first observed in 1982. *Phragmites* occurred in both water-managed areas (4 clones) and in unmanaged areas (17 clones).

Table 2-2. Area (m²) of *Phragmites* clones from initial appearance in aerial photography until 1998. No clones > 5 m in diameter were visible at that time on 1933 and 1958 photographs. Clones 1, 5, 6, 15 and 27 were not visible in 1985 due to the small scale of the photography. Two stands present in 1998 were three converged clones each.

Clone	1968	1978	1982	1985	1995	1998
1	-	-	61	-	163	570
4	-	-	94	125	450	785
5	-	-	417	-	2537	3935
6	10	38	54	-	173	265
7	41	188	483	784	1895	2281
8 total	127	385	1266	1948	3446	3463
8A	64	193	633	974	Converged	Converged
8B	46	138	443	742	Converged	Converged
8C	17	55	190	232	Converged	Converged
9	-	33	178	389	1642	1639
10 total	64	199	693	1056	2855	3109
10A	32	100	347	528	Converged	Converged
10B	11	51	270	415	Converged	Converged
10C	21	49	77	113	Converged	Converged
11	-	41	118	173	850	975
12	-	-	49	96	310	584
13	-	-	13	34	96	198
14	12	52	57	99	436	539
15	-	-	42	-	68	174
18	-	-	14	95	-	577
21	204	401	920	2256	7003	11471
24	44	194	770	1243	4520	7307
27	29	79	236	-	2439	4986
28	6	32	220	435	1431	3569

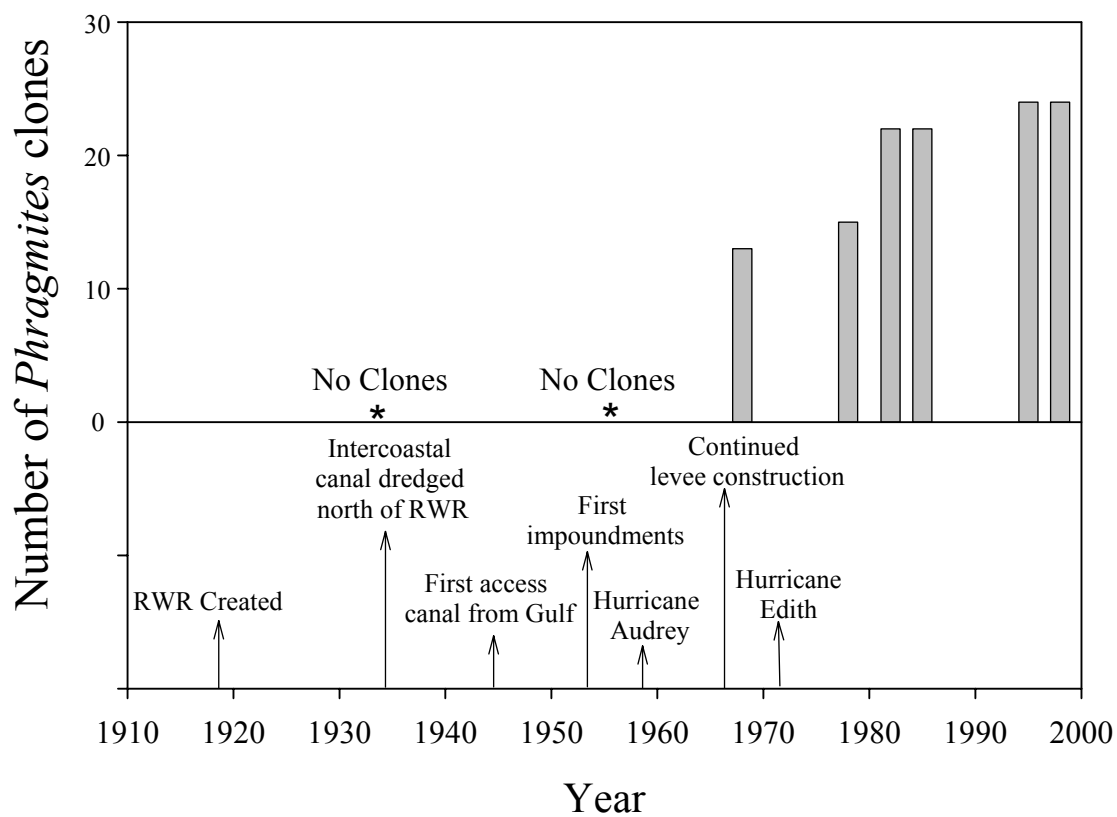


Figure 2-3. Cumulative number of *Phragmites* clones >5 in diameter detected on aerial photography between 1933 and 1998 in the westernmost 1000 hectares of coastal marsh. The lower timeline indicates major natural and anthropogenic impacts occurring in the Chenier plain during the same time period.

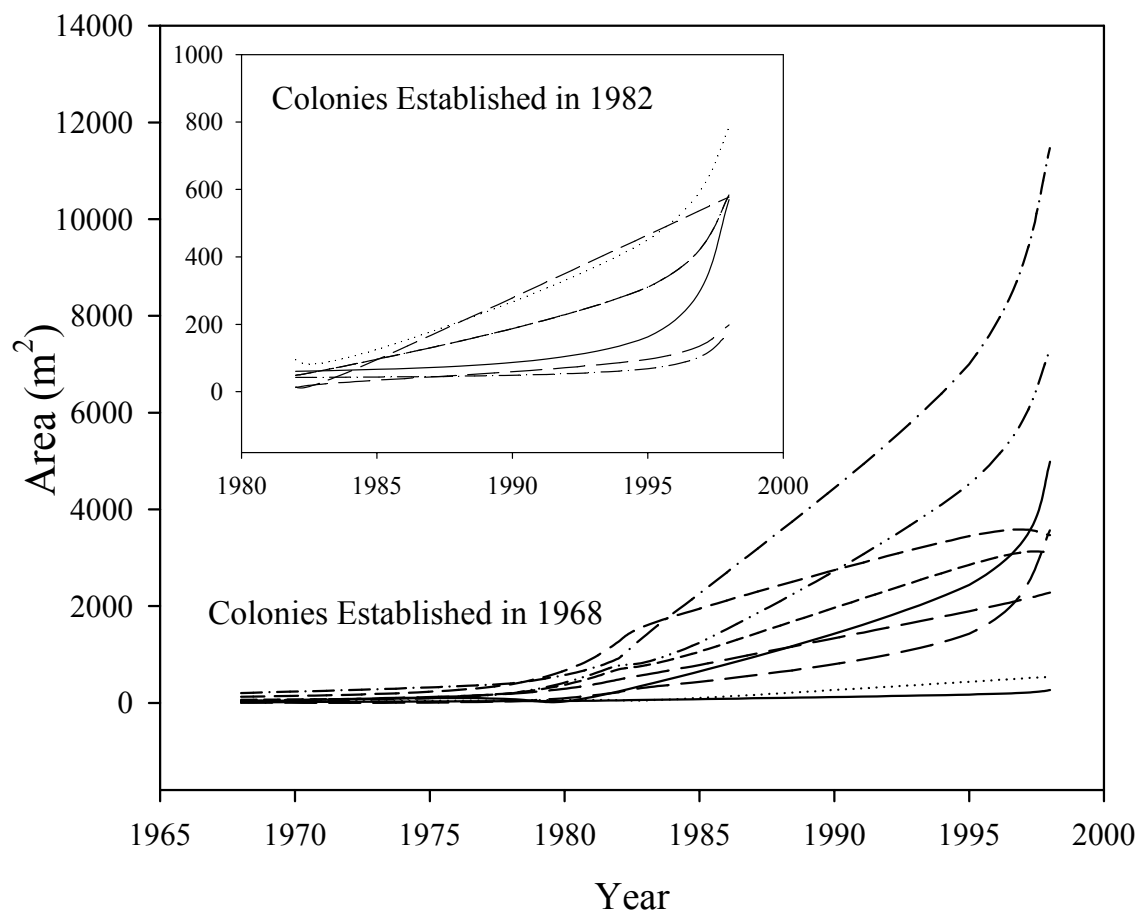


Figure 2-4. Area (m²) of *Phragmites* clones over time since initial detection in 1968. The inset graph depicts area of *Phragmites* clones over time that were initially detected in 1982. Lines are curved segments connecting time points between measured areas (m²). Time points for each measurement from 1968 clones include 1968, 1978, 1982, 1985 and 1995. Time points for each measurement from the 1982 clones include 1982, 1985 and 1995. No clones of *Phragmites* were identified on 1933 and 1955 photography.

Table 2-3. Summary of colony growth rate estimates from the non-linear Malthusian equation and growth estimates calculated using the fixed effects modeling, both with associated standard errors. The slope estimate is a measure of growth rate. Those denoted with * are not significantly different from zero.

Table 2-3.

Clone Number and Starting Areas					Nonlinear Regression Malthusian Exponential Growth Model with Iterations (Area = (Area) _o exp(b _{1t}))					Linear Regression (fixed effects, by colony) (log(area) = b _o + b _{1t})		
Clone	n (n-1)	Year Initially Observed	Starting Area (Area) _o	Log (start area) (b _o)	Slope Estimate (r-value) (b _{1t})	Approx. S. E.	Intercept Estimate (b _o)	S. E.	Predicted Establishment	Slope Estimate (b ₁)	S. E.	Predicted Establishment
1	2	1982	60.74	4.1066	0.1194	0.0132	4.00	0.4864	1946	0.1146	0.0379	1981
4	3	1982	94.47	4.5483	0.1297	0.0035	4.49	0.0771	1948	0.1311	0.0074	1981
5	2	1982	417.49	6.0343	0.1399	0.0006	6.03	0.0144	1939	0.1398	0.0012	1980
6	4	1968	10.37	2.339	0.1070	0.0012	2.46	0.1045	1945	0.1036	0.0053	1971
7	5	1968	41.34	3.7218	0.1364	0.003	3.99	0.2503	1940	0.1341	0.013	1973
8.1	3	1968	63.66	4.1529	0.1601	0.0048	4.02	0.2974	1942	0.1624	0.0255	1969
8.2	3	1968	46.20	3.8329	0.1618	0.0049	3.69	0.3065	1944	0.1635	0.0254	1969
8.3	3	1968	17.42	2.8577	0.1556	0.0071	2.76	0.2973	1950	0.1588	0.0246	1969
9	4	1978	33.32	3.5062	0.2027	0.0097	4.14	0.409	1958	0.1827	0.0333	1979
10.1	3	1968	32.09	3.4685	0.1647	0.0049	3.33	0.3129	1947	0.1672	0.0259	1969
10.2	3	1968	11.12	2.4084	0.2149	0.0057	2.25	0.4027	1957	0.2186	0.0333	1970
10.3	3	1968	20.97	3.0432	0.0965	0.0029	3.00	0.0834	1936	0.0972	0.0069	1965
11	4	1978	41.41	3.7236	0.1629	0.0053	3.96	0.1638	1954	0.1557	0.0133	1979
12	3	1982	48.85	3.8887	0.1526	0.0038	3.99	0.1263	1955	0.1444	0.0121	1981
13	3	1982	12.65	2.5378	0.1692	0.0049	2.76	0.2373	1965	0.1528	0.0228	1981
14	5	1968	11.87	2.4737	0.1290	0.0015	2.47	0.1303	1948	0.1288	0.0068	1974
15	2	1982	42.31	3.745	0.0767*	0.0201	3.67	0.5113	1930	0.0729*	0.0429	1977
18	2	1982	14.30	2.6605	0.2312	0.0072	3.24	0.7199	1968	0.2035*	0.0767	1982
21	5	1968	204.43	5.3202	0.1334	0.0011	5.04	0.248	1930	0.1411	0.0129	1974
24	5	1968	43.67	3.7767	0.1711	0.0012	3.88	0.2402	1946	0.1721	0.0125	1974
27	4	1968	28.98	3.3667	0.1700	0.0017	3.05	0.2616	1948	0.1763	0.0133	1974
28	5	1968	6.18	1.8207	0.2103	0.0021	1.93	0.3956	1959	0.2103	0.0206	1975

Phragmites Expansion Rates: Nonlinear Expansion Model

Most *Phragmites* clones increased in size over time (Figure 2-4). Several clones increased exponentially after what appeared to be a period of persistence with little or no increase in area (lag in expansion); other clones increased gradually in size.

The exponential model was fit to the data of each of the 21 clones (Table 2-3). The intrinsic rate of increase for each clone was estimated using least squares (PROC NLIN, SAS 1999; Table 2-3). The associated standard errors were very small, indicating a good fit of the model to the data. The estimated intrinsic rate of increase in area of each of the 21 clones of *Phragmites* ranged from 0.0767 to 0.2312 yr⁻¹ (Table 2-3). The predicted spread of clones in the exponential model was initially slow, indistinguishable from 0 in the early stages of growth, but increasing over time and producing rapid increases in area during the most recent time interval for many clones (Figure 2-4).

The exponential shape of the clone expansion curves (see Figure 2-4) and the absence of an asymptote (areas still growing in 1998) suggested that a log transformation of area would be appropriate for linear modeling. The log transformation was successful in linearizing the relationship.

Fixed Effects Analysis

A clone-specific analysis using a fixed effects model limits conclusions to only the measured clones in this study. The significant time by clone interaction indicated by the analysis of covariance linear model suggested differing expansion rates for each clone ($p < 0.0001$).

Separate regressions were fit for each clone for which there were at least 2 photographs beyond the starting time t_0 . The estimated slope was not significantly different from 0 for only two clones, 15 and 18 (Table 2-3). The other estimated slopes for these linear regression models

(on the log scale) ranged from 0.097 to 0.210, indicating an increase in area of 10% to 21% per year for each clone. Intercepts were included in the model to allow for variation in stand establishment at $t = 0$. The estimated slopes (growth rate) for the nonlinear and linear models were similar (Table 2-3), and the small standard errors associated with each of the models suggest that exponential expansion rates with a nonzero starting point can be used to predict changes in clone size over time.

Random Effects Analysis

The random effects model considers the observed clones to be a random sample from a potential population and thus gives one expansion estimate (intercept) and associated standard deviation. There were significant differences between the initial areas (intercepts) and expansion rates (slopes) for the different clones observed in this study (intercepts, $p < 0.001$; slopes, $p = 0.001$, SAS PROC MIXED, 1999). The significance of these random effects was determined by likelihood ratio tests that iteratively deleted each effect and tested the fit of the model at each stage.

The estimated intercept distribution (clone area) had a mean of 3.5 ± 0.85 (s.e.) m^2 and a standard deviation of 0.8471 on the transformed scale. A 95% confidence interval for the mean of the log transformed starting areas for a population of *Phragmites* clones was 1.89 to 5.21. The corresponding interval for the median observed starting area was 6.604 to 182.783. Although this confidence interval is rather wide, it is representative of a population of starting areas and also includes any error encountered in the quality of the aerial photography.

The estimated expansion rates of clones had a mean of 0.15 yr^{-1} and a standard deviation of 0.03 on the log transformed scale. A 95% confidence interval for the expected change in the $\log(\text{area})$ for 1 year was 0.1 to 0.21. The predicted percent increase in area for 1 year for a

population of such clones ranged from 10.5% to 22.8%. For 3 years, the minimum time between photo observations, the corresponding interval for the median increase was 35.1% to 85.1%.

Phragmites Expansion Contrasts

Both the non-linear and the linear procedures provided similar expansion estimates. A regression relating both data sets yielded an r^2 value of 0.95.

Expansion rates were not different based on the age of *Phragmites* colonies (Figure 2-5). The non-linear analysis indicated no significant differences ($p = 0.55$) in expansion rates between clones first observed in 1968 ($0.15 \text{ yr}^{-1} \pm 0.01$), 1978 ($0.18 \text{ yr}^{-1} \pm 0.02$) or 1982 ($0.15 \text{ yr}^{-1} \pm 0.02$). There were also no significant differences ($p = 0.46$) in expansion rates based on observation dates in the linear analysis (1968 ($0.16 \text{ yr}^{-1} \pm 0.01$); 1978 ($0.17 \text{ yr}^{-1} \pm 0.01$); 1982 ($0.14 \text{ yr}^{-1} \pm 0.02$); Figure 2-5).

Phragmites clonal expansion was not different based on growing environment (Figure 2-6). For the non-linear analysis, there was no significant difference ($p = 0.142$) between clones adjacent to water in unmanaged areas ($0.1286 \text{ yr}^{-1} \pm 0.0134$), clones adjacent only to vegetation in unmanaged areas ($0.1635 \text{ yr}^{-1} \pm 0.0122$) and clones adjacent only to vegetation in managed areas ($0.1712 \text{ yr}^{-1} \pm 0.0157$). However, when using the results from the linear analysis, a significant difference ($p = 0.05$) was found between clones adjacent to water in unmanaged areas ($0.12 \text{ yr}^{-1} \pm 0.01$) and clones in managed areas surrounded by vegetation (0.18 ± 0.01), yet no significant difference between those and colonies in unmanaged areas surrounded by vegetation ($0.16 \text{ yr}^{-1} \pm 0.01$, Figure 2-6).

Prediction of *Phragmites* Establishment Dates: Fixed Effects Analysis

The predicted establishment dates for the *Phragmites* clones estimated by the non-linear model ranged from 1930 to 1968, whereas the linear model gave establishment estimates ranging

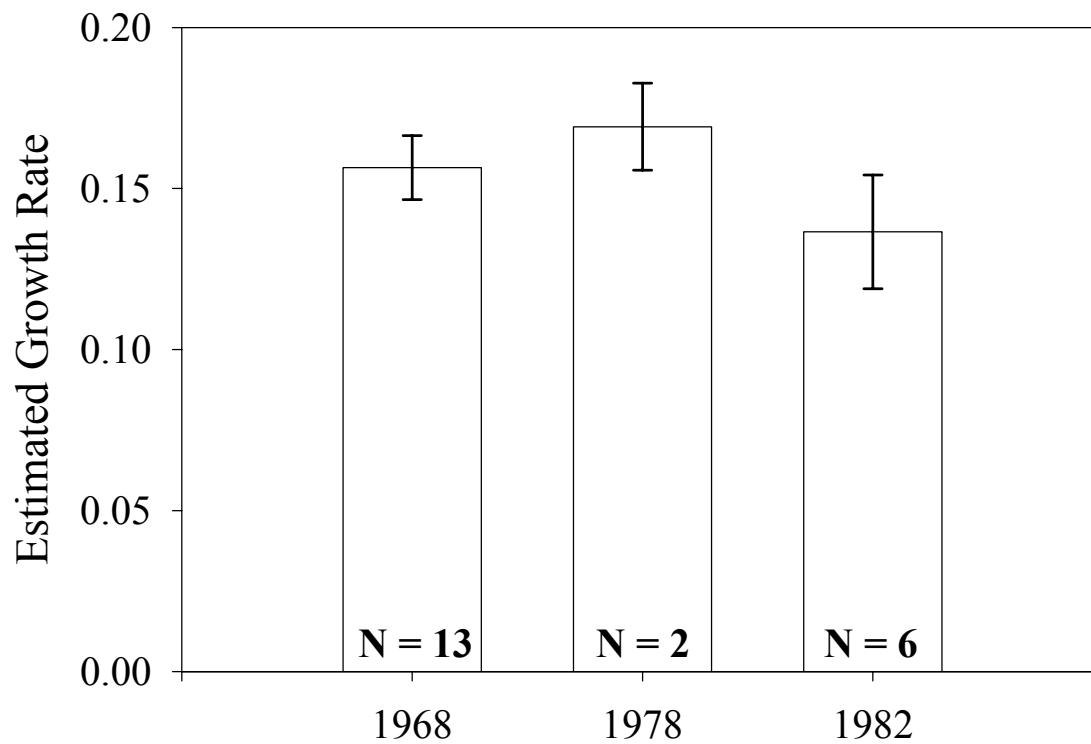


Figure 2-5. Estimate of expansion rates (yr^{-1}) from linear modeling of *Phragmites* clones, based on establishment times analyzed using a Student t-test. Means \pm standard errors are depicted by horizontal lines and vertical bars ($p = 0.458$).

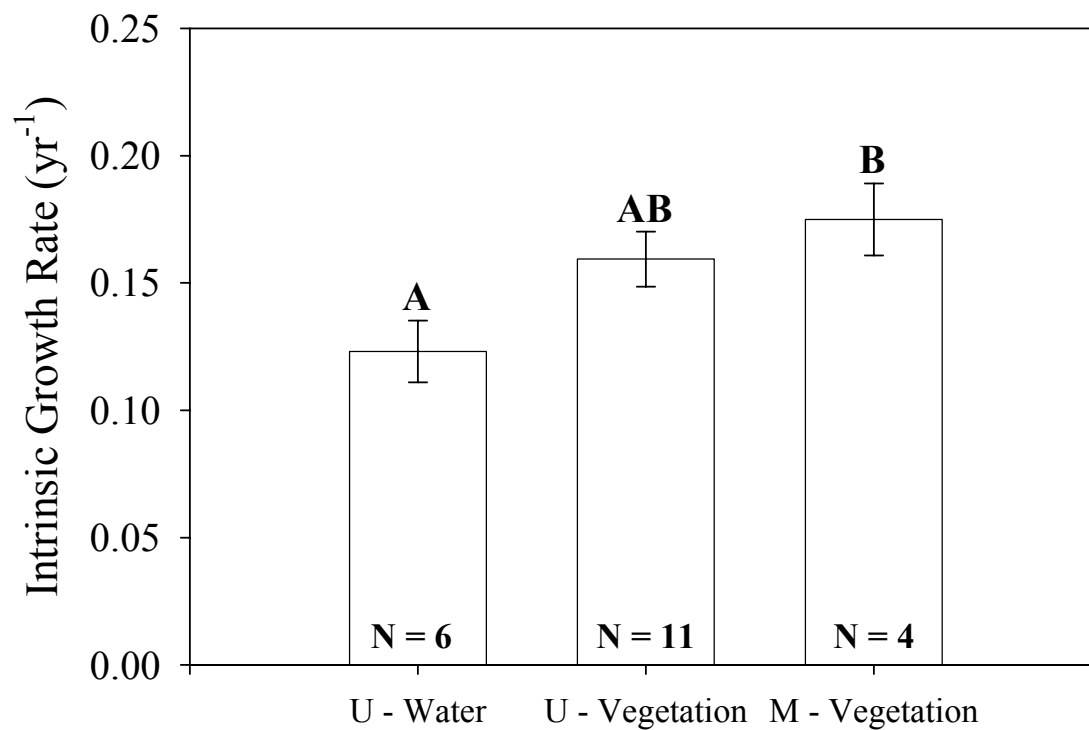


Figure 2-6. Intrinsic Growth Rate of *Phragmites* clones in managed areas completely surrounded by vegetation (M-vegetation), unmanaged areas surrounded by vegetation (U-vegetation), and unmanaged areas adjacent to water (U-water) at Rockefeller Wildlife Refuge. Analyses performed using a Student t-test. Means \pm standard errors are depicted by horizontal lines and vertical bars.

from 1965 to 1982 (Table 2-3). Calibration of the non-linear model suggests that for a given clone, the time for predicted establishment using the estimates (value of zero $\log(\text{area})$, assumes $\text{area} = 1 \text{ m}^2$ is noticeable on aerial photography) would be $-b_0/b_1$ (where b_0 and b_1 are the estimates of earliest observed area and growth rate). For example, colony 27, in the non-linear model, first observed in photos of 1968 would have an estimated starting time ($-3.3667 / 0.1763 = -19.1$ years) in late 1948, and in the linear model would be the x-intercept at 1974. Colony 21, also first observed in 1968, would have a non-linear estimated starting time ($-5.3202 / 0.1411 = -37.9$ years) in early 1930 and 1974 for the linear x-intercept. Each of the non-linear point estimates for establishment has an associated standard error that differs for each colony and is based on the number of observations of each colony on the aerial photography.

Prediction of *Phragmites* Establishment Dates: Random Effects Analysis

Those colonies initially observed in 1968 were used in the random coefficients model in an attempt to predict the average time at which that set of colonies may have become established. Prediction intervals for this set of colonies were centered at -19.5 years or mid 1949.

Discussion

Disturbances, both anthropogenic and natural, have been shown to exacerbate the dispersal, establishment and spread of invasive species (Elton 1946;1958; Platt 1975; Hobbs and Huenneke 1992; Horvitz et al. 1998). For example, draining wetland areas through ditching may suppress water tables, giving species less tolerant to waterlogging stress the opportunity for invasion (Bart and Hartman 2000). Drainage will have long lived effects on edaphic conditions, allowing these species to persist and spread. Natural events, such as hurricanes, may spread seed or propagules to other locations where they did not exist before. If conditions are favorable, populations establish, spread and ultimately change vegetative community structure. Thus both

human induced and natural events may provide windows of opportunity for the establishment and expansion of invasive species.

Widespread Landscape Scale Changes

The marshes within the Louisiana Chenier Plain began forming about 3000-4000 years ago during periods when the Mississippi River followed a westerly course (Gould and McFarlan Jr. 1959; Gosselink et al. 1979). Expansive mudflats were created with westward shifts of the Mississippi River causing large quantities of riverine sediments to be deposited on the gulf shore. At the end of a delta building sequence, the river shifted eastward and erosion reworked the gulf shoreline to form a beach ridge (Chenier) parallel to the shoreline, consisting of shell and sand, and typically higher elevation than the surrounding marshes. The repetition of this cycle resulted in a series of shore-parallel ridges separated by inter-ridge marshes that comprise the Chenier Plain.

The hydrology of this natural coastal system has been altered extensively (see timeline, Figure 2-3). During the 1930's, the Intracoastal Waterway connecting White and Grand Lake was completed. This canal continued east and west, interrupting the north-south flow of fresh water and redirecting it east and west. The installation of locks and impoundments throughout the watershed has reduced water flow, disrupting the natural drainage in these marshes (Gammill 2002). In addition, highway construction (LA Hwy 82 and 27) further impeded the north-south flow of fresh water.

Within RWR, the formation of canals and impoundments exacerbated the hydrologic disconnection. In 1944 the Humble Canal, the first oil exploration canal in the RWR, was excavated. This also resulted in increased drainage of water from the interior portions of the refuge (Wicker and Endres 1995). In 1954-55, the first impoundments were built in intermediate

(oligohaline) marsh areas using existing oil access canal spoil banks and stranded/remnant beach ridges through the refuge. These impoundments were periodically drained and flooded to enhance production of waterfowl foods.

Nichols (1959a) identified and measured 4 stranded beach ridges running roughly parallel to the shoreline in RWR. These subsided ridges, which are 2-3 cm higher in elevation than the surrounding marsh, are not usually discernable by changes in vegetation. Nichols did identify *Phragmites* occurring in the northern most portion of one of these ridges, which was situated within an intermediate marsh. The next ridge, located 2.5 km to the south, was situated in a brackish marsh and was not, at that time, colonized by populations of *Phragmites* (Nichols 1959b)

The construction of the Intracoastal Waterway, creation of impoundments and canal excavation throughout the watershed most likely did not result in the invasion of *Phragmites* because it was not present in brackish marshes in either early surveys (O'Neil 1949; Nichols 1959a) or on the early aerial photography. However, the combination of these events likely lowered water levels relative to stranded/remnant beach ridges found in the interior brackish marshes south of the Chenier ridge. The combination of a lowered water table in the interior portions of the marsh and the interruption of fresh water sheet flow from the north likely generates suitable conditions for the establishment of species such as *Phragmites* in areas with slightly higher elevation.

Phragmites Dispersal

Between 1955 and 1968, two major events occurred that may have provided a window of opportunity for the establishment of *Phragmites*. In 1954-55, the first impoundments were built in intermediate marsh areas using existing oil access canal spoil banks and stranded/remnant

beach ridges through the refuge. These impoundments were periodically drained and flooded to enhance production of waterfowl foods. Some of the clones first apparent on the 1968 aerials are located inside these impoundments. Not all of the clones that appear in the 1968 aerials, however, are located inside impoundments. Some are located along an undisturbed stranded/remnant beach ridge at the western edge of RWR. Establishment of these clones may have also occurred following Hurricane Audrey in 1957 (Figure 2-7). The center of the eye of this large category IV hurricane crossed the Louisiana coastline about 100 km west of RWR, produced tidal surges of 3-4 m at RWR and winds of 120 km/hr. The influx and egress of water was associated with large-scale movement of vegetation, possibly resulting in rhizome fragments being transported into the brackish marsh from the more inland intermediate marsh. Regardless of the origin of *Phragmites* in impoundments or transport by the hurricane, clones present in 1968 did not expand rapidly; these clones took at least a decade to initiate the more rapid growth that I documented in this study.

Natural disturbances may influence the post-invasion dynamics of *Phragmites* spread. Prior field and greenhouse experiments indicate low rates of seedling emergence in populations of *Phragmites* at RWR (see Ekstam and Forseby 1999; Ekstam et al. 1999; Pellegrin and Hauber 1999; Mauchamp et al. 2001). We propose that post-invasion spread of *Phragmites* most likely arises through physical transport of rooted culms or rhizomes to new sites. Plants arising from such fragments would be more resistant to increased salinities (Lissner and Schierup 1997) and could remain viable even through severe drought conditions (L. E. Stanton, personal observation). In contrast, seedlings often are sensitive to harsh conditions and can take up to 2 years to become successfully established (Haslam 1971).

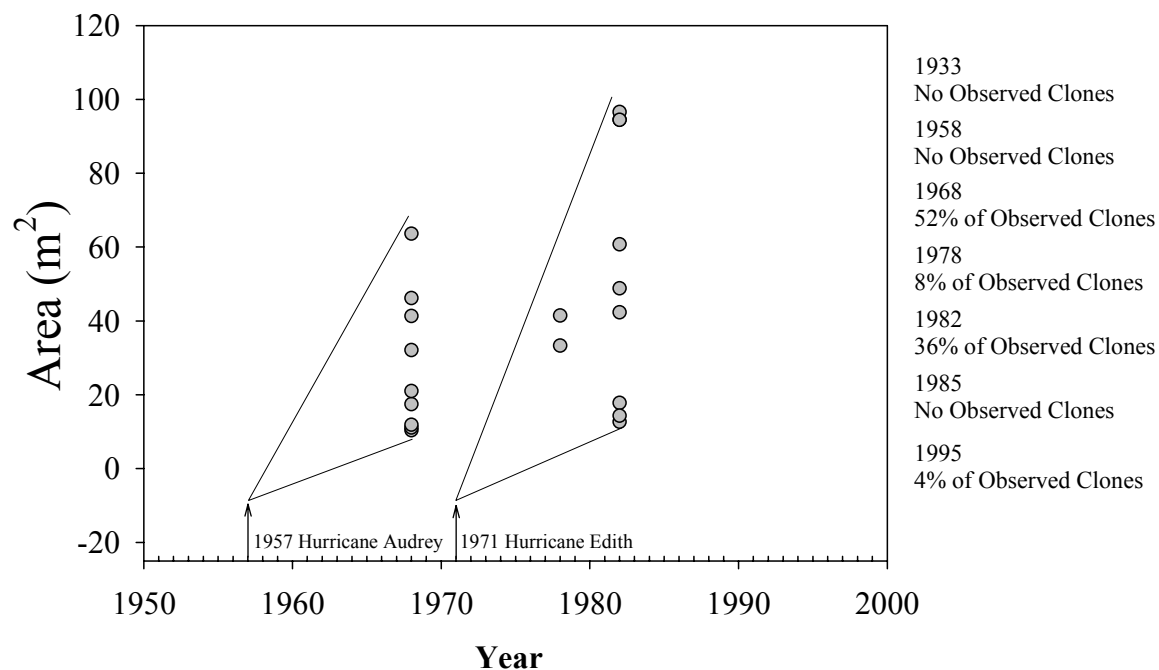


Figure 2-7. Size of *Phragmites* clones (m²) in year of initial appearance in aerial photography. Arrows denote major hurricanes that affected Rockefeller Wildlife Refuge. Note the larger numbers of new clones observed 10 years after each storm event.

The results from our analysis suggest that establishment of *Phragmites* clones did not coincide with major storm events affecting RWR. Table 2-3 lists the estimated establishment times for each individual colony using both the linear and non-linear data. In addition, a prediction using the random effects analysis for colonies that first appeared on the 1968 photographs did not coincide with a storm event, as suggested in Figure 2-7. The 1968 colonies were predicted to have established in mid 1949, which was 8 years before Hurricane Audrey made landfall.

Both the exponential and the linear models “bracket” establishment times for each of the *Phragmites* colonies in this study. The exponential model did not accurately predict establishment times because it estimated establishment well before Nichols (1959a) and O’Neil (1949) conducted their studies and the 1955 aerial photography, none of which identify *Phragmites* in the study area (Table 2-3). In contrast, the linear model often predicts *Phragmites* establishment after the clones had been identified on aerial photography (Table 2-3). This disparity suggests that the rate of clonal spread has changed, such as a lag in clonal expansion after establishment, or the initial density of culms in establishing clones was too low for detection on the aerial photography. Thus, these models do not have the resolution to incorporate changes in expansion rates and therefore yield incorrect establishment times. As a result, the hypothesis that storm events may be responsible for the establishment of new *Phragmites* colonies cannot be discounted.

Phragmites Expansion

Historically, *Phragmites* has existed in North American marshes for thousands of years (Orson et al. 1987), yet the reasons for recent expansions in its range and increases in abundance within its historical range have not been delineated. Rapid expansion of area occupied can be

expected if invasion is followed by dispersal to new areas not adjacent to existing clones (Moody and Mack 1988). *Phragmites* is capable of dispersing new ramets (either clonal fragments or by seeds) far enough that clones are not likely to spread as a front, but rather as a saltatorial spread. Many smaller *Phragmites* clones can occupy a greater area as they expand than could one large clone (Mack 1985). In addition, each independent clone has the capability to further distribute seed or clonal fragments to additional sites, thus increasing the overall rate of the invasion process.

The occurrence of *Phragmites* clones has increased in relatively undisturbed interior portions of brackish marsh in southwest Louisiana over the last 50 years. The clones examined in this study were, in most instances, unbounded by physical barriers such as levees or other changes in topography (six of the 22 colonies were adjacent to water). There were no vegetation barriers such as shrubs or trees that prevented clone expansion (Havens et al. 2002). Stands of *Phragmites* have become pervasive in many areas previously occupied by native short graminoids, typically comprised of a mixture of *Spartina patens*, *Schoenoplectus robustus* and *Distichlis spicata*.

Phragmites is a dominant competitor, both above and belowground. *Phragmites* has a distinct height advantage (culms 3-4 m) to capture more light than shorter graminoid species (<1 m tall). In addition, *Phragmites* has a deep well-developed rhizome network (>1 m depth) that can access different belowground resources (Burdick et al. 2001) and remain protected in the event of fire (Cross and Fleming 1989). Furthermore, the extensive rhizome network is integrated, allowing translocation of resources among ramets (Amsberry et al. 2000). These morphological and physiological characteristics, coupled with an extended growing season beginning in March and lasting through October, may result in accelerated expansion rates in

Louisiana marshes. Thus, it seems likely that the spread of these isolated *Phragmites* clones will continue unchecked in interior marshes until they merge with other *Phragmites* clones, reach a physical barrier, or exhibit a reduction in growth due to environmental or biological changes.

The densities of the culms in *Phragmites* clones are sparse initially. When ground-truthing was conducted in 1998, several small clones were observed and delineated with GPS. However, the low densities of the clones made efforts to locate them on the 1998 aerial photography unsuccessful. It is likely that sparse clones are present even when no visual identification is made when using aerial photography. It is not known how long clones remain sparse, or what densities are necessary to become observable in aerial photography. A distinct lag phase was demonstrated by colonies first observed in 1968 and in 1982. In both cases, the lag time between establishment and rapid increases in expansion are between 10 and 15 years (Figure 2-3). Change in the rate of clonal spread might occur in brackish areas once the rhizome network becomes established and may be a partial explanation for the lag in growth seen in the colonies studied. Burdick (2002) suggests that *Phragmites* rhizomes can utilize fresh water trapped beneath a lens of higher salinity water near the surface. Higher salinities near the marsh surface may reduce clonal growth rates of establishing stands. However, once deep rhizomes are produced, clonal expansion rates may increase due to improved nutrient absorption and water acquisition capacity.

The growth form of *Phragmites* may facilitate its invasion into sub-optimal environments. In previous studies, *Phragmites* establishment has been associated with disturbances that reduce harsh environmental conditions (Bart and Hartman 2000) or has occurred along a sharp environmental gradient (Amsberry et al. 2000). In New England marshes, elevation gradients are horizontally compressed, creating sharp environmental

gradients. Therefore, *Phragmites* establishment occurs in areas with optimum environmental conditions, and clonal integration between ramets facilitates invasion of less-optimum environments (Amsberry et al. 2000; Bart and Hartman 2000). However, in Gulf Coast marshes, changes in elevation along the coast are small, resulting in a gradual gradient between harsh and benign environmental conditions. In such unbounded marshes, this same clonal integration appears to result in ever increasing rates of clonal expansion. Losses of areas containing short graminoids to *Phragmites* are likely to accelerate over time, resulting in rapid takeover of a marsh once clones reach critical sizes.

Phragmites invasions are prevalent in many coastal areas (Rice et al. 2000). The post-invasion expansion of *Phragmites* along the Mid-Atlantic Coast has been described using deterministic non-linear expansion models (Rice et al. 2000). Bailey (1997) reported intrinsic rates of increase in sizes of clones in a Delaware low salinity marsh (0-10ppt) as 0.0024 yr^{-1} between the years of 1979-1988 and 0.057 yr^{-1} between 1988 and 1993. These rates of clonal expansion are less than rates ranging from 0.0160 yr^{-1} to 0.1175 yr^{-1} in a mesohaline marsh and 0.1221 yr^{-1} to 0.2123 yr^{-1} in an oligohaline marsh found by Rice et. al (2000). The intrinsic rates of increase found in this study ranged from 0.0767 to 0.2312 yr^{-1} in managed marshes with salinities between 7 and 15ppt and 20-42ppt in unmanaged areas, which fall within the upper range reported for *Phragmites* expansion in previous studies.

Expansion Rates Based on Age and Environment

For some clonal species, there is a decline in expansion rates as the genet ages (Cheplick 1998). Rice and others (2000) indicated that the intrinsic rate of increase in clones of *Phragmites* established prior to 1985 along the Mid-Atlantic coasts had decreased or stabilized in both fresh water and mesohaline marshes. This may be due to *Phragmites* clones merging with

other clones or reaching a physical or environmental barrier. In comparisons between different aged *Phragmites* clones in this study, there was no evidence to indicate that stand age had any effect on the intrinsic rate of increase (Figure 2-5). Thus, we do not expect a decrease in outward expansion of *Phragmites* in these habitats unless environmental conditions become less favorable for growth or until a physical barrier is reached.

Post-invasion spread of *Phragmites* is not affected by being in managed or unmanaged areas. The expansion rates of *Phragmites* clones located in water level managed portions of Rockefeller Wildlife refuge were not greater than those in unmanaged areas and managed areas. Although clonal expansion rates were lowest for clones adjacent to water, this is most likely because expansion is retarded in submerged environments and the clones are only expanding in one direction (van der Valk 1994; Rea 1996).

Conclusion

Phragmites has become established and spreading throughout coastal areas of Louisiana. This establishment is most likely not a direct result of any single natural or anthropogenic disturbance, but rather a combination of compounding disturbances. Once established, *Phragmites* does not appear to persist until a genetic shift releases competitive restraints or if environmental conditions improve. Expansion rates are consistent from the time clones are detectable, many exhibiting exponential spread. Thus, *Phragmites* is demonstrating the same characteristics as non-native invasive species. Since unchecked growth occurs immediately once established, managers should begin control efforts as soon as an invasion is noticed.

It is obvious that the brackish marsh of southwestern Louisiana is a favorable habitat for *Phragmites*. Our data suggest that initial establishment occurred at least 70 years ago. Post-invasion spread is occurring rapidly regardless of whether marsh management techniques are

practiced. However, the mechanism by which new clones of *Phragmites* establish remains unclear. What seems likely is that *Phragmites* expansion and spread will continue unchecked until harsh environmental conditions overcome the species tolerance levels and surpass the benefits of clonal integration, competition with woody species impedes growth or a physical barrier is reached. This will occur at the expense of the indigenous short graminoids that have historically occupied these marshes and will ultimately change the nature of coastal Louisiana marshes.

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CHAPTER 3

THE EFFECT OF DISTURBANCE AND NUTRIENT INTERACTIONS ON COMMUNITY INVASIBILITY AND THE ESTABLISHMENT OF *PHRAGMITES* *AUSTRALIS* IN A BRACKISH MARSH IN SOUTHWESTERN LOUISIANA

Introduction

As biological invasions have become a common phenomenon throughout the world, ecologists have intensified efforts to understand and predict why natural communities are susceptible to invasion (Elton 1958, Crawley 1987, Richardson and Bond 1991, Robinson et al. 1995, Wiser et al. 1998, Stohlgren et al. 2003). With the understanding that biological invasions will continue to intensify in response to increasing human populations and global climate change (Thompson et al. 2001), many ecological investigations have focused on identifying specific characteristics of communities vulnerable to invasion and the invading species (Elton 1958, Crawley 1987, Tilman 1999, Naeem et al. 2000, Prieur-Richard and Lavorel 2000, Hector et al. 2001, Kennedy et al. 2002, Prieur-Richard et al. 2002).

Although the susceptibility of a natural community to invasion has most commonly been correlated with species richness (Elton 1958, Tilman 1999, Naeem et al. 2000, Hector et al. 2001, Kennedy et al. 2002, Pennings et al. 2002), inconclusive results have caused a shift from an emphasis on richness/invasibility relationships to examinations of landscape scale changes in disturbance regimes and availability of resources as determinates of invasibility (Orians 1984, Heywood 1989, Schierenbeck et al. 1994, Burke and Grime 1996, Higgins and Richardson 1998, Horvitz et al. 1998, Wiser et al. 1998, Levine and D'Antonio 1999, Smith and Knapp 1999, Hector et al. 2001, Stohlgren et al. 2003). For example, in some communities disturbances such as fire and grazing may influence an invaders success directly by altering resource availability (Pickett and White 1985, Burke and Grime 1996) or indirectly by changing biotic interactions

(competition) and subsequently community structure (Richardson and Bond 1991, Hobbs and Huenneke 1992). Furthermore, nutrient enrichment from agricultural and urban areas can favor fast growing exotic species, effectively creating a shift in community structure and ultimately changing ecosystem functions (Burke and Grime 1996, Hector et al. 2001). Yet when communities are subject to both disturbance and eutrophication, the mechanisms directly and indirectly affecting community stability and invasibility are often difficult to separate.

Coastal wetlands have become more vulnerable to invasive species in the last 50 years (Thompson et al. 1987, Chambers et al. 1998, Galatowitsch et al. 1999, Bart and Hartman 2000, Stohlgren et al. 2003). Even though wetland communities are disturbed naturally by wrack deposition (Bertness and Ellison 1987, Brewer and Bertness 1996, Minchinton 2002), periodic fires (Hackney and de la Cruz 1981, Ceulean and Engstrom 1993, Nyman and Chabreck 1995) and intense herbivory events (Taylor and Grace 1995, Gough and Grace 1998), it has been suggested that disturbances resulting from increased urbanization and development in coastal areas have surpassed that which wetlands are typically subject and may be responsible for the increased prevalence of invasive species (Wilcox 1995, Chambers et al. 1998, Chambers et al. 1999, Detenbeck et al. 1999, Ekstam et al. 1999, McKee and Baldwin 1999). Furthermore, coastal wetlands occupy fringing and estuarine landscape positions that continue to receive elevated nutrients via rivers, watersheds and drainage basins (Morris 1991, Gale et al. 1994, Rabalais 2002, Rabalais et al. 2002, Turner and Rabalais 2003), which could further enhance community vulnerability.

However, invading species can only become established if they are pre-adapted to existing environmental conditions of the invaded community (Wilson 1961, Ewel 1986). In addition to the natural and anthropogenic disturbances to which wetlands are exposed, these

habitats are subject to constant environmental stressors such as waterlogging (Jones 1970, Gleason and Zieman 1981, Mendelssohn and McKee 1992, Bornette and Amoros 1996), elevated salinities (Parrondo et al. 1978, Morris 1984, Mendelssohn and McKee 1992), sulfides (Havill et al. 1985, Patterson and Mendelssohn 1991, McKee et al. 2004) as well as root oxygen deficiency (Mendelssohn et al. 1981, Howes and Teal 1994). Thus, the successful wetland invasive species must be physiologically adapted to rather stressful conditions independent of the disturbances that can alter resource availability or provide an opportunity for establishment.

As urbanization of the coastal zone continues, higher levels of disturbance and increased nutrient loading may provide windows of opportunity for the establishment and spread of invasive species in coastal plant communities. Marsh plant recovery and resulting zonation patterns have been examined after small-scale disturbances (Bertness and Ellison 1987, Hartman 1988, Shumway and Bertness 1994) and in response to nutrient enrichment (Levine et al. 1998, Pennings et al. 2003). However, the effects of disturbance and nutrient enrichment on the successful establishment of an invading species and on how these factors control community invasibility have not received scientific scrutiny.

Hence, I have investigated the mechanisms controlling community invasibility of a brackish coastal marsh by the common reed, *Phragmites australis* (hereafter referred to as *Phragmites*), in the Northern Gulf of Mexico. Although largely considered a native species (Neiring and Warren 1980, Orson 1987), an invasive non-native strain of *Phragmites* has been identified along the eastern seaboard of the U.S. and is known to be responsible for the observed spread in those areas (Saltonstall 2002). Although it isn't known if these Northern Gulf Coast populations are of that non-native strain, it has been identified along the Mississippi River Delta and could possibly have spread to other areas of coastal Louisiana (Saltonstall 2003).

Phragmites has become invasive in many freshwater, tidal brackish and salt marsh communities along the Atlantic and Gulf Coasts of the United States over the last 75 years, forming large monospecific stands in habitats where it had not occurred previously (Meyerson et al. 2000).

Although coastal marshes are subject to nutrient enrichment and disturbance, it remains unknown if these events increase susceptibility to *Phragmites* invasion. Therefore, I addressed several questions related to brackish marsh invasibility in this study: (1) How does the intensity of disturbance influence natural recruitment into a tidal wetland? (2) Is the invasibility of a natural community enhanced in non-lethally and lethally disturbed areas when an invasive species is purposefully introduced? (3) Furthermore, is invasibility promoted by nutrient enrichment in conjunction with both non-lethal and lethal disturbances? And (4) are disturbed areas more susceptible to establishment by seedlings or rhizome fragments? To answer these research questions, I tested the invasibility of a South Louisiana brackish marsh by manipulating both nutrient levels and disturbance regimes in conjunction with purposeful introductions of *Phragmites* seed and rhizome material. My results show that the natural marsh community quickly recovered from disturbance treatments and responded positively to fertilization. Although no seedlings emerged, one third of the *Phragmites* plants introduced to undisturbed and disturbed plots in this study remained viable, even during two record setting drought seasons. This study demonstrates that *Phragmites* has the potential for active growth and spread once environmental conditions improve, and that brackish marshes are likely susceptible to *Phragmites* invasion.

Methods

Study Site

Rockefeller Wildlife Refuge (29°55' N 92°30' W; hereafter RWR) lies within the southeastern portion of the Chenier Plain Region of coastal Louisiana (Cameron Parish, Figure 3-1). It is bordered on the south by the Gulf of Mexico, on the north by the Grand Chenier Ridge complex, and contains about 32,000 hectares. Present-day RWR was purchased by the Rockefeller foundation in 1914, and subsequently deeded to the state of Louisiana in 1920 under the mandate to “preserve, maintain, and improve, whenever practical, the refuge lands in perpetuity”. The majority of the refuge is actively managed through the use of water control structures to maximize germination of annual plants important as food for waterfowl (Wicker et al. 1983).

The study site is located in a 1000-hectare portion of brackish marsh on the western border of the refuge. This marsh is bounded to the south by the Gulf of Mexico, and the majority of this area has remained unmanaged since the inception of the refuge. It is comprised of *Spartina patens* (hereafter *Spartina*) and *Distichlis spicata* (hereafter *Distichlis*), with sparse inclusions of *Schoenoplectus robustus* (hereafter *Schoenoplectus*) and *Juncus roemerianus*. *Spartina alterniflora* is also present, but is restricted to areas immediately adjacent to water bodies (Nichols 1959). Although discreet populations of *Phragmites* have become established within this area, this experiment was conducted in an area where *Phragmites* has not invaded.

Experimental Design

Treatments were arranged in a split-plot design in strips with the main factors being level of disturbance (control, non-lethal, and lethal) and fertilization (ambient and fertilized). Blocks ($n = 5$) were 21 m in length and 6 m in width, with 2 m separating each treatment combination.

Figure 3-1: The location of Rockefeller Wildlife Refuge in coastal Louisiana, and the experimental design used in this study. The refuge lies in southwestern Louisiana on the border between Cameron and Vermillion Parishes and borders the Gulf of Mexico. The study design is a split-plot in strips with main treatment factors being disturbance (undisturbed, non-lethal and lethal) and nutrient additions (fertilized and ambient). Within each treatment combination is propagule addition (control, seed and rhizome) to test *Phragmites* establishment under different main treatment conditions. This figure depicts one block of five total.

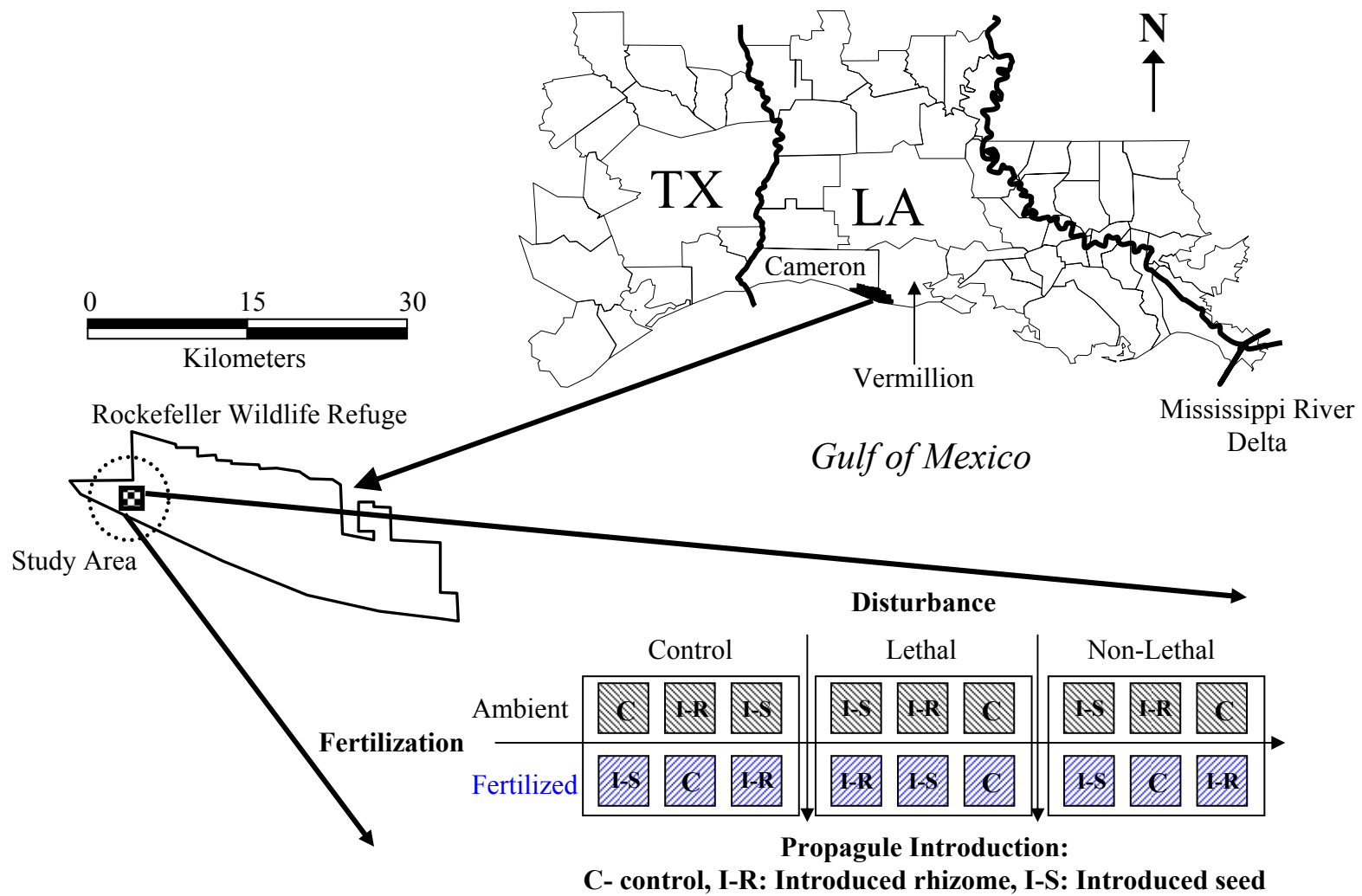


Figure 3-1

Experimental plots (1 m²) were manipulated at two different levels to mimic natural disturbances that commonly occur in coastal marsh ecosystems (fire/grazing and burial by wrack- McKee and Baldwin 1999). Undisturbed, or control plots, were not modified, while plots that mimicked a fire/grazing disturbance (non-lethal) were mechanically clipped with a weed trimmer to remove aboveground vegetation. To imitate complete plant dieback (lethal disturbance), such as that occurring after severe burial by vegetative wrack or other debris, one third of the experimental plots were treated repeatedly with a short-lived systemic herbicide (Roundup[®], Monsanto). Once aboveground plant material died, remaining standing dead biomass was mechanically clipped using a weed-trimmer. Additional clipped plant material from non-lethally disturbed plots was added to create a uniform wrack depth of 15 cm across the entire plot. Fertilized plots received a total of 500 Kg N ha⁻¹ y⁻¹ applied in three equal portions once every 4 months and two weeks prior to sampling (Mendelssohn 1979). Fertilization treatments began in May 1999.

To determine how dispersal mechanism (seed or rhizomes) would favor *Phragmites* establishment, three 1 m² plots, spaced 1 m apart were established within each treatment combination (Figure 3-1). Plots receiving seed had approximately 20 panicles from nearby *Phragmites* populations evenly distributed within the plot and anchored in place with 2.5 cm monofilament mesh. Those plots receiving live *Phragmites* rhizome material received 1 sod of *Phragmites*, standardized to approximately 20 cm in diameter and 30 cm deep. Sods were collected from nearby populations of *Phragmites*. Each culm was clipped to ground level and the remaining sod with rhizomes was placed in the center of the 1 m² plot and anchored with plastic coated aluminum wire to prevent movement. The third plot within each treatment combination was left unplanted to measure natural recruitment. A total of 5 blocks of each

treatment combination was created with each disturbance/nutrient arrangement containing three plots for propagule additions (seed, rhizome and control). Both main treatments (disturbance and fertilization) and propagule types were assigned randomly within each block.

Vegetative Measurements

Species composition and cover were measured every 4 months (5 times over the course of the study) within each plot using a 0.25 m² quadrat divided into 100 sections to obtain a nondestructive measure of vegetative success. All measurements were averaged to obtain overall cover and compared by each disturbance/nutrient combination. At the conclusion of the experiment (November 2000), all aboveground vegetation within a 0.5 m² area in the center of each plot was clipped at ground level and sorted to species. Once sorted, 6 stems of both *S. patens* and *D. spicata* were randomly selected and the length measured. All plant material was then dried to constant weight at 70 °C and weighed.

At the conclusion of this experiment, all *Phragmites* plants were collected by the complete removal of all above and belowground material. Rhizomes were excavated, collected and tested with a tetrazolium assay to determine viability (Parker 1953, Steponkus and Lanphear 1967).

Environmental Measurements

To ascertain soil oxidation status within each disturbance/nutrient combination, Eh (redox potential) measurements were taken in the field within the upper one to two cm of soil (n = 3; hereafter referred to as surface Eh) and at a depth of 15 cm (n = 3; hereafter referred to as depth Eh). Measurements were made using a calomel reference electrode, bright platinum electrodes and a portable pH-mV meter. Each reading was standardized to a standard hydrogen electrode by adding 245 mV to each reading (Faulkner et al. 1989). Soils were classified as

aerated (> 300 mV), moderately reduced (100 to 300 mV), reduced (-100 to 100 mV) and strongly reduced (< -100 mV), following Patrick's (1980) classification. Eh readings were not corrected for pH.

Interstitial sulfide and ammonium concentrations, salinity, and pH were measured within each disturbance/nutrient combination. Sediment cores were taken 3 times annually for 22 months to a depth of ~ 15 cm using an aluminum corer 6 cm in diameter. Soil was extruded into 500 ml centrifuge tubes and sealed. To ensure an anaerobic environment, the samples were immediately purged with nitrogen gas and placed on ice for transport to the laboratory. The samples were then centrifuged at 10,000 g at 4 °C for ten minutes. Immediately after opening each tube, an aliquot of the supernatant was added to an antioxidant solution (NaOH, ascorbic acid, sodium salicylate) and analyzed for total soluble sulfide concentration (Sulfide Electrode, Lazar Research Laboratories, Los Angeles, CA). Another unfiltered 10 ml aliquot of supernatant was set aside to measure salinity and pH. Salinity was measured with a handheld field refractometer and pH with an Altex Model 3560 Digital pH meter and a Corning General Purpose Combination Electrode. A final 10 ml aliquot of supernatant was filtered through a 0.45 micron Millipore syringe filter and frozen for $\text{NH}_4\text{-N}$ analysis using the Colorimetric, Automated Phenate Method (U.S. Environmental Protection Agency 1979).

Long term trend in rainfall patterns were also examined and annual precipitation data were collected from the meteorological station located at The Rockefeller Wildlife Refuge from 1965 to present (Louisiana Climatic Survey, LSU).

Statistical Analysis

Both biomass and stem length data were analyzed using a split-plot in strips design with disturbance (undisturbed, non-lethal and lethal disturbances) and fertilization (fertilized and

ambient) as main factors and propagule introduction (I-rhizome, I-control) as the sub-factor (Figure 3-1). Introduced seed plots (I-S) were omitted because no *Phragmites* seedlings emerged in these treatments. Environmental variables were also analyzed using the split-split design, but with repeated measures over 5 sample periods (June 1999, September 1999, January 2000, June 2000 and September 2000). Environmental measurements were only taken within main treatment combinations (disturbance and nutrient) and were not distinguished by propagule introductions. Biomass and environmental data were normalized using a square root transformation while stem lengths were normalized using a log transformation. These data were then analyzed using the PROC MIXED procedure of the SAS statistical package (Institute 2003). All differences noted in results are significant unless otherwise noted.

Cover measurements were analyzed for each main treatment and sub-factor combination using the PROC MIXED procedure of the SAS statistical package (SAS Institute 2003) with sample date as a repeated measure. Comparisons between cover estimates for each species were not independent from one another; as such, a Bonferroni connected LSD was used to compare between groups of data. Five groups, *Phragmites*, *Distichlis*, *Spartina*, *Schoenoplectus* and cumulative cover, were tested. The initial alpha level of 0.05 was divided by the number of contrasts conducted resulting in an alpha level of 0.01. Although some statistical differences might be overlooked, this lowers the chance of making a Type I error (Moltuski 1995). *Phragmites* was only found in study plots receiving rhizomes and therefore was not analyzed by propagule type or higher order interactions containing propagule type. All differences are significant unless otherwise noted.

Results

Phragmites biomass and cover measurements were greatest in non-lethally disturbed plots, yet was unaffected by elevated nutrients. In contrast, the natural plant community responded strongly to both disturbance and nutrient enrichment. *Spartina patens* and *Distichlis spicata* biomass was 41 and 10 times, respectively, that produced by *Phragmites* in unfertilized non-lethally disturbed treatments. In fertilized non-lethal treatments, *S. patens* and *D. spicata* produced 80 and 30 times, respectively, the biomass produced by *Phragmites*. At the end of the experiment, more than 30% of *Phragmites* plants survived in undisturbed and non-lethally disturbed treatments even though severe drought conditions (Figure 3-2, (McKee et al. 2004). Although nutrient enrichment increased interstitial ammonium concentrations, the other environmental variables were not affected by nutrient enrichment or disturbance. The muted response of environmental variables was most likely a result of drought conditions.

Vegetation Response

Percent Vegetative Cover

Overall, *Spartina* and *Distichlis* were the dominant vegetation in this brackish marsh, with a combined percent cover of approximately 75% (Figure 3-3(b) and (c)). *Schoenoplectus* is a minor component of this vegetative community with cover values less than 5% (Figure 3-3(d)). *Phragmites* was not present initially, but introduced sods quickly grew culms that comprised 5% of the total community over the duration of the experiment (Figure 3-3(a)).

COVER RESPONSE OVER TIME

Phragmites and *Distichlis* cover changed over time (Table 3-1). Since introduced *Phragmites* culms were clipped to ground level, initial *Phragmites* cover was zero (Figure 3-3(a)). Culms immediately grew to almost 6% maximum cover in September 1999, but steadily

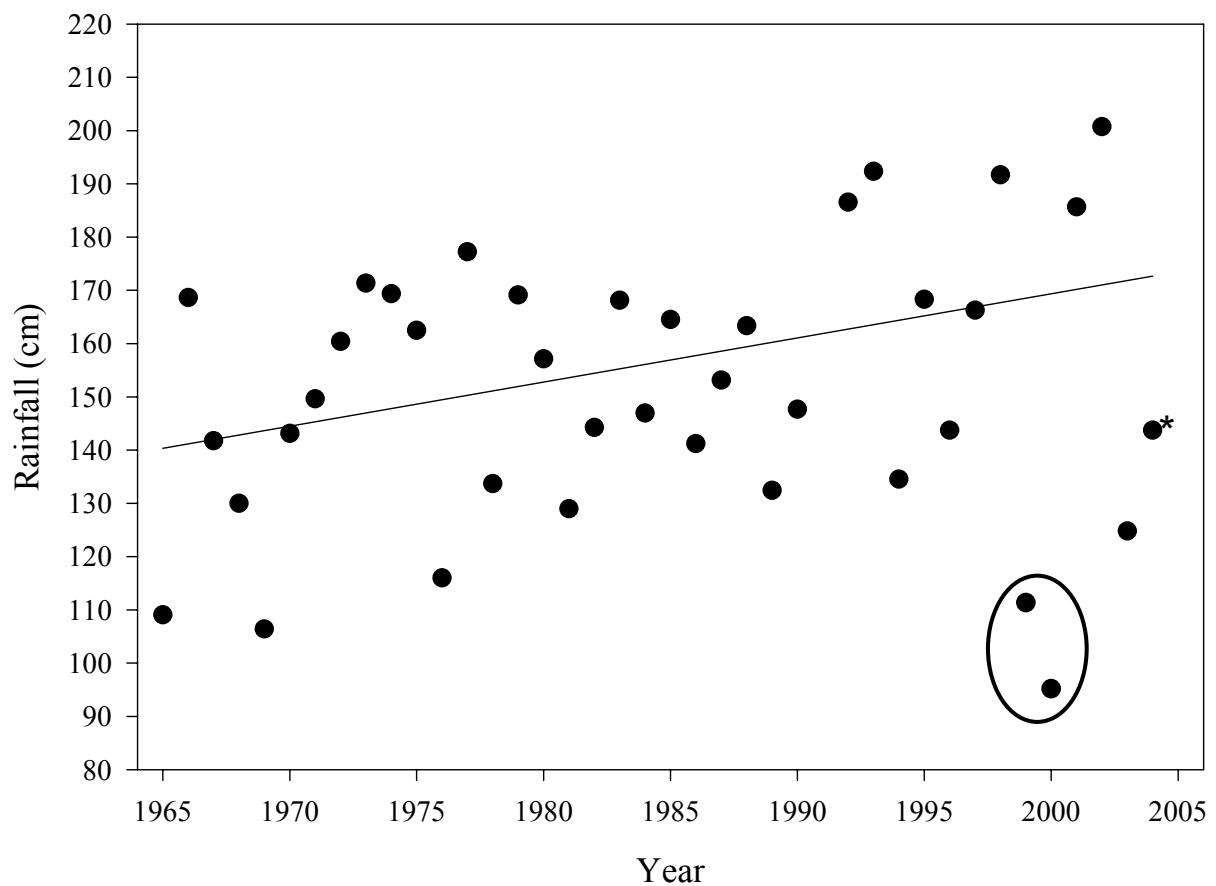


Figure 3-2: Annual rainfall recorded at Rockefeller Wildlife Refuge, Cameron Parish, Louisiana, for the years 1965 to 2004. The regression was calculated with 1999 and 2000 removed, thus reflecting typical rainfall patterns. The 2004 data is marked with an asterisk (*) and shows cumulative rainfall from January through October only. Rainfall is expressed in cm.

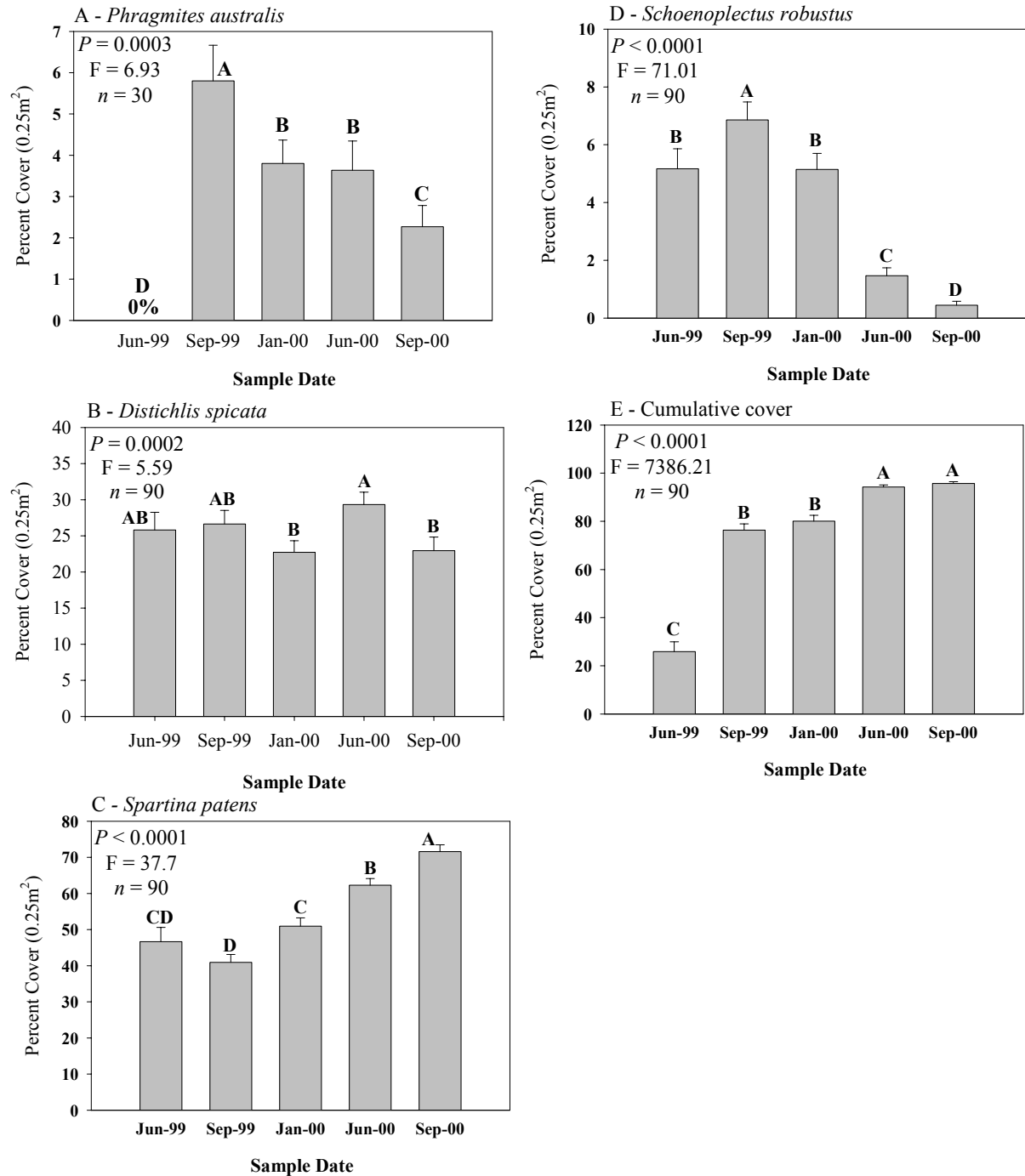


Figure 3-3: Average percent cover of *Phragmites australis*, *Distichlis spicata*, *Spartina patens*, *Schoenoplectus robustus* and cumulative cover by sample date (June 1999, Sept 1999, January 2000, June 2000 and Sept 2000). Cover is expressed in percent present in the 0.25 m² center of each experimental plot. Measurements are averaged over disturbance, nutrient and propagule introduction. Error bars represent standard error and bars that share letters are not significantly different.

Table 3-1. ANOVA table of percent cover analyzed using PROC MIXED with time as a repeated measure. Comparisons made within this group were not independent of one another; as such, a Bonferroni connected LSD was used to compare between groups of data. Five groups, *Phragmites*, *Distichlis*, *Spartina*, *Schoenoplectus* and cumulative cover, were tested. The initial alpha level of 0.05 was divided by the number of contrasts being conducted resulting in an alpha level of 0.01. *Phragmites* was only found in plots receiving rhizome material, therefore the effect of propagule type was not tested for *Phragmites*. Bold indicate significance at $\alpha = 0.01$.

Cover		<i>Phragmites</i>		<i>Distichlis</i>		<i>Spartina</i>		<i>Schoenoplectus</i>		Cumulative Cover	
Source	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Time (T)	4	6.93	0.0003	5.59	0.0002	37.7	<0.0001	71.01	<0.0001	7386.21	<0.0001
Nutrient (N)	1	1.76	0.1877	0.21	0.6496	8.19	0.0045	11.12	0.001	23.05	<0.0001
T x N	4	1.86	0.1413	2.75	0.0285	2.58	0.0376	2.57	0.038	1.1	0.3551
Disturbance (D)	2	22.47	<0.0001	162.49	<0.0001	17	<0.0001	32.38	<0.0001	2593.04	<0.0001
T x D	8	0.2	0.9755	2.55	0.0202	20.62	<0.0001	6.8	<0.0001	1590.26	<0.0001
N x D	2	0.45	0.6366	2.06	0.1287	1.43	0.2402	0.23	0.7981	0.18	0.8314
T x N x D	8	0.8	0.5726	0.73	0.6224	1.46	0.1898	2.11	0.0525	1.17	0.3136
Propagule (P)	2	--	--	6.06	0.0026	1.73	0.1781	2.71	0.0681	7.55	0.0006
T x P	8	--	--	1.06	0.3936	1.15	0.3285	1.6	0.1247	2.51	0.0115
N x P	2	--	--	0.14	0.8724	2.17	0.1156	0.46	0.6321	2.92	0.0552
T x N x P	8	--	--	0.18	0.9937	0.47	0.8772	0.74	0.6602	1.13	0.3442
D x P	4	--	--	0.83	0.5042	0.91	0.4586	0.78	0.5368	8.5	<0.0001
T x D x P	16	--	--	0.58	0.8593	0.83	0.6188	0.66	0.7912	3.08	<0.0001
N x D x P	4	--	--	0.02	0.9988	2.25	0.0639	0.96	0.4314	2.03	0.0894
T x N x D x P	16	--	--	0.58	0.8596	0.95	0.5015	0.34	0.9819	0.88	0.5958

Note: Block was tested as a random effect.

decreased over the course of the experiment with the lowest cover in September 2000 (Table 3-1). Although *Distichlis* cover changed between sample dates, these changes did not demonstrate a clear trend (Figure 3-3(b)). *Distichlis* cover was greatest in June 2000 and lowest in both January and September 2000. Cover values in June and September 1999 were not different from any other cover value.

However, for *Spartina* and *Schoenoplectus*, the response in cover over time was dependent on the level of disturbance (Table 3-1). *Spartina* cover steadily increased over the course of the experiment (Figure 3-3(c)), while *Schoenoplectus* cover steadily decreased (Figure 3-3(d)). The change in cumulative cover over time was also dependent on disturbance and propagule introduction (Table 3-1). Even though, as species recovered from disturbance and responded to fertilization, total cumulative cover increased (Figures 3-3(e)).

RESPONSE TO DISTURBANCE

All species reflected a change in cover in response to level of disturbance (Table 3-1). Both *Phragmites* and *Distichlis* had higher cover in non-lethally disturbed plots than in undisturbed control plots (Figures 3-4.1(a) and 3-4.2(a)), and cover in control plots and non-lethally disturbed plots were higher than in lethally disturbed plots.

The response of both *Spartina* and *Schoenoplectus* cover to level of disturbance was also dependent upon sample date (Table 3-1). *Spartina* had higher percent cover in undisturbed plots and the lowest cover in non-lethally disturbed plots (Figure 3-4.3(a)) and *Schoenoplectus* had higher cover in non-lethally disturbed plots (3-4.4(a)). The response of cumulative cover to disturbance was also dependent upon both time and propagule introduction (Table 3-1). Cumulative cover was greatest in undisturbed and non-lethally disturbed plots when compared to lethally disturbed plots (Figure 3-4.6(a)).

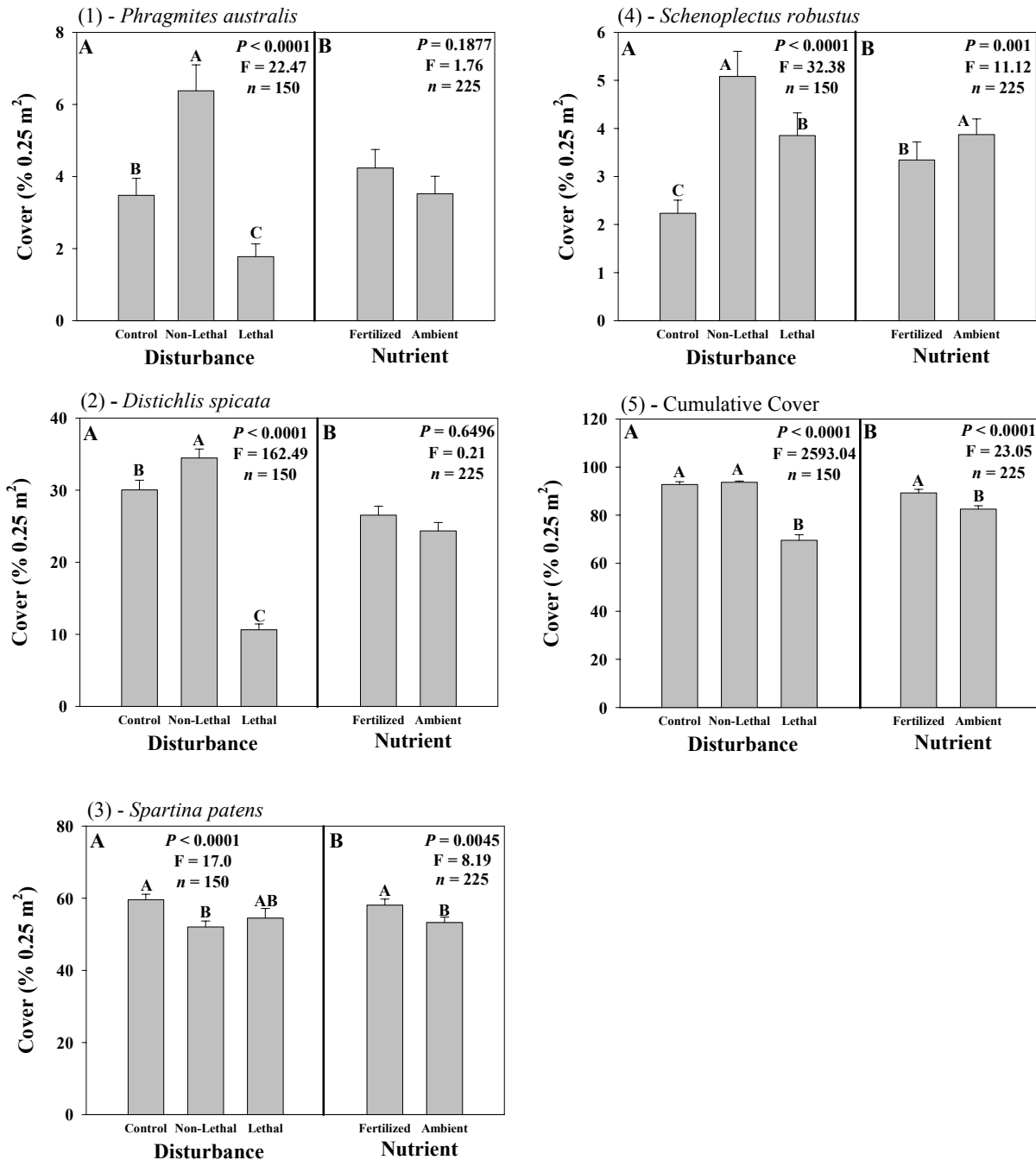


Figure 3-4: Average percent cover of *Phragmites australis*, *Distichlis spicata*, *Spartina patens*, *Schoenoplectus robustus* and cumulative cover within (a) disturbance (control, non-lethal and lethal) and (b) nutrient (fertilized and ambient) treatment. Cover is expressed in percent present in the 0.25 m² center of each experimental plot. Measurements are averaged over five sampling dates. Error bars represent standard error and bars that share letters are not significantly different.

RESPONSE TO NUTRIENTS

Spartina, *Schoenoplectus* and cumulative cover changed in response to nutrient additions (Table 3-1). Both *Spartina* and cumulative cover increased under fertilized conditions (Figures 3-4.3(b) and 3-4.6(b)) while *Schoenoplectus* decreased under elevated nutrient conditions (Figures 3-4.4(b) and 3-4.5(b)). In contrast, fertilization had no effect on either *Phragmites* or *Distichlis* cover (Figures 3-4.1(b) and 3-4.2(b)).

PERCENT COVER BY SAMPLE DATE AND DISTURBANCE

Although the initial cover for non-lethally and lethally disturbed plots was zero, most species re-colonized within three months (Figure 3-5). The response of *Spartina* and *Schoenoplectus* cover was dependent on both sample date and level of disturbance (Table 3-1). Although initial *Spartina* cover was zero in lethally disturbed plots, it increased even above cover in undisturbed control plots and in non-lethally disturbed plots on the last two sample dates (Figure 3-5(c)). Conversely, *Schoenoplectus* cover in both non-lethally and lethally disturbed plots responded immediately to disturbances with a two-fold increase in cover when compared to undisturbed plots. In contrast, *Schoenoplectus* cover in undisturbed plots steadily decreased over the course of the study (Figure 3-5(d)). Even with the immediate increase, *Schoenoplectus* cover in disturbed plots sharply decreased, ultimately matching percent cover in undisturbed plots on the last two sample dates.

Over all, cumulative cover increased over time as species recovered from initial disturbances (Figure 3-5(e)). However, the response of cumulative cover to disturbance over time was also dependent on propagule introduction (Table 3-1).

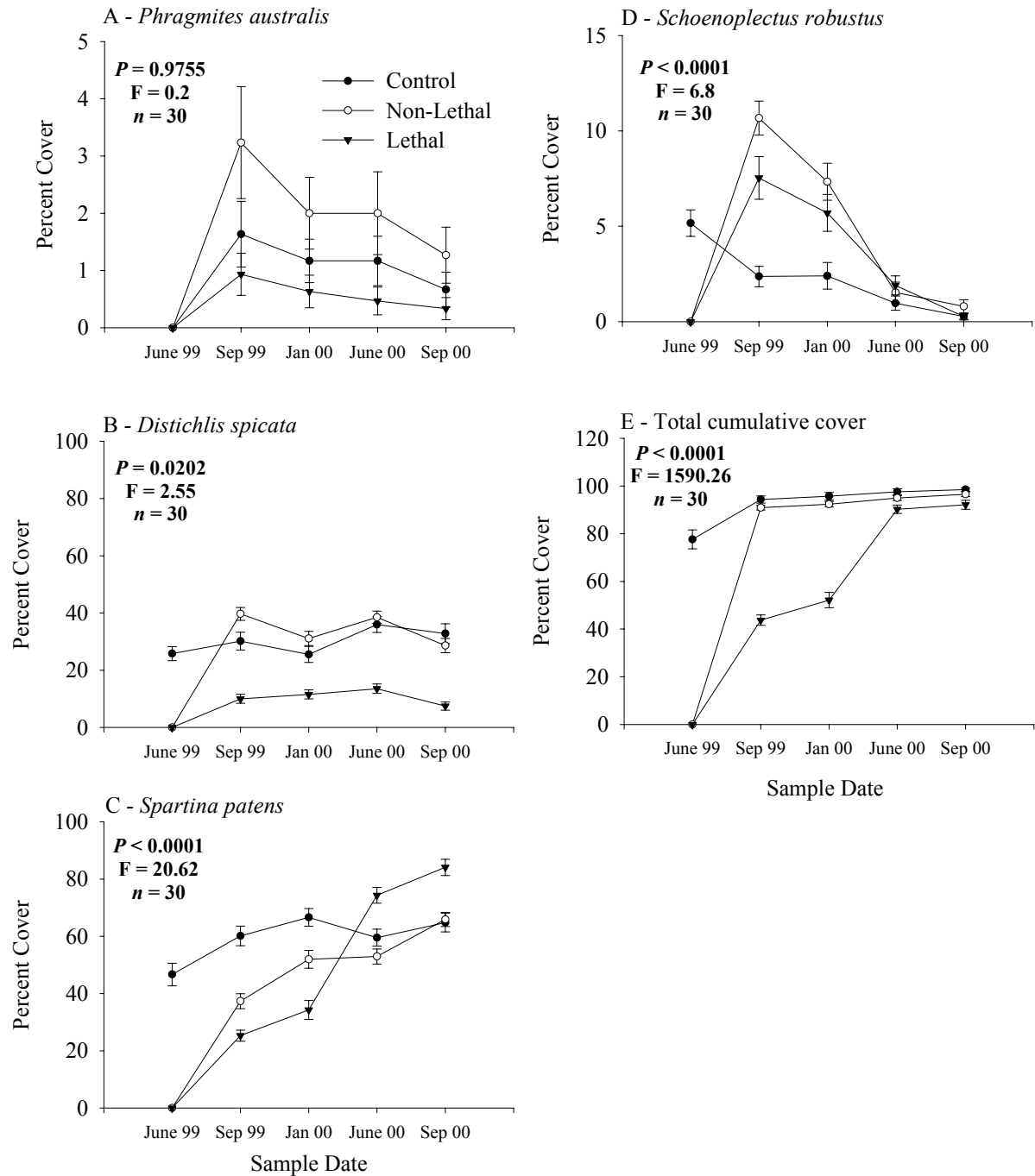


Figure 3-5: Percent cover of *Phragmites australis*, *Distichlis spicata*, *Spartina patens*, *Schoenoplectus robustus* and cumulative cover within each disturbance (control, non-lethal and lethal) on each sample date. Cover is expressed in percent present in the 0.25 m² center of each experimental plot and error bars represent standard error.

PERCENT COVER AS AFFECTED BY *PHRAGMITES* INTRODUCTION

The physical presence of sod occupied space that was normally vegetated, thus reducing cover for certain measurements. Introducing *Phragmites* sods reduced *Distichlis* cover when compared to control plots (Table 3-1; Figure 3-6.1(a)). Cumulative percent cover was also affected by a propagule introduction (Table 3-1, Figure 3-6.1(b)) but this response was dependent on level of disturbance (Table 3-1). Cumulative percent cover was less in undisturbed plots receiving introduced *Phragmites* sods when compared to undisturbed plots receiving seed (I-S) or undisturbed plots receiving no propagules (Figure 3-6.2).

However, the combined effects of propagule introduction and level of disturbance on cumulative percent cover was also dependent on the change in vegetative cover over time (T x D x P; Table 1). In June 1999, *Phragmites* sods reduced cumulative cover in undisturbed plots, while both non-lethal and lethal disturbances resulted in 0% cover in disturbed plots (Figure 3-6.3). In September 1999 and January 2000, the presence of *Phragmites* sods was not nearly as evident as the reduction in cover associated with lethally disturbed treatments. Cumulative cover in June and September 2000 were not different regardless of disturbance or propagule introduction. It appears the initial reduction of cumulative cover in plots receiving *Phragmites* sods was eventually masked by growth of vegetation in control plots around rhizomes and the re-growth of vegetation in disturbance plots.

Biomass

Phragmites biomass was greater in non-lethally disturbed plots when compared to lethally disturbed plots (Table 3-2; Figure 3-7.1(a)). Biomass in undisturbed plots was not different in either lethally disturbed or undisturbed plots. In addition, there was no fertilization effect or interaction between fertilization and disturbance on *Phragmites* biomass (Table 3-2;

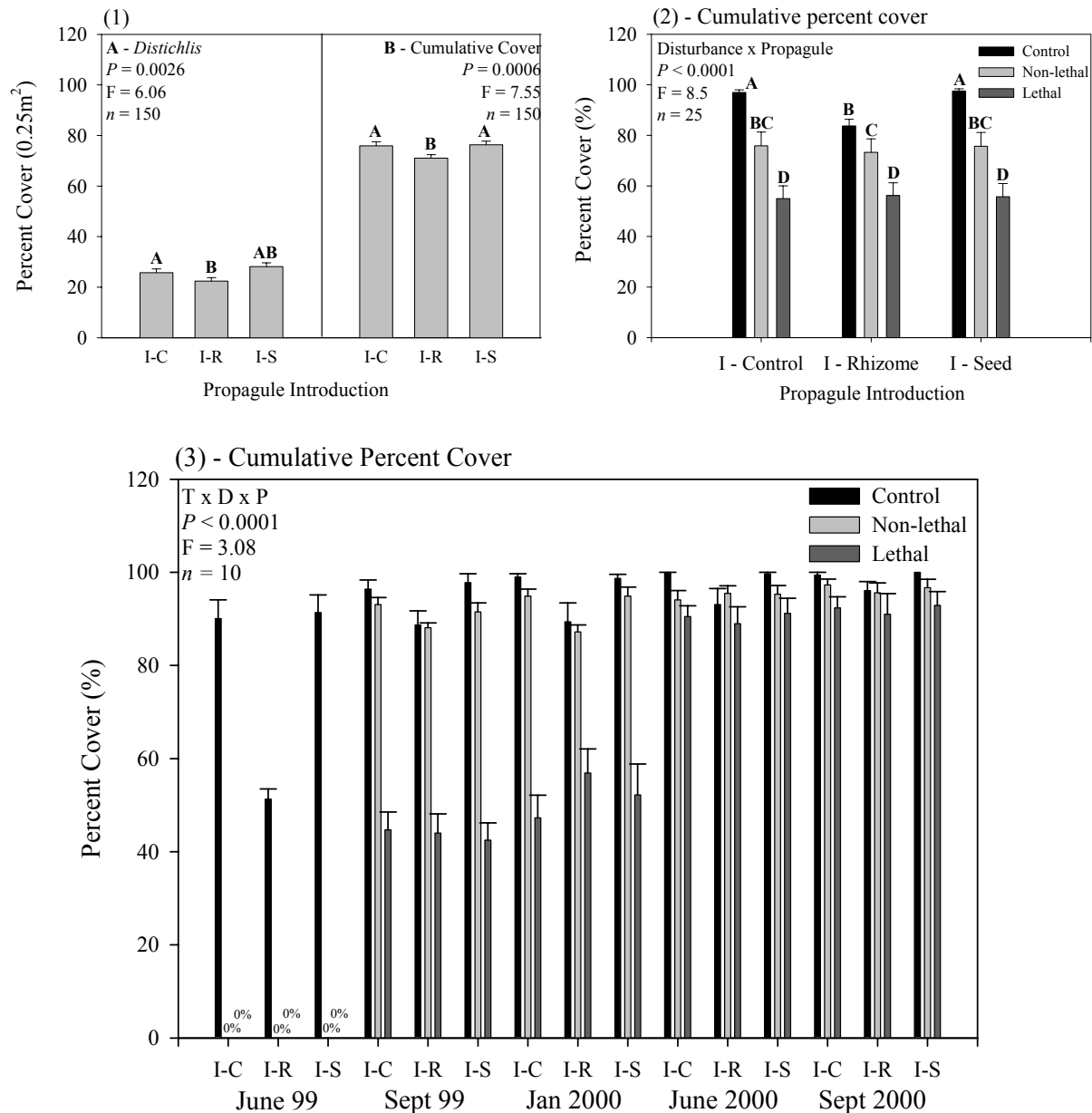


Figure 3-6: Percent cover of *Distichlis* (3-6.1(a)) and cumulative cover (3-6.1(b)) by propagule introduction. Figure 3-6.2 demonstrates the interaction between propagule introduction and disturbance on cumulative cover. Figure 3-6.3 depicts the three-way interaction between sample date, level of disturbance and propagule introduction on cumulative cover. In all figures, error bars represent standard error and where present, bars that share letters are not significantly different.

Table 3-2. ANOVA table of vegetative biomass analyzed using PROC MIXED. Bold indicates statistical significance at $\alpha = 0.05$. *Phragmites* was only found in study plots receiving rhizomes and therefore was not analyzed by propagule type or higher order interactions containing propagule.

Biomass		<i>Phragmites</i>		<i>Distichlis</i>		<i>Spartina</i>		<i>Schoenoplectus</i>		Cumulative	
Source	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Disturbance (D)	2	3.88	0.0376	47.88	<0.0001	5.54	0.0068	7.56	0.0015	23.03	<0.0001
Nutrient (N)	1	1.08	0.3114	16.27	0.0002	13.12	0.0007	0.86	0.3596	77.07	<0.0001
D x N	2	1.60	0.2271	1.7	0.1944	0.79	0.4616	3.96	0.0263	1.77	0.1914
Propagule (P)	1	--	--	0.36	0.5535	3.03	0.0882	1.43	0.2385	2.78	0.1083
N x P	1	--	--	0.84	0.3637	0.19	0.6663	4.85	0.033	0.3	0.5907
D x P	2	--	--	0.06	0.9465	0.24	0.7873	0.57	0.5681	0.38	0.6866
N x D x P	2	--	--	0.02	0.9781	0.59	0.5559	0.02	0.9808	1.61	0.2201

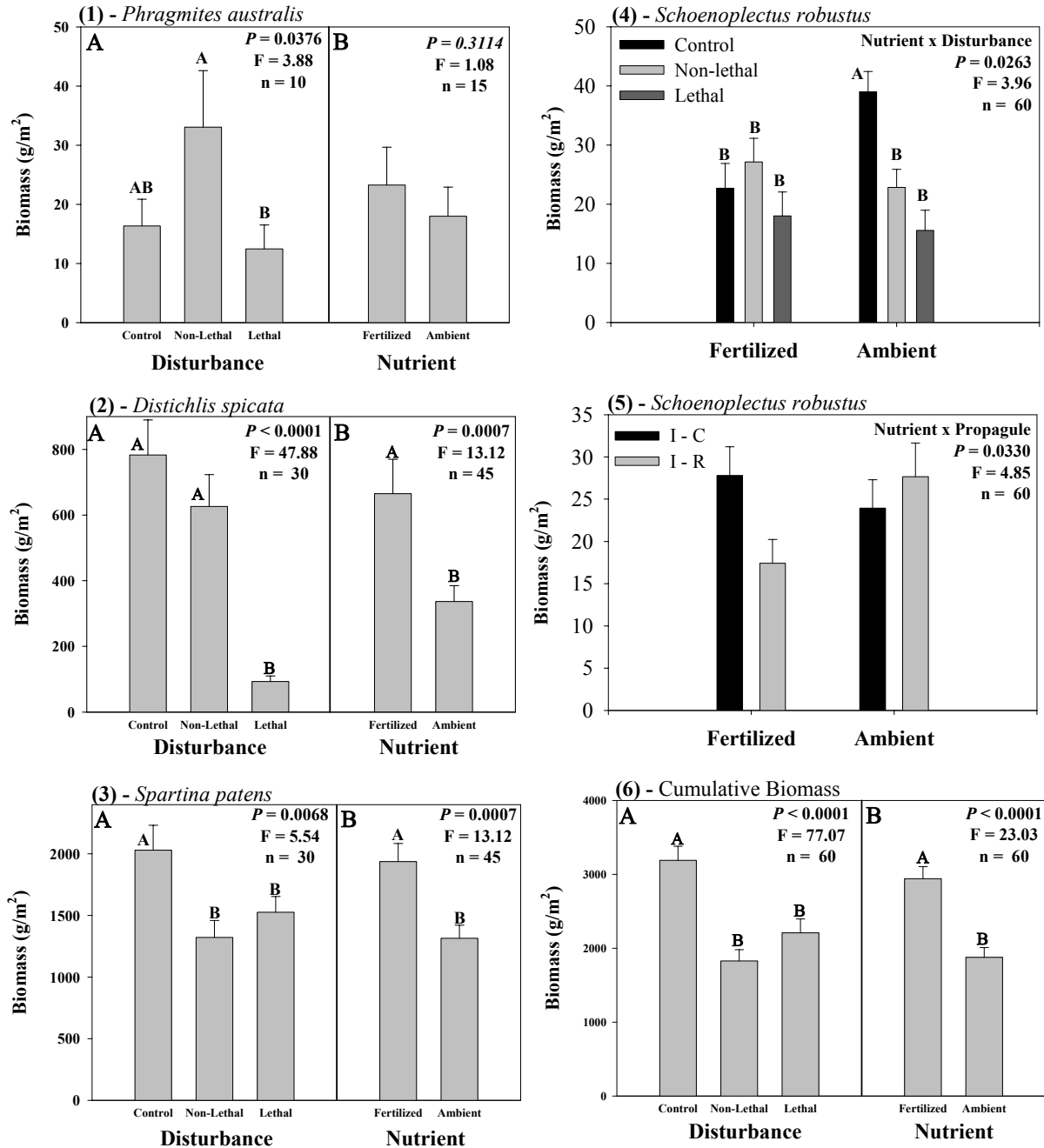


Figure 3-7. Graphs demonstrating the main effects of disturbance and nutrient additions on biomass. Graphs 1-3 and 6 reflect biomass measurements tested by (a) disturbance (control, non-lethal and lethal) and (b) nutrient (fertilized and ambient) for *Phragmites*, *Spartina patens*, *Distichlis spicata* and cumulative biomass. Graphs 4 and 5 reflect the interactions between nutrient x disturbance and nutrient x propagule introduction for *Schoenoplectus robustus*. All biomass measures are expressed as grams dry weight m^{-2} and error bars reflect SE. Bars that share letters are not significantly different.

Figure 3-7.1(b)). Since *Phragmites* was only present in plots receiving rhizome material, biomass was not analyzed by propagule treatment (Table 3-2).

Distichlis biomass in fertilized treatments was greater than biomass in unfertilized plots (Table 3-2, Figure 3-7.2(b)). In addition, *Distichlis* biomass was not adversely affected by non-lethal disturbance and was not different than undisturbed plots (Table 3-2; Figure 3-7.2(a)). In fact, *Distichlis* biomass from both undisturbed and non-lethally disturbed plots was three-fold higher than in lethally disturbed plots (Table 3-2, Figure 3-7.2(a)). There was no interaction between nutrient additions and disturbance for *Distichlis* biomass (Table 3-2).

Spartina also yielded more biomass in both undisturbed plots and in fertilized plots (Table 3-2). Biomass in fertilized plots was nearly 25% greater than that in unfertilized plots (Figure 3-7.3(b)). However, *Spartina* recovery in non-lethally disturbed plots did not respond as quickly as *Distichlis*. *Spartina* biomass in both non-lethally and lethally disturbed plots was a third less than in undisturbed plots (Figure 3-7.3(a)). There was no interaction between nutrient additions and disturbance for *Spartina* biomass (Table 3-2).

Although *Schoenoplectus* biomass was affected by disturbance, this response was dependent on fertilization and also with propagule introduction (Table 3-2; N x D; N x P). When averaged over disturbance, *Schoenoplectus* biomass was unaffected by introducing *Phragmites* rhizomes, while fertilized plots receiving rhizomes had less biomass than plots that received no introduction (Figure 3-7.4). When averaged over propagule introduction, disturbance had no effect on *Schoenoplectus* biomass under fertilized conditions (Figure 3-7.5). However, in unfertilized plots, undisturbed plots had greater biomass than those that were subjected to non-lethal or lethal disturbances.

Cumulative live biomass was greatest in fertilized plots and in undisturbed control plots (Table 3-2; Figure 3-7.6(a) and (b)). Total biomass in non-lethal and lethally disturbed plots was less than in undisturbed plots. Biomass in non-lethal and lethally disturbed plots was different from each other. Overall, biomass in fertilized treatments was 30% higher than in unfertilized treatments.

Stem Height

Stem height for both *Spartina* and *Distichlis* was greatest in undisturbed and fertilized treatments (Table 3-3; Figures 3-8.1(a) and (b) and 3-8.3(a) and (b)). *Distichlis* stem height was lowest in lethally disturbed plots (Figure 3-8.1(a)), while *Spartina* stem height was lowest in non-lethal disturbances (Figure 3-8.3(a)). *Distichlis* stem height was also significantly different in each disturbance treatment, with tallest stems in undisturbed plots, and shortest stems in lethal disturbances. However, *Distichlis* stem height in disturbance treatments was dependent on fertilization (Table 3-3; Figure 3-8.2). Under unfertilized conditions, *Distichlis* stem height was highest in undisturbed plots, yet was not different between non-lethal and lethal disturbances. Similar to ambient conditions, *Distichlis* stem height under fertilized conditions was also highest. However, stem height in fertilized non-lethally disturbed plots was lower than undisturbed plots and higher than lethally disturbed plots.

Phragmites Viability

Once the experiment was terminated and all above ground vegetative material was harvested, all remaining *Phragmites* rhizomes and roots were excavated and returned to the laboratory to determine viability with tetrazolium azide (Parker 1953, Steponkus and Lanphear 1967). Of the 30 sods planted in the experiment, 1/3 remained viable even under drought conditions (Figure 3-9). Four of the 10 found alive were in undisturbed plots, 5 were in non-

Table 3-3. ANOVA table of *Distichlis* and *Spartina* stem length analyzed using PROC MIXED. Bold indicates statistical significance at alpha = 0.05.

Stem Length		<i>Distichlis</i>		<i>Spartina</i>	
Source	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Disturbance (D)	2	37.82	<0.0001	22.89	<.0001
Nutrient (N)	1	610.23	<0.0001	134.14	<.0001
D x N	2	3.18	0.0428	1.17	0.3421
Propagule (P)	1	0.2	0.6584	4.02	0.0564
N x P	1	0.01	0.9062	1.36	0.2553
D x P	2	0.68	0.5092	2.71	0.0871
N x D x P	2	0.56	0.5721	1.92	0.1683

lethally disturbed plots and 1 remained viable in a lethally disturbed plot. Six plants remained viable under ambient nutrient conditions while 4 remained viable in fertilized plots.

Environmental Variables

Although there were no differences for most environmental variables with respect to experimental treatments, there was a significant time effect (Table 3-4).

Sulfide, Salinity and pH

Interstitial sulfide concentrations and pH were not different between any nutrient or disturbance treatment, yet both of these environmental variables changed over time (Tables 3-4 and 3-5). Sulfide concentrations steadily decreased throughout the study while pH fluctuated between 6.48 and 7.34 (Table 3-6). Low water tables as a result of the drought conditions prevented sulfide concentrations from reaching a biologically significant level (i.e., growth limiting) and pH levels were within normal ranges reported for brackish marshes (Anastasiou and Brooks 2003). Although salinity generally increased over time as a result of drought conditions and there was a slight difference in salinity between disturbance treatments, there was an interaction between time and level of disturbance (Table 3-4). On the June 1999 and January

Figure 3-8: Stem height of *Spartina patens* and *Distichlis spicata*. Graphs 1 and 3 reflect stem height tested by the main effects of (a) disturbance (control, non-lethal and lethal) and (a) nutrient (fertilized and ambient) for total *Distichlis spicata* and *Spartina patens*. Graph 2 shows the significant interaction of disturbance and nutrient on *D. spicata* stem height. Error bars represent standard error and bars that share letters are not significantly different.

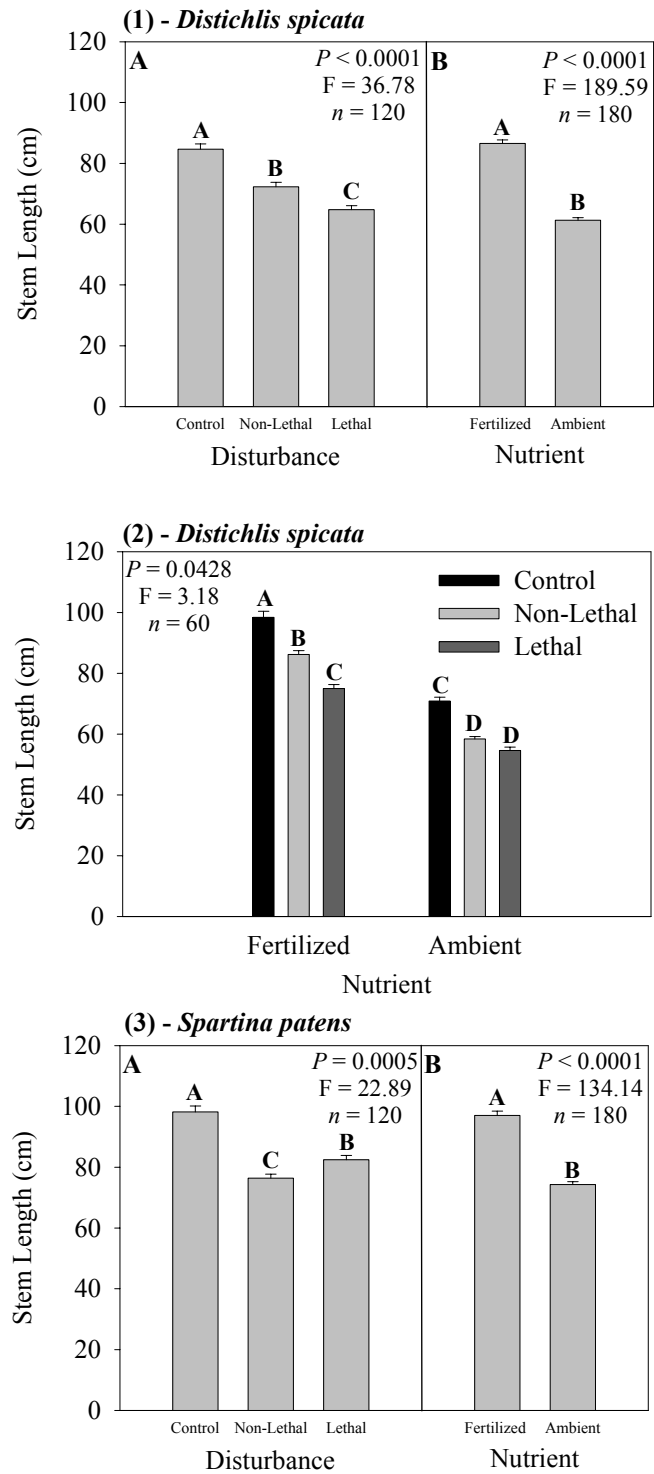


Figure 3-8.

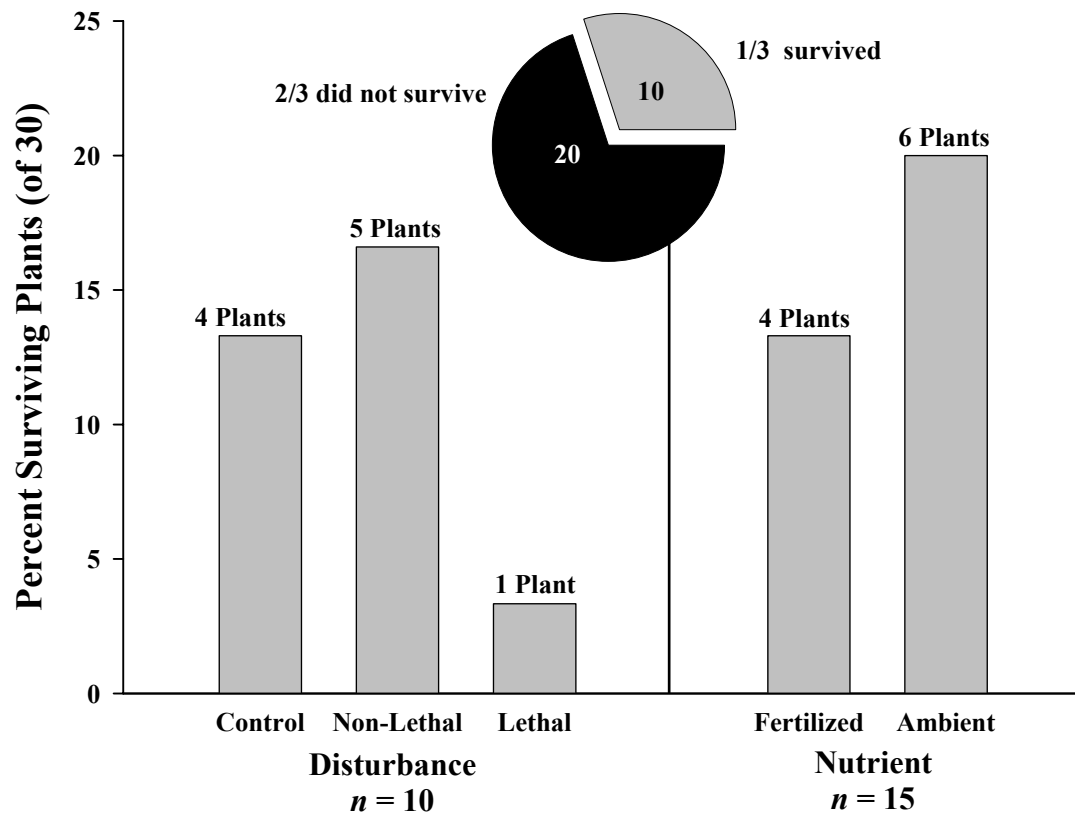


Figure 3-9: Results of the tetrazolium assay for determination of viable *Phragmites* rhizomes. The pie chart represents the number of viable versus non-viable exhumed rhizomes while the bar graph indicates the percentage of surviving plants from each disturbance/nutrient treatment.

Table 3-4. ANOVA table of interstitial environmental variables analyzed using PROC MIXED and time as a repeated measure. Bold indicates statistical significance at $\alpha = 0.05$.

Environmental Variables		Sulfide (uM)		Salinity (ppt)		pH		Ammonium (μ M)		Eh (mV-Surface)		Eh (mV-Depth)	
Source	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Time (T)	4	3.67	0.0074	315.98	<0.0001	48.10	<0.0001	27.26	<0.0001	258.65	<0.0001	126.39	<0.0001
Nutrient (N)	1	0.10	0.7471	0.16	0.6882	0.43	0.5128	126.68	0.0004	2.35	0.1277	0.30	0.5839
T x N	4	0.16	0.9561	0.74	0.5667	0.42	0.7904	8.04	0.0009	2.14	0.0798	0.25	0.9083
Disturbance (D)	2	0.91	0.4048	6.59	0.0019	1.20	0.3045	6.47	0.0213	1.09	0.3400	0.19	0.8278
T x D	8	0.87	0.5427	6.78	<0.0001	0.59	0.7841	3.63	0.0041	0.61	0.7682	1.85	0.0744
N x D	2	0.96	0.3846	1.14	0.3221	1.24	0.2934	4.43	0.0507	0.91	0.4039	2.14	0.1222
T x N x D	8	0.84	0.5703	0.63	0.7516	0.55	0.8138	2.05	0.0743	0.88	0.5382	3.18	0.0026

Table 3-5. Environmental variables measured in this study and compared by disturbance and nutrient treatment. All measurements are \pm SE, and statistical significance is denoted by bold letters and corresponding p-values adjacent to each parameter.

Environmental Variable	<i>n</i>	Disturbance			Nutrient	
		Control	Non-Lethal	Lethal	Ambient	Fertilized
Sulfide (μ M)	50, 75	0.0424 \pm 0.0154	0.067 \pm 0.447	0.0151 \pm 0.006	0.036 \pm 0.011	0.047 \pm 0.03
Salinity (ppt) (p = 0.0019)	50, 75	27.88 \pm 0.943 (B)	28.86 \pm 0.888 (A)	27.48 \pm 0.977 (B)	27.93 \pm 0.731	28.21 \pm 0.798
pH	50, 75	6.95 \pm 0.055	7.03 \pm 0.060	7.01 \pm 0.047	7.01 \pm 0.043	6.98 \pm 0.046
NH ₄ (μ M) (dist: p = 0.0559) (nut: p = 0.0006)	50, 75	292.53 \pm 91.24 (B)	317.59 \pm 79.78 (B)	1100.08 \pm 447.62 (A)	37.90 \pm 4.15 (B)	1102.23 \pm 301.76 (A)
Eh surface (mV)	300, 450	293.48 \pm 16.65	292.43 \pm 16.09	292.93 \pm 16.19	301.55 \pm 13.05	284.34 \pm 13.52
Eh depth (mV)	300, 450	125.38 \pm 14.40	154.09 \pm 16.42	163.28 \pm 15.49	145.80 \pm 12.45	149.36 \pm 12.86

Table 3-6. Environmental variables measured in this study and compared by sample date. All measurements are \pm SE, and statistical significance is denoted by bold letters and corresponding p-values adjacent to each parameter.

Environmental Variable	<i>n</i>	Sample Date				
		June 1999	Sept 1999	Jan 2000	June 2000	Oct 2000
Sulfides (μ M) ($p = 0.0053$)	30	0.1582 ± 0.076 (A)	0.039 ± 0.0092 (B)	0.009 ± 0.001 (B)	0.0012 ± 0.0003 (B)	$9.16e^{-5} \pm 6.54e^{-6}$ (B)
Salinity (ppt) ($p < 0.0001$)	30	24.23 ± 0.334 (D)	27.6 ± 0.569 (C)	19.73 ± 0.332 (E)	30.96 ± 0.497 (B)	37.83 ± 0.437 (A)
pH ($p < 0.0001$)	30	6.48 ± 0.022 (D)	7.34 ± 0.086 (A)	6.96 ± 0.025 (C)	7.18 ± 0.039 (B)	7.02 ± 0.032 (C)
NH ₄ (μ M) ($p = 0.0492$)	30	60.34 ± 8.70 (B)	128.88 ± 56.79 (B)	1386.88 ± 721.53 (A)	745.32 ± 208.88 (AB)	528.93 ± 150.05 (AB)
Eh surface (mV) ($p = 0.0001$)	180	147.50 ± 9.54 (C)	383.98 ± 10.46 (B)	25.07 ± 12.77 (D)	458.48 ± 7.48 (A)	449.72 ± 9.32 (A)
Eh depth (mV) ($p = 0.0001$)	180	109.60 ± 8.23 (B)	38.04 ± 12.37 (C)	-49.80 ± 9.12 (D)	321.32 ± 17.47 (A)	318.74 ± 12.21 (A)

2000 sample dates, there were no differences between salinities regardless of level of disturbance (Figure 3-10). However, in September 1999 and in June 2000, salinities were highest in non-lethally disturbed treatments. In contrast, salinities were highest in both undisturbed and lethally disturbed plots in October 2000. No clear pattern emerged for porewater salinity in respect to level of disturbance even though porewater salinity levels had reached a level well above that typical for brackish marshes by the end of the study (Table 3-6).

Ammonium

Ammonium was the only variable in this study to demonstrate a clear treatment effect (Table 3-4). Ammonium concentrations were higher in fertilization treatments and in lethally disturbed plots (Table 3-5). However both disturbance and fertilization effects were both dependent on time (Table 3-4). Fertilization took place once every four months, two weeks prior to sampling. Porewater ammonium concentrations steadily accumulated in sediments during this time as a result of the drought and resulting low water tables (Figure 3-11.1). With reduced rainfall amounts (Figure 3-2), it is likely that ammonium was not flushed through the sediments. In addition, ammonium concentrations were further influenced by level of disturbance (Table 3-4). Initial ammonium concentrations were greater in non-lethal plots in June 1999 (Figure 3-11.2). In September 1999, ammonium concentrations were highest in both undisturbed and non-lethally disturbed plots when compared to lethally disturbed plots on that sample date. Although porewater ammonium concentrations in disturbance treatments were not different for the remainder of the study, concentrations increased over time in all fertilized plots, with the highest concentrations in January and June 2000.

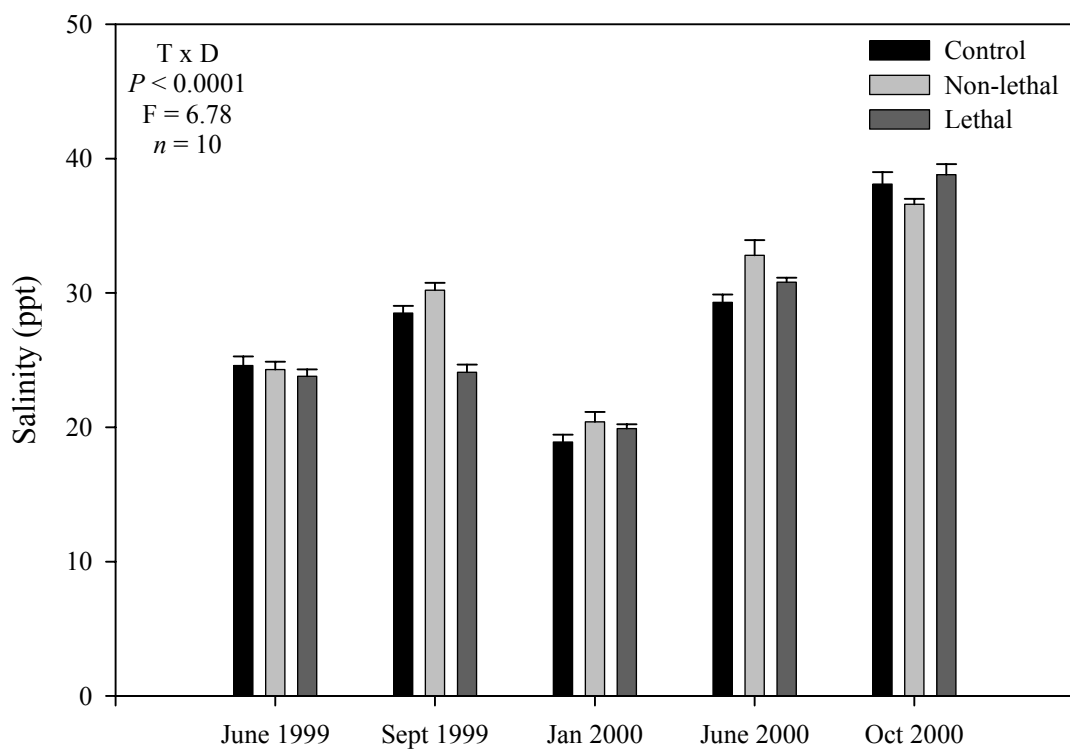


Figure 3-10: Porewater salinities (ppt) by sample date and level of disturbance. Error bars reflect SE.

Figure 3-11: Ammonium concentrations (μM) by Sample date and Nutrient enrichment (3-11.1), and ammonium concentrations (μM) by Sample date and Disturbance (3-11.2). Error bars reflect SE.

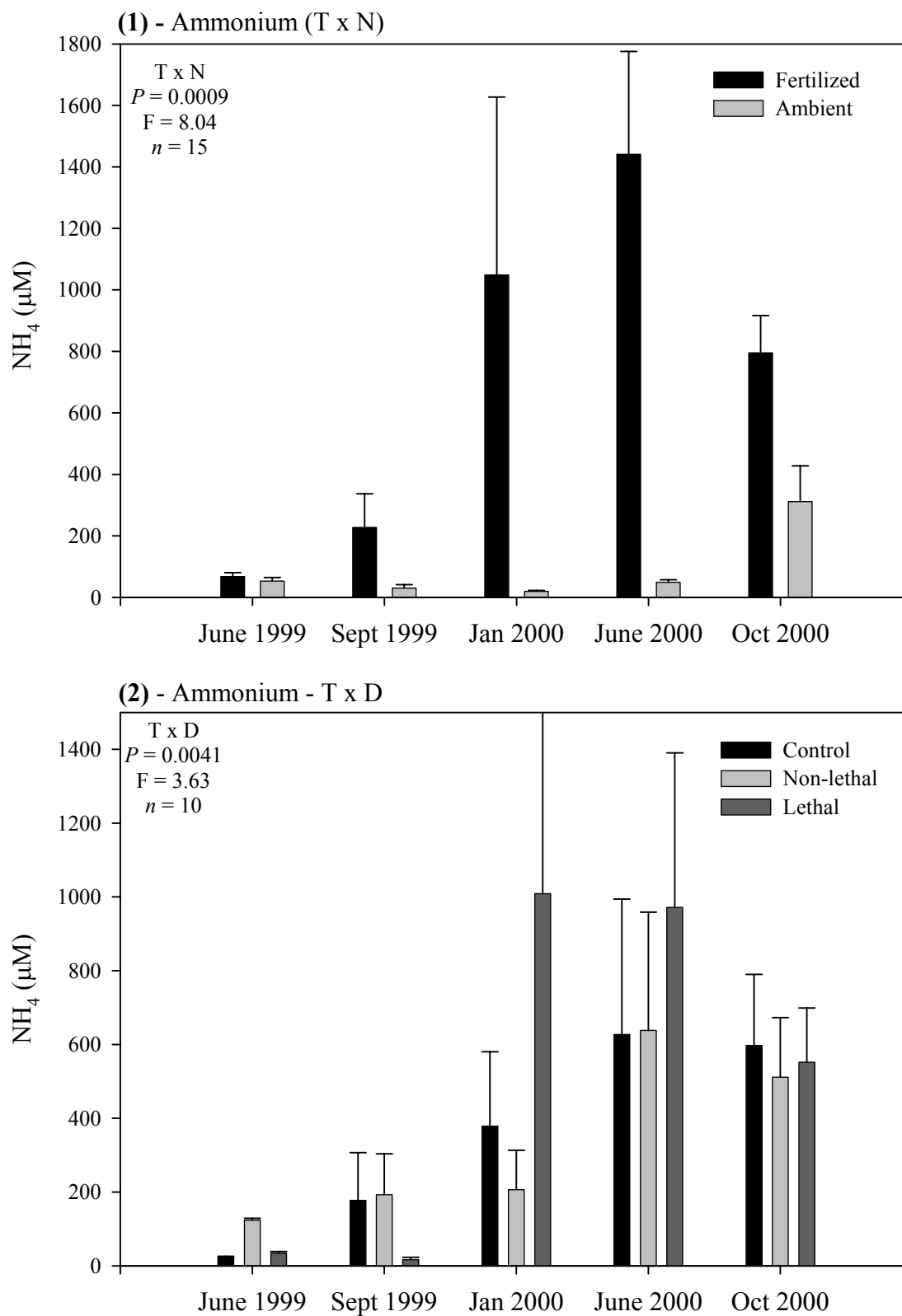


Figure 3-11

Sediment Eh

Soil redox taken at both the sediment surface and at 15 cm depth was not affected by disturbance or fertilization treatments in this study (Tables 3-4 and 3-5). In general, Eh in the upper 1-2 cm of the soil surface was, on average, 150 mV higher than at 15 cm depth. Even

though no treatment effects were realized, surface redox changed over time (Tables 3-4 and 3-5). Based on Patrick's (1980) classification, sediments in this study were only reduced in September 1999 and January 2000, moderately reduced in June 1999 and aerated in June and September 2000. Throughout the study, strongly reduced conditions never occurred, most likely due to low soil moisture as a result of drought conditions.

Although Eh at 15 cm depth changed over time, this response was dependent on both fertilization and level of disturbance (Table 3-4; Figure 3-12). Although Eh changed markedly between sample dates, nutrient and disturbance treatments had an additional effect on Eh. In June 1999, January 2000 and September 2000, Eh was not different between nutrient or disturbance treatments. However, in September 1999, Eh was lowest in control and non-lethally disturbed fertilized treatments. In unfertilized treatments that same sample date, Eh was lowest only in non-lethally disturbed plots. A similarly perplexing pattern was observed in Eh measurements taken in June 2000 (Figure 3-12), where Eh measurements in fertilized undisturbed treatments were lower than in non-lethal or lethally disturbed plots. Under unfertilized conditions, lethally disturbed plots had the lowest redox.

Discussion

One of the major questions surrounding invasive species ecology is whether native communities demonstrate characteristics that influence the success of invading species. We tested the invasibility of a brackish marsh by manipulating both nutrient levels and disturbance

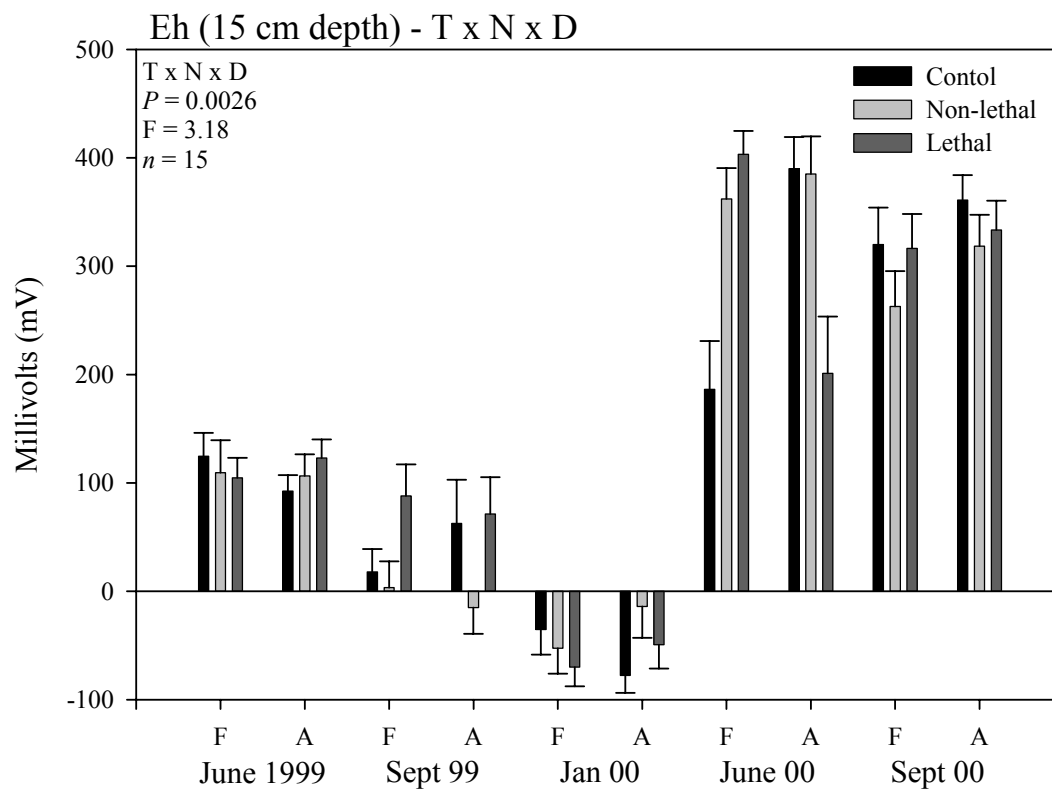


Figure 3-12. Sediment Eh levels (mV) taken at 15cm depth by sample date, nutrient enrichment and disturbance. Error bars reflect SE

regimes in conjunction with purposeful introductions of *Phragmites*, a species that has been increasingly invasive in higher salinity wetlands over the last fifty years (Winogrand and Kiviat 1997, Chambers et al. 1999, Rice et al. 2000). Contrary to our hypotheses, the natural community demonstrated a greater response to disturbances and nutrient additions than did the introduced *Phragmites*. Yet, a third of introduced *Phragmites* plants remained viable through the experiment, even over two-growing seasons of drought. Hence, that persistence of an introduced species until environmental conditions improve could be an important pathway of invasion of some species, and *Phragmites* in particular.

Community invasibility was first correlated with species richness (Elton 1958, Tilman 1982, Crawley 1987, Tilman 1988, Pyle 1995, Smith and Knapp 1999), yet positive correlations between invasibility and both species-poor and species-rich communities exists (Fox and Fox 1986, Crawley 1987, Rejmanek 1989, Richardson and Bond 1991, Knops et al. 1995, Robinson et al. 1995, Tilman 1997, Wisser et al. 1998). Brackish marshes have relatively low species diversity (Mitsch and Gosselink 1993) and are characterized in the Northern Gulf of Mexico by *Spartina patens* and *Distichlis spicata*. The low diversity is likely a product of harsh environmental conditions (e.g., salinity and soil waterlogging) where only species adapted for those conditions can survive (Von Holle et al. 2003). Yet, in the last 40 years, invasion by the common reed, *Phragmites*, has become prevalent in brackish areas where it has not historically been found (Chapter 2, Chambers et al. 1999, Bart and Hartman 2000, Rice et al. 2000).

The frequency and intensity of disturbance is one of the principal factors considered to regulate community invasibility (Fox and Fox 1986, Hobbs 1989). Disturbances alter resource supply in communities by creating gaps, opening space, altering hydrology or nutrient levels (Pickett and White 1985). Because of their position in the landscape, wetlands experience

natural disturbances typical for both terrestrial (e.g., fire) and aquatic (e.g., tidal/storm surges, sedimentation) ecosystems (McKee and Baldwin 1999). Yet, as population growth continues to climb in nearshore areas, development pressures have increased in the coastal zone. As a result, wetland communities have become subject to both increased intensities and frequencies of anthropogenic disturbance (Chambers et al. 1999, McKee and Baldwin 1999, Bart and Hartman 2000). Much like physical disturbances, wetlands are exposed to increased nutrient loads which can result in shifts of plant community composition and diversity (Levine et al. 1998, Boyer and Zedler 1999, Pennings et al. 2002).

Both disturbance intensity/frequency and eutrophication can serve as a source of temporal and spatial heterogeneity (Sousa 1984), altering both species composition and community structure (Suding and Goldberg 2001). It impacts the relative abundances of populations and in some cases, provides ideal opportunities for invasive species to establish (Hood and Naiman 2000, Brewer 2002). In marsh communities, vegetative recovery after physical disturbances is most often promoted by rapid growth of clonal species (Hartman 1988, Bertness 1991, Allison 1995), whereas seedling establishment tends to be a rare phenomenon in the recolonization process (Shumway and Bertness 1992). This brackish marsh community is dominated primarily by *Spartina patens* and *Distichlis spicata*, with sparse inclusions of *Schoenoplectus robustus*. Within three months of enacting both lethal and non-lethal disturbances, *Spartina* and *Distichlis* recovered to almost 50% of natural cover densities (Figures 3-5(b) and (c)). In fact, *Distichlis* cover in non-lethally disturbed plots exceeded that demonstrated in control plots in the initial three months (Figure 3-5(b)). Both *Spartina* and *Distichlis* have been observed to quickly revegetate denuded areas through vegetative growth even in the absence of seedling establishment (Allison 1995). Surprisingly, the non-dominant

species *Schoenoplectus* initially responded very strongly to disturbances, far exceeding densities reflected in control plots, yet declined over the course of the study (Figure 3-5(d)). Although increased salinities (Table 3-6) resulting from the drought could be responsible for the reduction in *Schoenoplectus* cover and biomass (Figures 3-4.4, 3-5(d) and 3-7.4), it is more likely a result of increased competition with *Spartina* and *Distichlis*. Both *Spartina* and *Distichlis* biomass, stem height and cover rapidly increased in fertilized disturbed treatments often laying over and smothering adjacent vegetation (Figures 3-4.3, 3-7.2, 3-7.3, and 3-8). Furthermore, the addition of *Phragmites* rhizomes in fertilized plots in the form of sods may have further prevented *Schoenoplectus* from reaching levels found in control plots with no propagule introduction (Figure 3-7.5).

Louisiana experienced two record setting drought seasons in both 1999 and 2000 (Figure 3-2). As a result, water tables were depressed and porewater salinities ranged from 20 to 38 ‰, which exceeded that normally measured in brackish communities (Table 3-6; Mitsch and Gosselink 1993). It is very likely that this extreme meteorological event depressed treatment responses of measured variables such as pH, salinity, redox, and sulfide concentrations (Table 3-5). As expected, ammonium concentrations were positively correlated with fertilization treatments (Table 3-6; Figure 3-11.1). However, ammonium concentrations increased over time, indicating that nutrients were accumulating in fertilized plots and that more and more exchange sites were becoming saturated. This is likely due to the decrease in flushing associated with drought conditions (Figure 3-2). Regardless of the drought conditions, both *Distichlis* and *Spartina* responded vigorously to fertilization treatments, with a two-fold increase in *Distichlis* biomass and a third more *Spartina* biomass in fertilized plots (Figures 3-7.2(b) and 3-7.3(c)) when compared to unfertilized treatments.

Success of *Phragmites* Introductions

Although introduced *Phragmites* rhizomes began growing immediately in all disturbance and nutrient treatments, no seedlings emerged in treatments receiving seed introductions. Previous field and greenhouse experiments indicate that seedling emergence in populations of *Phragmites* located in the study area is a rare phenomenon (Stanton, unpublished data). Seed incubated under optimum conditions (see Ekstam and Forseby 1999, Ekstam et al. 1999) in a climate controlled growth chamber did not germinate, and furthermore, field plots inoculated with seed did not give rise to any seedlings under natural conditions. Germination of *Phragmites* seed is generally infrequent (Pellegrin and Hauber 1999, Mauchamp et al. 2001), and if germination does occur, seedlings are sensitive to harsh conditions (i.e., high salinities and drought) and can take up to 2 years to become successfully established (Haslam 1971). In contrast, plants arising from root and rhizome fragments are more resistant to increased salinities and have a higher chance of survival (Lissner and Schierup 1997, Bart and Hartman 2002).

Phragmites rhizomes introduced into disturbance and nutrient treatment plots began to grow immediately, with rhizomes in non-lethally disturbed plots responding with more biomass and higher cover measurements than in lethally disturbed or undisturbed treatments (Figures 3-5(a) and 3-7.1(a)). Furthermore, *Phragmites* rhizomes exhumed from 5 non-lethally disturbed plots and 4 undisturbed plots receiving rhizome introductions remained viable at the conclusion of the experiment (Figure 3-9). This response may be a result of facilitation of harsh physical conditions by neighboring plants (Franco and Nobel 1988, Bertness and Callaway 1994, Bertness and Hacker 1994). *Spartina*, *Distichlis* and *Schoenoplectus* were present in undisturbed plots and re-vegetated non-lethally disturbed treatments more quickly than in lethally disturbed plots (Figures 3-5(b-d)). The presence of aboveground vegetation most likely buffered drying

conditions with increased shade. Furthermore, the greater *Phragmites* cover and biomass measured in non-lethally disturbed plots when compared to undisturbed plots may be a result of reduced competition for light capture. *Phragmites* ability to capture light for initial growth would have been greater in non-lethally disturbed plots relative to undisturbed control plots where neighboring vegetation remained. Thus, non-lethal disturbances might be more susceptible to *Phragmites* establishment and subsequent invasion than lethal disturbances. Although harsh conditions would be reduced in undisturbed areas, competition between resident and establishing species could potentially favor the residents.

One of the most important results of this study was the persistence and viability of introduced *Phragmites* plants (Figure 3-9) through two consecutive record-breaking drought seasons (Figure 3-2). Lodge (1993) describes that the ecological resistance to an invading species occurs in part because of environmental, demographic and biotic factors influencing the arrival and establishment of invading species. Environmental conditions (i.e., drought) during the invasion process acts as a major physiological filter that can preclude a species altogether or induce a significant lag time between establishment and spread of an invading species. Thus, an organism's ability to persist under unfavorable conditions will increase its chances of spreading once conditions improve. Of the 30 *Phragmites* sods planted in this study, 10 remained viable at the conclusion of the experiment (Figure 3-9). All *Phragmites* vegetation (above- and belowground) was excavated at the end of the experiment and tested using the tetrazolium viability assay (Parker 1953, Steponkus and Lanphear 1967). Of the 10 surviving *Phragmites* plants, 6 were located in fertilized treatments and 4 were in non-fertilized treatments (Figure 3-10). Although 5 *Phragmites* plants survived in non-lethally disturbed plots and 4 survived in control plots, only one remained viable in lethally disturbed plots. Even though the

environmental conditions in lethally disturbed plots may have been harsher than in other disturbance treatments, the persistence of *Phragmites* rhizomes through harsh environmental conditions is clear. Its ability to persist until benign environmental conditions return could be a likely mechanism increasing establishment success and hastening *Phragmites* expansion.

Response of the Natural Community to Invasion

A community is invulnerable when an introduced species is able to establish and persist or expand (Burke and Grime 1996). One barrier to invasion is competition from established native species (Crawley 1986, Crawley 1987, Rejmanek 1989, Burke and Grime 1996, Rejmanek 2000, Thompson et al. 2001). However, the success of an invading species is also dependent on competitive ability, growth rate and ability to persist in a new environment (Chambers et al. 1999, Windham and Lathrop 1999, Rice et al. 2000, Saltonstall 2003). In this brackish marsh, both *Spartina* and *Distichlis* responded to disturbance and fertilization treatments with much greater cover and biomass than *Phragmites* (Figures 3-5 and 3-8). At the end of the experiment, unfertilized *Spartina* biomass was approximately 65 times as great as unfertilized *Phragmites*, and 85 times more when in fertilized treatments (Figure 3-7). Likewise, fertilized *Distichlis* biomass was 26 times more than fertilized *Phragmites*, and 15 times more in unfertilized treatments (Figure 3-7). Although the increase in biomass and cover of the resident vegetation did restrict success and establishment of *Phragmites* in some cases, 30% of *Phragmites* plants remained viable even through drought conditions (Figure 3-9). This indicates that even under extreme environmental conditions, this brackish marsh is susceptible to *Phragmites* invasion.

Conclusion

It is clear that *Phragmites* is invading brackish marshes where it has not occurred previously (Chapter 1, Cronk and Fuller 1995, Chambers et al. 1999, Galatowitsch et al. 1999).

Although an invasive genetic variant originating from Europe has been identified, and is known to be responsible for much of the spread along the Eastern Seaboard of the United States, it isn't known if the populations in this study are of the same genetic origin (Burdick et al. 2001).

Phragmites has many characteristics that enable it to be a dominant competitor once it establishes in brackish marshes: It's larger morphology with tall fast growing clonal culms (3-4 m) and a deep (~1 m) integrated rhizome network can effectively out-compete natural marsh vegetation (D'Antonio 1993, Pyle 1995, Brewer 2002). Additionally, a deep rhizome network may enable *Phragmites* to utilize nutrients that are unavailable to other species with a shallower root zone, or utilize a deeper water table that is lower in salinity than porewater found closer to the marsh surface (Myers 1983, Milbau et al. 2003). Furthermore, the time required for *Phragmites* to develop a rhizome network and carbohydrate reserve after establishment could answer questions concerning observed lag times between establishment and active spread.

Invasion ecology has sought to answer community invasibility questions through closer examinations of disturbance regimes (Burke and Grime 1996) of natural communities in combination with the characteristics of invading species . Invasions seem particularly successful when the invaders exhibit certain traits such as fast growth, wide environmental tolerances, and greater size . Even though *Phragmites* cover declined over the course of the study, one third of the *Phragmites* plants introduced to undisturbed and disturbed plots in this study remained viable even during two record setting drought seasons. The persistence of *Phragmites* indicates the potential for active growth and spread once conditions improve, and thus demonstrates that brackish marshes are likely susceptible to *Phragmites* invasion even under severe environmental conditions.

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CHAPTER 4

THE ECOSYSTEM EFFECTS OF *PHRAGMITES AUSTRALIS*, AN INVASIVE CLONAL PLANT SPECIES IN SOUTHWESTERN LOUISIANA

Introduction

The increasing prevalence of invasive species and their ensuing impact on natural community structure has become a primary concern for ecologists (Mooney and Drake 1986, Vitousek 1992, Carroll and Dingle 1996, Vitousek et al. 1996, Cox 1999). There are ever increasing reports of invasive species colonizing natural areas (Cox 1999), and in many cases threatening natural species diversity and potentially altering ecosystem services and function (Vitousek 1984, Gordon 1998). Thus, it seems logical that invasive species that are competitive enough to invade natural habitats are also likely to have significant impacts to community structure, composition, and least apparently but most importantly, ecosystem services that the natural community provides (D'Antonio and Vitousek 1992).

Although non-indigenous animals have long been recognized to have significant impacts to resource availability, community structure, and ecosystem functioning (Elton 1958, Vitousek 1984, Cloern and Alpine 1991, Schoessler and Nalepa 1996, Cox 1999), non-native plants also have major effects (Vitousek 1984, 1992, Gordon 1998, Levine 1999, Levine et al. 2003). Non-native plants can use resources in different manners than native species, alter flow of energy or biomass by changing food webs, and also alter disturbance regimes that often facilitate further colonization of non-native species (Vitousek 1990, Crooks 2002).

Often, non-native plant species that possess markedly different growth forms or habits can modify the physical structure of the ecosystem itself (i.e., ecosystem engineering), many times irreversibly (Zavaleta 2000, Crooks 2002). For example, the growth form of *Lolium perenne*, an invasive perennial grass, increases fire frequencies in coastal chaparral areas in

California thus preventing successful establishment of native species (Zedler 1995). Similarly, tall invasive species may out-compete shorter competitors for sunlight or conversely, even promote the establishment of other species by reducing salinities in coastal environments or increasing soil moisture content in arid environments (Franco and Nobel 1988, Bertness and Yeh 1994, Holmgren et al. 1997). Deep rooted invasive species, such as *Tamarix* in arid and semi-arid riparian areas of southwestern U.S., have significantly higher transpiration rates than native species, effectively drawing down water tables and lowering flow rates of waterways (Vitousek 1984, Zavaleta 2000). It seems apparent that invasive organisms demonstrating a different morphology or physiology can have an immediate effect on native species, and furthermore, are likely to alter ecosystem processes and subsequent ecosystem services (Ehrenfeld 2001).

Although shifts in community structure are immediately noticed when invading species displace native species, it is much more difficult to identify the nature of ecological impacts to ecosystem function and services. Plants can alter soil structure over time through litter build up and hummock formation, changing flooding regime and the rates of nutrient renewal and storage (Bowden 1987), yet once those effects are realized the invasion is often too widespread to examine the rate at which ecosystem functions change over time.

Phragmites australis (Cav.) Trin. Ex Steud., the common reed, has expanded its distribution in North America during the past 50 years (Bailey 1997, Rice et al. 2000, Warren et al. 2001). Although long considered a native species, a genetic variant originating from Europe has been identified and thought to be responsible for the observed spread throughout many inland fresh water marshes, coastal brackish and salt marshes of the mid-Atlantic and Gulf Coast regions of the United States (Neiring and Warren 1980, Orson 1987, Chambers et al. 1999, Saltonstall 2002). *Phragmites australis* (hereafter referred to as *Phragmites*) often forms large

mono-specific stands in habitats where it had not occurred previously (Winogrand and Kiviat 1997, Galatowitsch et al. 1999, Clevering and van der Toorn 2000, Rice et al. 2000). Like many of the native marsh plants it replaces, *Phragmites* is also a grass. However, its clonal morphology is strikingly different with culm heights in excess of 3 m replacing natural brackish marsh vegetation that seldom exceeds 1 m. In addition, *Phragmites* rhizomes can penetrate marsh sediments to a depth of a meter (Burdick et al. 2001) where native graminoid rooting depth seldom exceeds 30 cm (Mitsch and Gosselink 1993).

With a distinctly different morphology, it is not surprising that *Phragmites* invasions have been correlated with changes in ecosystem characteristics of invaded areas. In New Jersey brackish marshes, Windham and Lathrop (1999) found that *Phragmites* biomass was 10 times greater than that of neighboring un-invaded marsh, and invaded areas had higher redox levels while both salinities and water levels were reduced. Furthermore, soil properties were correlated with both age and biomass of *Phragmites* communities. Water levels and micro-topographic relief can be reduced in as little as three years while other variables may take up to 15 years to stabilize at peak difference from adjacent un-invaded communities (Windham and Lathrop 1999). *Phragmites* also can decrease ammonium concentrations relative to adjacent un-invaded *Spartina alterniflora* or *S. patens* marsh (Chambers 1997, Windham and Ehrenfeld 2003).

Phragmites is invading relatively undisturbed brackish marshes in Southwestern Louisiana, often forming circular mono-specific stands (L. Stanton, personal observation). Similar establishment patterns have been reported in brackish marshes in the Mid-Atlantic United States coast (Lathrop et al. 2003). Although it isn't known if these *Phragmites* populations are the non-native European strain, the rapidly increasing numbers and sizes of these populations have attracted the attention of the public and marsh managers (Tom Hess, LWDF,

Louisiana Department of Wildlife and Fisheries). By using a time series of historic aerial photographs, the establishment time and spreading rate has been determined for several large mono-specific *Phragmites* stands (Chapter 2). These circular stands appear to originate from a single establishment point, spread outwardly in all directions and range in size from 100 to 150 m in diameter. Thus, it is intuitive that the area in the center of these *Phragmites* “islands” has been occupied by *Phragmites* for the longest period of time while the areas closer to the edge of these colonies have been occupied by *Phragmites* the shortest period of time. The presence of these circular *Phragmites* communities provides an opportunity to examine differences in ecosystem functioning between different vegetation types over measurable time scales.

To determine if *Phragmites* does alter ecosystem functions in a Northern Gulf of Mexico brackish marsh, I addressed several research questions: (1) Do brackish marshes dominated by *Phragmites* exhibit environmental characteristics different than those in un-invaded marsh? (2) Are soil decomposition rates affected by *Phragmites* invasion? (3) Do physical characteristics (i.e., elevation, peat accumulation, sediment composition) of brackish marsh change over time when invaded by *Phragmites*? (4) Does aboveground biomass production change as *Phragmites* invades brackish marsh areas? To answer these research questions, four distinct successional community types were identified (un-invaded marsh, ecotone, the edge of mono-specific *Phragmites* and the center of mono-specific *Phragmites*) along transects extending from the center of three *Phragmites* colonies outward to natural un-invaded brackish marsh. My results show that *Phragmites* has greater aboveground biomass and organic matter accumulation relative to un-invaded marsh. This study demonstrates for the first time that *Phragmites* increases marsh surface elevation relative to un-invaded marsh by affecting soil composition, peat development and lower cellulose decomposition rates. These effects may allow *Phragmites* dominated

marshes to better tolerate increasing water levels due to sea-level rise/land subsidence than short stature graminoids.

Methods

Study Site

Rockefeller Wildlife Refuge (hereafter RWR, 29°55' N 92°30' W) lies within the southeastern portion of the Chenier Plain Region (Cameron Parish; Figure 4-1). It is bordered on the south by the Gulf of Mexico, on the north by the Grand Chenier Ridge complex, and contains about 32,000 hectares. Present-day RWR was purchased by the Rockefeller foundation in 1914, and subsequently deeded to the state of Louisiana in 1920 under the mandate to “preserve, maintain, and improve, whenever practical, the refuge lands in perpetuity”. The majority of the refuge is actively managed through the use of water control structures to maximize germination of annual plants important as food for waterfowl (Wicker et al. 1983).

The study site, Price Lake Unit, is located in the southwestern corner of the Rockefeller Wildlife Refuge and is bordered to the south by the Gulf of Mexico (Wicker et al. 1983). Price Lake Unit is passively managed with fixed crest weirs and low hurricane levees (Phillips 2002). It contains approximately 7500 acres of brackish to saline marsh and shallow open water bodies. The crest of the weirs is set to 15 cm below the average marsh level to reduce the inflow and out flow of water over an average tidal cycle. This prevents excessive draining of marsh ponds during periods of sustained low tides and result in a stabilization of water levels and a reduction in hydrological energy (Wicker et al. 1983). The brackish marsh in Price Lake Unit is comprised primarily of *Spartina patens* and *Distichlis spicata*, with sparse inclusions of *Schoenoplectus robustus*. Discreet circular populations of *Phragmites* have become established within this area,

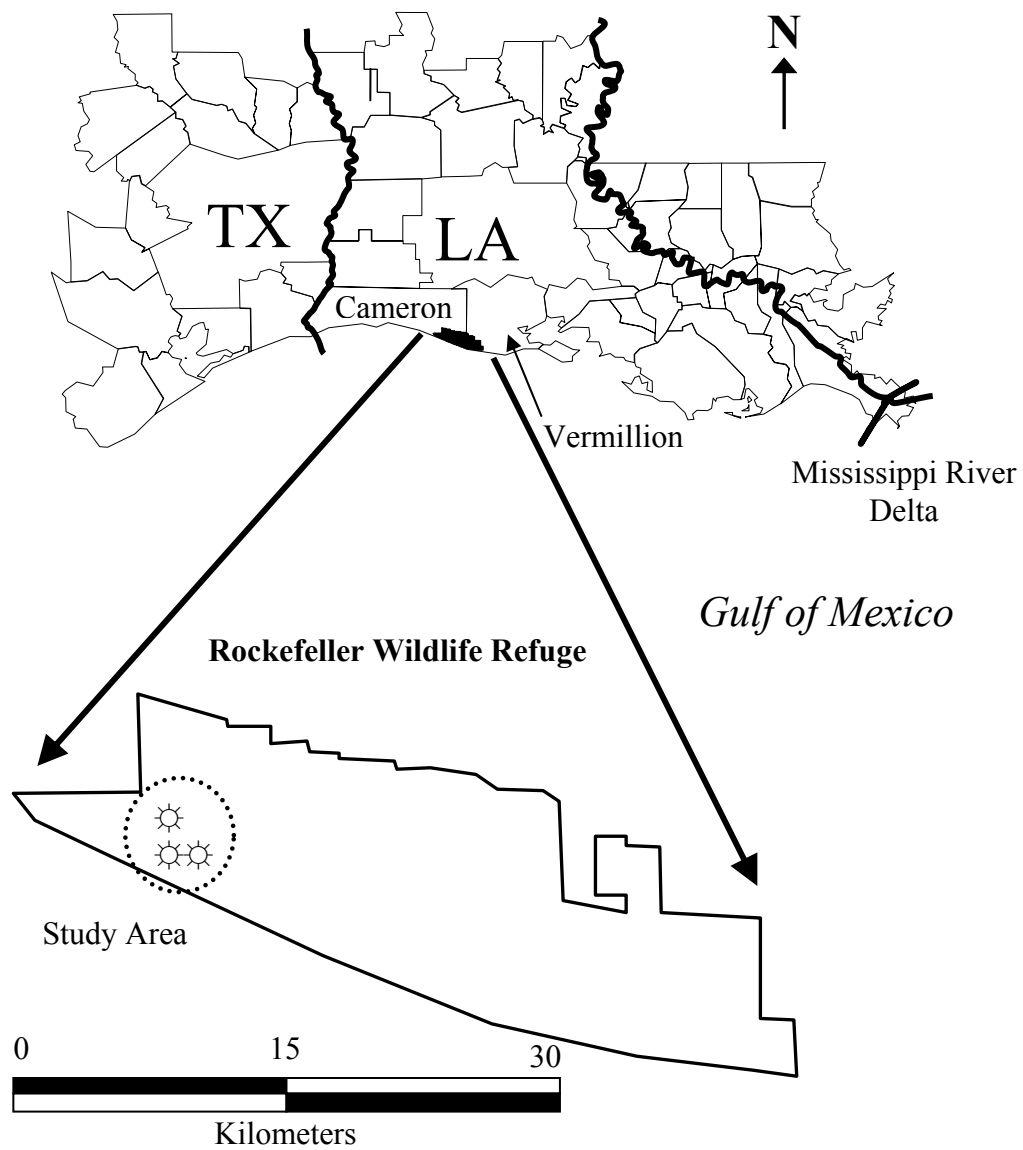


Figure 4-1: Location of Rockefeller Wildlife Refuge, Louisiana. The refuge lies in southwestern Louisiana on the border between Cameron and Vermillion Parishes.

and have actively spread over the last 40 years. Hereafter in this study, these species will be referenced by their generic names, *Spartina*, *Distichlis*, *Schoenoplectus* and *Phragmites*.

Experimental Design

Three discrete circular *Phragmites* invasions were located within the Price Lake Unit at RWR. Each of these stands was first observed on aerial photography of that area in 1968 and have steadily increased in size (Chapter 2). A transect was extended due south from the center of each *Phragmites* colony into the natural un-invaded short graminoid marsh. This created, in essence, a “chronosequence” of the marsh area occupied by *Phragmites*. Along this *Phragmites* chronosequence, four distinct community types were identified; the first is the un-invaded marsh (no *Phragmites*), the second is the ecotone between the un-invaded marsh and *Phragmites* (*Phragmites* age ~3 years), the third is the community at the edge of mono-specific *Phragmites* (age ~7 years) and the fourth is the center of the mono-specific *Phragmites* stand (age ~40 years). A randomized block design was employed, with each invasion serving as a block. Within each community type, three 1-m² plots were randomly established at least 2 m apart in which environmental and vegetative data were collected. In the center of each colony, sample plots were randomly arranged so that elevation transects would not disturb the plots. For each statistical analysis, community type and sample date (when applicable) were analyzed as fixed effects in order to study spatial and temporal variation in the study site, while block (or colony) was analyzed as a random effect to allow inferences to other *Phragmites* colonies in this study area. Unless otherwise noted, all statistical analyses were performed using the PROC MIXED procedure of the SAS Statistical Package (SAS Institute 2003). All significant main effects were further investigated using Tukey’s post-comparison test. In order to improve normality and

homogeneity of variance, some data transformations were required. All differences indicated in results are significant unless otherwise noted.

Environmental Measurements

At four different times during a 16-month period, sulfide concentration, salinity, and pH were measured from porewater within each subplot in each community type within each colony. Porewater was removed from each plot in the 10-20-cm zone of the soil profile using a suction sampler (McKee et al. 1988, Koch and Mendelssohn 1989). The sampler consisted of a rigid plastic tube (3-mm inside diameter) with numerous small holes along the bottom 5-cm segment of the tube. The rigid tube was connected with Tygon tubing to a 50-ml syringe with a three-way valve. Approximately 30 ml of relatively clear interstitial porewater was collected at each sampling point. Five ml of unfiltered interstitial water was immediately mixed with 5 ml of anti-oxidant buffer and placed on ice for laboratory analysis of total soluble sulfide concentration (sulfide electrode, Lazar Research Laboratories, Los Angeles, CA, USA). Another unfiltered 15-ml aliquot was reserved for pH and salinity measurements. Salinity was measured using a handheld field refractometer and pH was measured using an Altex Model 3560 Digital pH meter with a Corning General Purpose Combination Electrode.

Both ammonium concentrations and nitrogen mineralization rates were measured in sediment from each of the community types on each sample date. Two soil cores (5-cm diameter x 9.5-cm height) were taken in each community type on each sample date. The first sample was sealed in a Ziploc freezer bag, placed on ice, and transported back to the lab for immediate extraction with 2N KCl to measure ammonium concentrations ($\text{NH}_4\text{-N}$ extraction following Bremner and Keeney 1966). The second sample was placed into a sealed Ziploc sandwich bag and placed approximately 15-cm deep into the marsh sediment to measure *in situ* nitrogen

mineralization (method following Eno 1960). The incubated bags were retrieved after 14 days, placed into Ziplock freezer bags and transported to the lab for extraction also with 2N KCl (Bremner and Keeney 1966) to determine the capacity of the soil to release inorganic nitrogen, and hence, influence soil fertility. After extraction, $\text{NH}_4\text{-N}$ samples were filtered through a 0.45 mm syringe filter and concentrations were measured using the Colorimetric, Automated Phenate Method (U.S. Environmental Protection Agency 1979).

Soil oxidation status (Eh, redox potential) was measured in each subplot within each community type within the upper one to two cm of soil ($n = 3$, hereafter referred to as surface Eh) and at a depth of 15 cm ($n = 3$, depth Eh). Measurements were made using a calomel reference electrode, bright platinum electrodes and a portable Cole-Parmer digital pH-mV meter. Each reading was standardized to a standard hydrogen electrode by adding 245 mV to each reading (Faulkner et al. 1989). Soils were classified as aerated (>300 mV), moderately reduced (100 to 300 mV), reduced (-100 to 100 mV) and strongly reduced (<-100 mV), following Patrick's (1980) classification. Eh readings were not corrected for pH.

Interstitial data was analyzed using a repeated-measures ANOVA (PROC MIXED; SAS Institute 2003). All significant main effects were further investigated using Tukey's post-comparison test. In order to improve normality and homogeneity of variance, NH_4 , pH, and salinity were log transformed while sulfides were square-root transformed. General trends in the data were revealed by plotting the mean and S.E. of the raw data for each community type.

Vegetative Measurements

In October (2001), the vegetation in each subplot of each community type within each colony was clipped to ground level (0.25 m^2) and collected. Collected vegetation was returned to the laboratory and sorted by species. Stem density was determined for each species. Stem

height and basal diameter was measured for each *Phragmites* stem, while a random sub-sample of 10 stems were selected for height measurements of each of the short graminoid species. All vegetation was then dried in paper bags to constant weight in a forced air oven at 70° C and weighed using a calibrated electronic balance. Both dry weight and stem densities were converted to a 1-m² basis for statistical analysis.

Decomposition Rates

Decomposition of cellulose in cotton strips was used as a proxy for evaluating the rates of decomposition of soil organic matter (Latter and Howson 1977, Harrison et al. 1988). Unlike natural litter bag tests, cotton strips are comprised almost totally of cellulose. Since cellulose comprises about 70% of the organic carbon compounds in plant tissue, its rate of decay is a key factor in plant decomposition. This technique has been used in a variety of different wetland environments to show relative rates of cellulytic activity and cellulose decomposition (French 1988, Harrison et al. 1988, Mendelssohn and Slocum 2004). Quantifying cellulose decomposition using cotton strips is based on the loss of tensile strength (TS) of cellulose fibers, referred to cotton tensile strength loss (CTSL; Shirley Institute, Didsbury, Manchester, UK).

In each community type (n = 4), 2 cellulose strips (12 x 30 cm) were inserted vertically into the soil substrate with a spade as described by Maltby (1988). Approximately 4 cm of the strip was left above the soil surface to facilitate retrieval. Once installed, the sediment surface was marked on each strip with a small lateral cut. The strips remained in the marsh for 14 days and were then retrieved. Reference cotton strips, used to quantify the TS of non-decomposed material, were inserted into the soil and immediately removed. Once collected, all strips were washed in tap water to remove the soil and other debris, and then washed in de-ionized water until clean. The strips were then air dried and stored in the dark in plastic bags until analysis.

For analysis, the strips were cut into horizontal strips 2.5-cm wide. These were reduced by fraying edges until each strip was exactly 2 cm wide, and corresponded to soil depths of 1, 4, 7, 10, 13, 16, 19, 22 and 25 cm. Tensile strength was measured in Newton's with a motorized tensiometer (Dillon Snapshot) equipped with spring loaded roller grips. To ensure standard conditions, all measurements were made at approximately 23 °C and 100% humidity. For each sub-strip, the CTSL was calculated as:

$$1) \%CTSL = ((1 - N/C) / D) \times 100$$

where N is the TS of the sub-strip in Newton's, C is the average TS of the reference sub-strips in Newton's, and D is the number of days the strips were left in the ground (14 days). CTSL is therefore expressed on a percent loss per day basis.

Community type was analyzed as a fixed effect to study temporal variation between un-invaded marsh and different-aged *Phragmites* stands. To determine how cellulose decomposition was affected by soil depth and community type, a factorial model was used with depth as a repeated effect. A separate factorial model was used to examine the effects of time, environmental measurements and community type on cellulose decomposition with time as a repeated measure.

A forward stepwise multiple-regression was used to assess how interstitial and physical data affected decomposition. Sediment temperature, water levels, Eh, elevation, bulk density, percent organic matter, and porewater pH, salinity and ammonium concentrations were included as independent variables while $CTSLd^{-1}$ was the dependent variable. This procedure correlated those abiotic variables that significantly affected decomposition at the 0.05 level of significance (SAS Institute 2003)

Elevation

In May 2002, 8-cm diameter steel pipe was driven ~16-m into the marsh at the edge of each *Phragmites* colony to serve as benchmarks for elevation measurements. True elevation at the top of each pipe was determined by OTS Surveying (2697 Grand Chenier Hwy, Grand Chenier, LA 70643) after installation.

A rotary laser transit was used to measure marsh elevation across each *Phragmites* colony. Four transects were created in each *Phragmites* colony using bush blade equipped weed trimmers in June 2002 (Figure 4-2(a)). Each transect began in the center of the colony and extended directly northwest, northeast, southeast and southwest so not to disturb the southward extending sampling transect. Allowances were made *a priori* at the center of each colony so that elevation transects would not affect sample plots. Swaths approximately 5-m wide were cut so that the line of sight along each transect would allow elevation measurements to be taken along the entire length without requiring transit relocation.

Elevation measurements were taken at 1-m intervals along each transect with reference to community type (un-invaded marsh, ecotone, mono-specific *Phragmites* at the edge and mono-specific *Phragmites* in the center, Figure 4-2(b)). At each sample point, the elevation was taken of the marsh surface and at the clay pan beneath the marsh peat. Peat was carefully removed by hand to ensure that the clay pan beneath was not disturbed. The difference between these two measurements yielded peat depth. The transect extended into the natural marsh 10-m beyond the edge of the *Phragmites* colony. After all measurements had been taken, transit height and benchmark elevation were rechecked to ensure data were accurate. All elevation data were

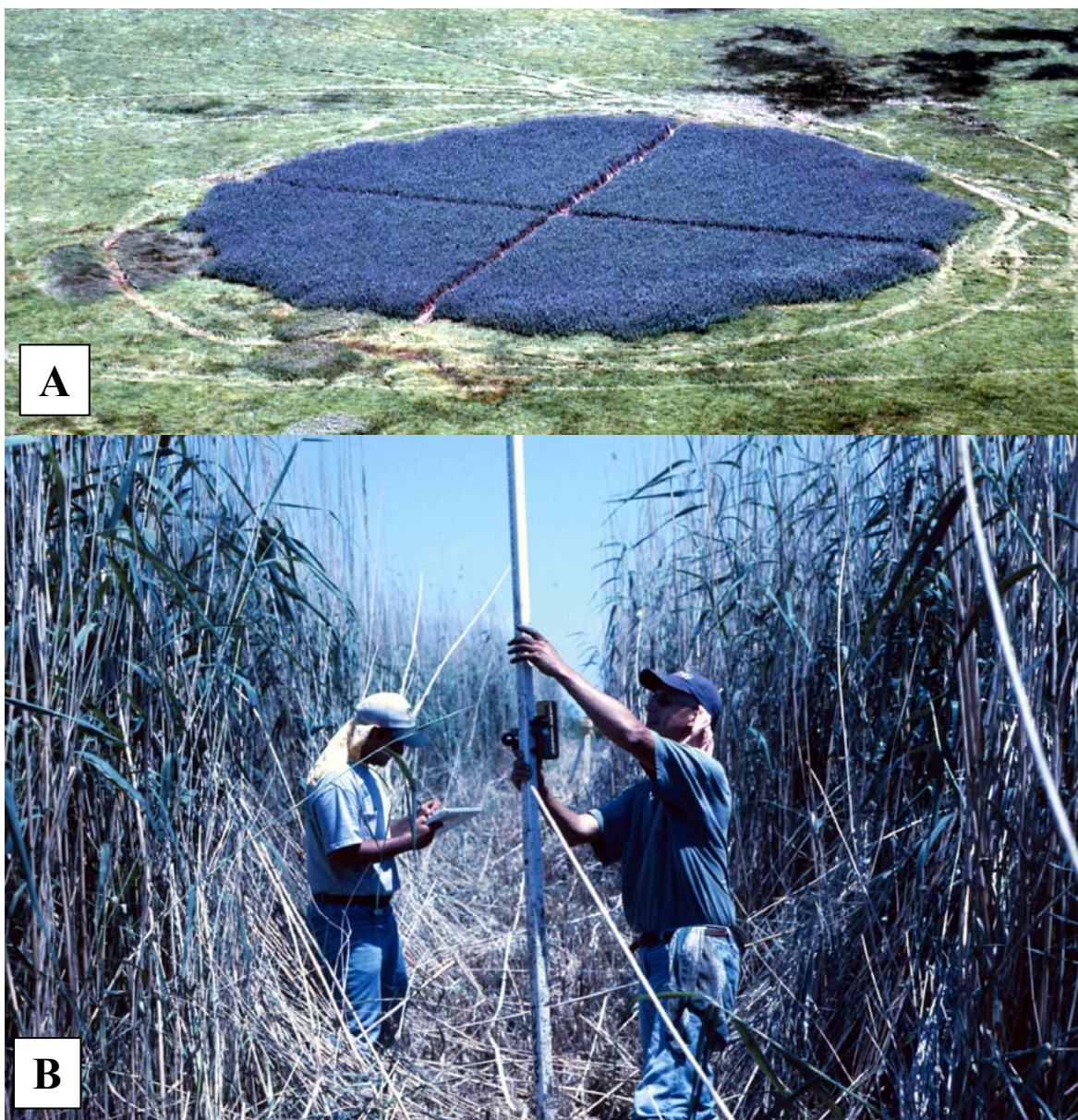


Figure 4-2(a) and (b). Figure A is an aerial photograph of a *Phragmites* colony approximately one week after conducting elevation surveys. Crossed pattern is a result of cutting line of sight swaths through the ~100 m diameter colony. Figure B demonstrates line of sight through the colony and measuring elevation using a transit and elevation rod. All measurements were corrected relative to sea level.

measured in inches, converted to centimeters and then corrected to true elevation. Elevation and peat thickness were analyzed with community type as a fixed effect and colony as a random effect.

Sediment Bulk Density and Percent Organic Matter Component

Sediment cores for measuring bulk density were collected from each community type ($n = 2$). The bulk density cores (5-cm diameter x 9.5-cm height) were dried at 65 °C to constant weight and mass determined. Once dried, cores were then combusted in a muffle furnace to determine ash-free dry weight. Muffle furnace temperature was incrementally ramped to 450 °C to prevent ignition and subsequent loss of material. Samples remained at 450 °C for 10 hours and allowed to slowly cool to 100 °C. To prevent erroneous weights due to water absorption, all samples were weighed at 100 °C. Percent organic component was then calculated for each sample. Both bulk density and percent organic data were not transformed prior to analyses.

Results

Elevation and Peat Thickness

Marsh elevation was highest in the center of the mono-specific *Phragmites* community type (Table 1; Figures 4-3(a)). Marsh elevation within mono-specific *Phragmites* at the edge was significantly higher than in the ecotone, and the ecotone was significantly higher than un-invaded marsh (Figure 4-3(a)). Elevation in the center of the *Phragmites* colony was nearly 10 cm higher than un-invaded marsh, 6 cm higher than the ecotone and nearly 3 cm greater than in the mono-specific *Phragmites* edge. Also, elevation differed by colony (Figure 4-3(b)).

Elevation in colony 3

Table 4-1. ANOVA table of elevation and peat thickness analyzed using PROC MIXED by colony and community type. Bold indicates statistical significance at $\alpha = 0.05$.

Elevation and Peat Thickness		Elevation		Peat Thickness	
Source of variation	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Colony (C)	2	62.11	<0.0001	52.14	<0.0001
Community type (Ct)	3	134.44	<0.0001	158.85	<0.0001
C x Ct	6	1.87	0.0846	2.61	0.0172

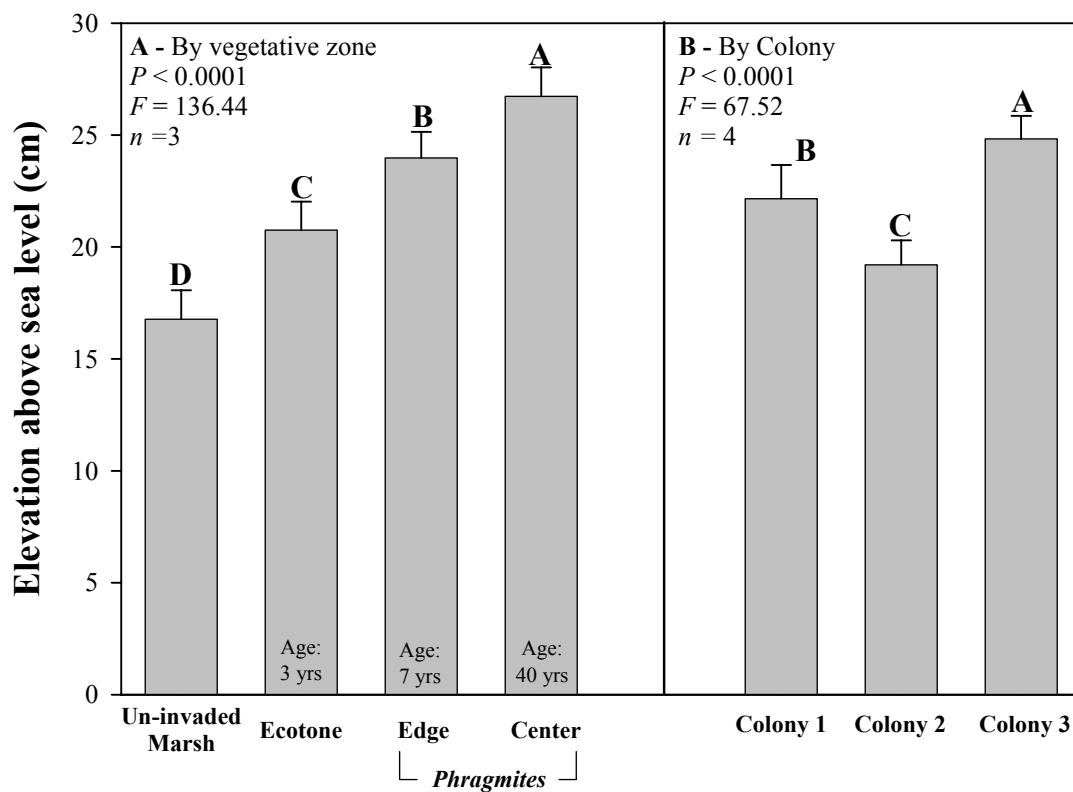


Figure 4-3(a) and (b). True elevation by (a) community type and by (b) colony. Error bars reflect SE and bars that share letters are not significantly different.

was higher than colony 1, and colony 1 was higher than colony 2. Although significant differences exist between the elevations of each colony, the largest difference between elevations was 6 cm (Figure 4-3(b)).

Peat thickness was significantly greater in the mono-specific *Phragmites* center than in the mono-specific edge *Phragmites*, ecotone or in un-invaded marsh (Table 4-1; Figure 4-4(a) and (b)). However, peat thickness by community type was dependent on colony (Table 4-1, Figure 4-5). In colony 2 and 3, peat thickness increased with *Phragmites* age and was significantly different between each community type. Peat thickness in colony 1 also increased with *Phragmites* age, yet, peat thickness in mono-specific *Phragmites* at the edge of the colony and in the center was not significantly different. When averaged over colony, peat layer in un-invaded marsh was less than 5 cm thick while peat thickness in the center *Phragmites* stand was over 16 cm. Peat thickness also varied by colony, with colony 1 (the largest colony) having 5 cm thicker peat than either colony 2 or 3 (Figure 4-4(b)).

Sediment Characteristics

Sediment bulk density was significantly highest in the un-invaded marsh (Table 4-2; Figure 4-6). On average, bulk density in the un-invaded marsh was approximately 0.30 g cc^{-1} , a third more than bulk density in the oldest *Phragmites* (0.20 g cc^{-1}). Bulk density steadily decreased with increasing age of *Phragmites*. Conversely, percent organic material was significantly greatest in the oldest part of each *Phragmites* colony, and steadily decreased with decreasing age of *Phragmites* and was lowest in the natural marsh (Table 4-2; Figure 4-7).

Cellulose Decomposition

Decomposition rates were significantly different between sample dates, community type and depth (Table 4-3). The change in decomposition rates among community types was

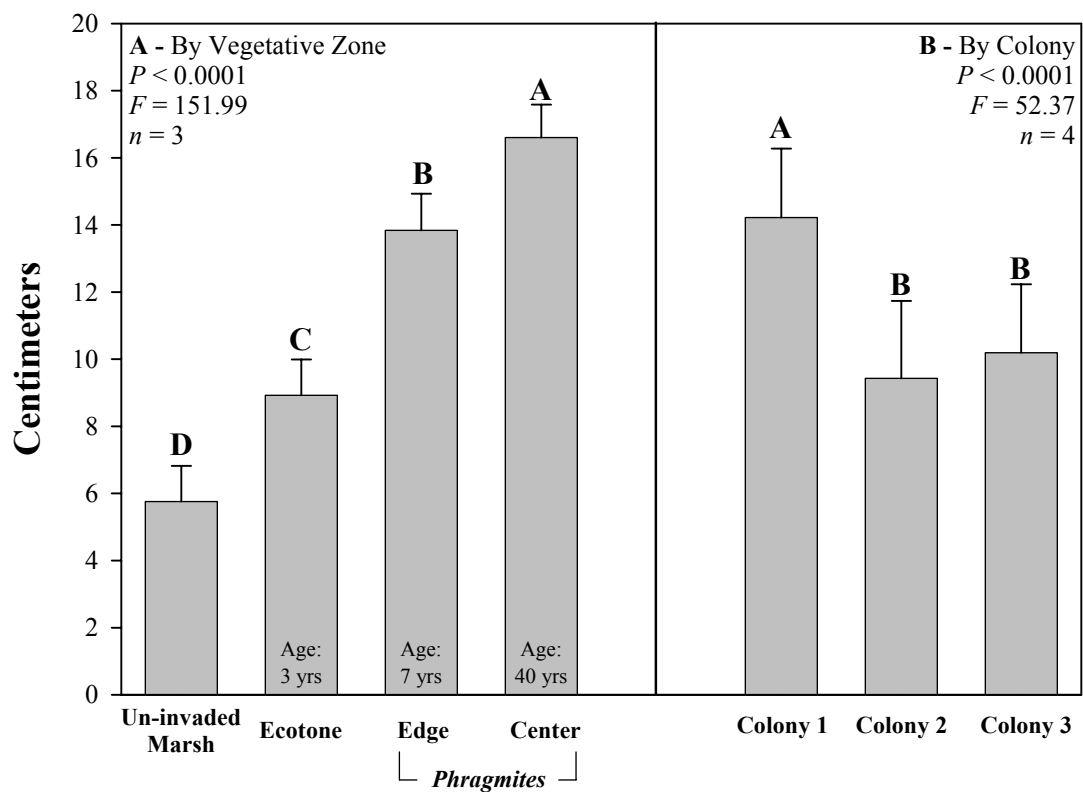


Figure 4-4(a) and (b). Peat thickness is reflected by (a) community type and (b) colony. Error bars reflect SE and bars that share letters are not significantly different.

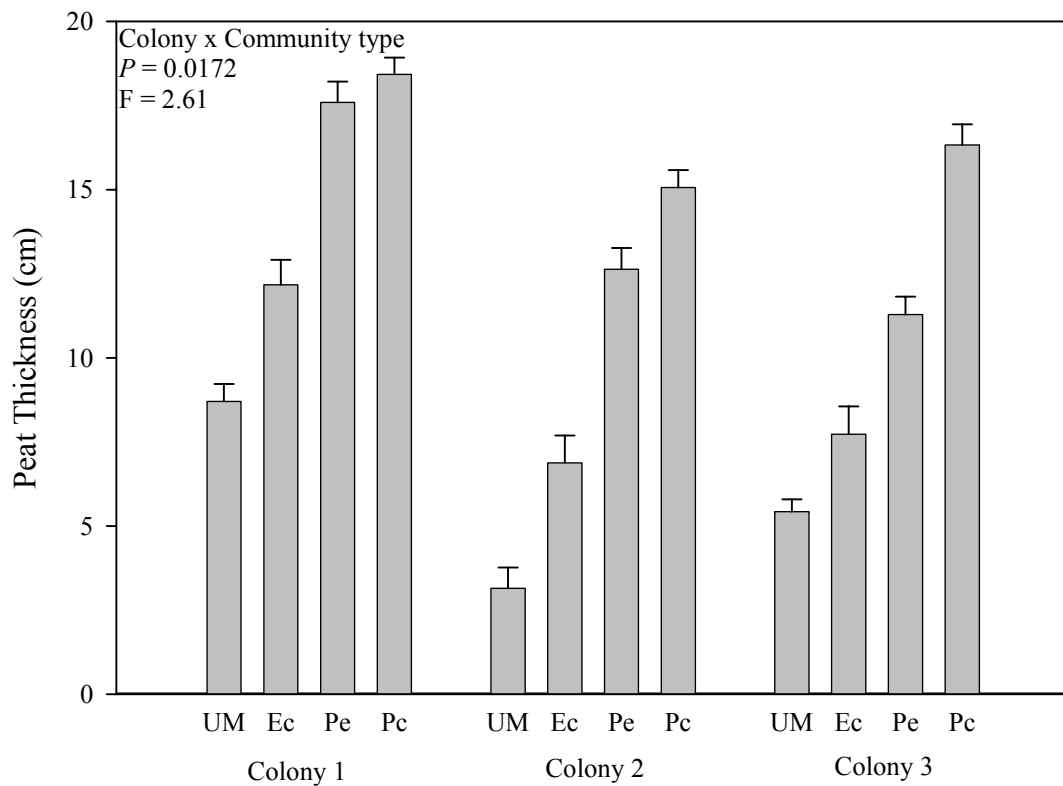


Figure 4-5. Peat thickness by community type and vegetative community. UM is un-invaded marsh, Ec is ectone, Pe is mono-specific *Phragmites* at the edge and Pc is mono-specific *Phragmites* in the center.

Table 4-2. ANOVA table of sediment characteristics analyzed by community type using PROC MIXED. Bold indicates statistical significance at $\alpha = 0.05$.

Sediment Characteristics		Bulk Density (g cc ⁻¹)		Organic Material (%)	
Source of variation	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Community type	3	8.05	0.0013	8.43	< 0.001

Note: Block was tested as a random effect.

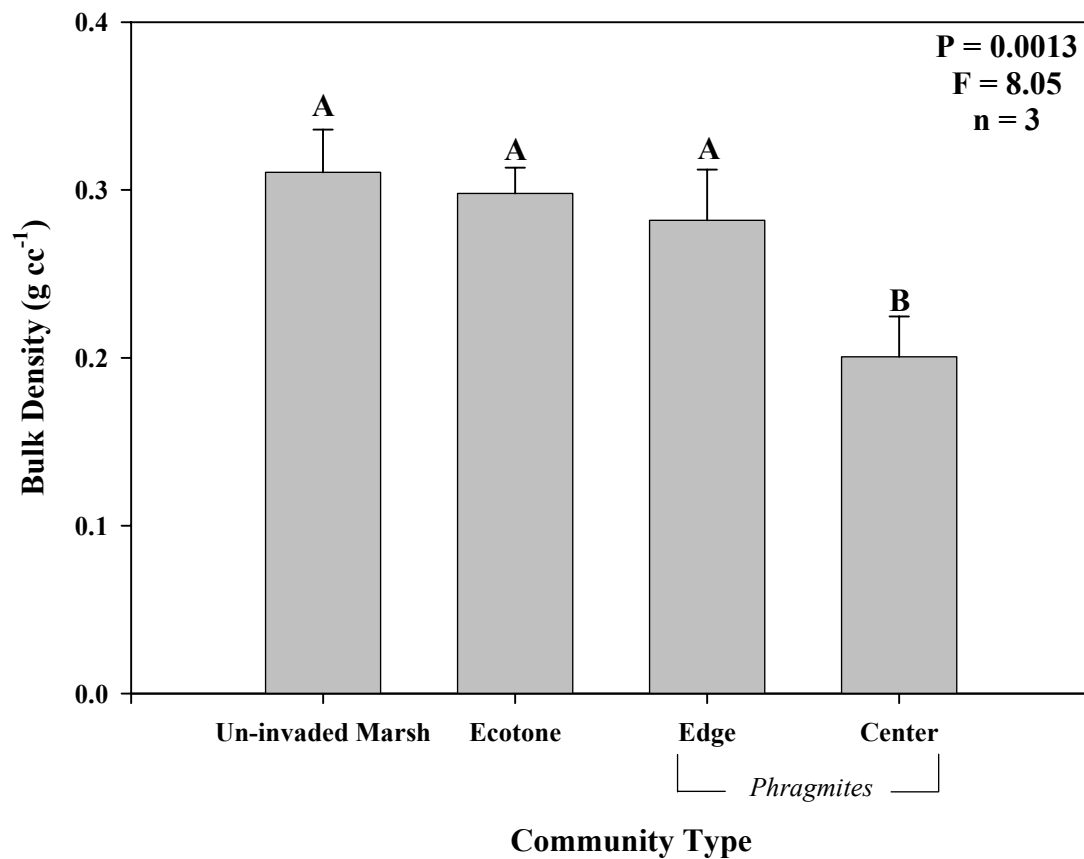


Figure 4-6. Sediment bulk density by community type. Error bars reflect SE and bars that share letters are not significantly different.

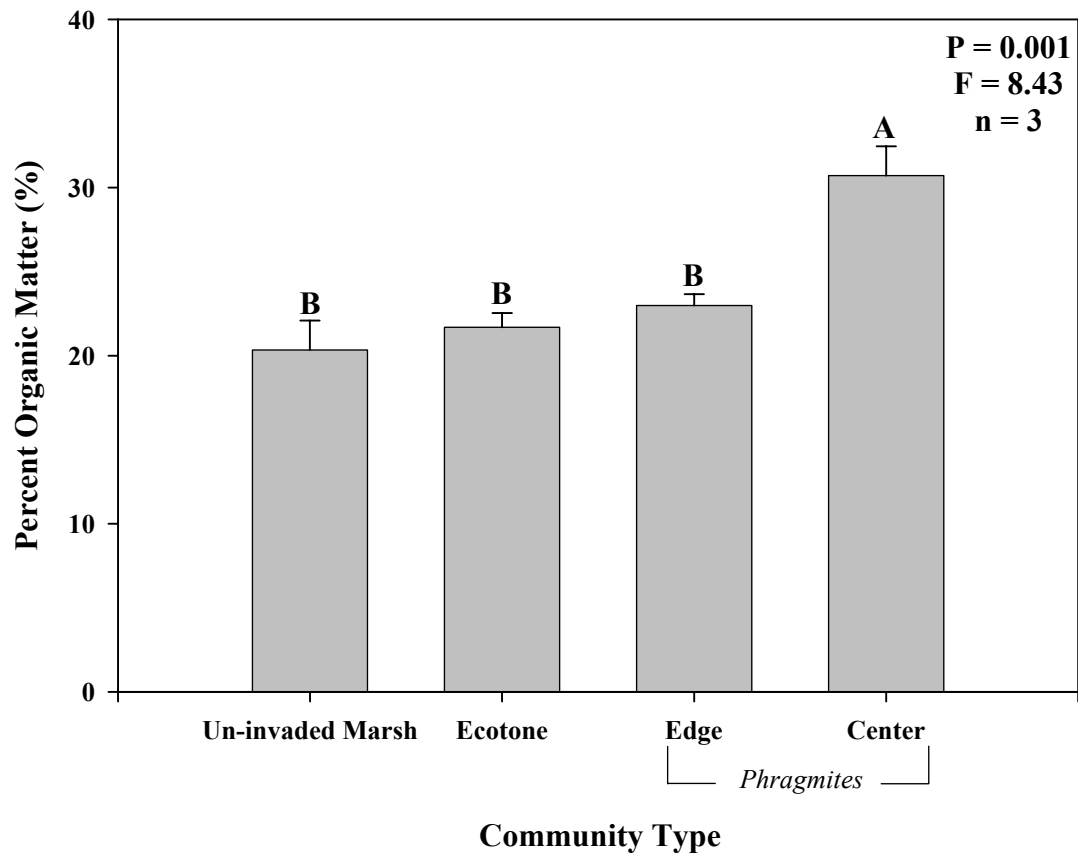


Figure 4-7. Percent organic component of bulk density cores by community type. Error bars reflect SE and bars that share letters are not significantly different.

Table 4-3. ANOVA table of cellulose decomposition analyzed using PROC MIXED and with time as a repeated measure. Bold indicates statistical significance at 0.05 level of significance.

Cellulose Decomposition			
Source of variation	df	<i>F</i>	<i>P</i>
Time (T)	3	16.29	0.0027
Community (C)	3	22.93	<.0001
T x C	9	3.97	<.0001
Depth (D)	8	9.94	<.0001
T x D	24	3.01	<.0001
C x D	24	1.13	0.3019
T x C x D	72	0.6	0.9966

Note: Block was tested as a random effect.

dependent on sample date. In addition, change in decomposition rates over depth was also dependent on sample date (Table 4-3, Figure 4-8(a)). Cellulose decomposition was lowest in the edge of the mono-specific *Phragmites* when compared to other communities (Figure 4-8(b)). Overall, decomposition was significantly higher in August 2001 than in December 2002 (Figure 4-8). On two occasions, decomposition was the same between community types (December 2001 and 2002). However, decomposition was significantly greater in un-invaded marsh than in the ecotone or the edge of mono-specific *Phragmites* in August 2001. Decomposition at the edge of the mono-specific *Phragmites* was significantly lower than in un-invaded marsh, the ecotone or in the center of the mono-specific *Phragmites* during the March 2002 sample period (Figure 4-8).

The significant time x depth interaction occurred due to an unexpected increase in decomposition rates as depth increased in March 2002 (Figure 4-9). In both August and December 2001, decomposition rates were negatively correlated with depth. In December 2002,

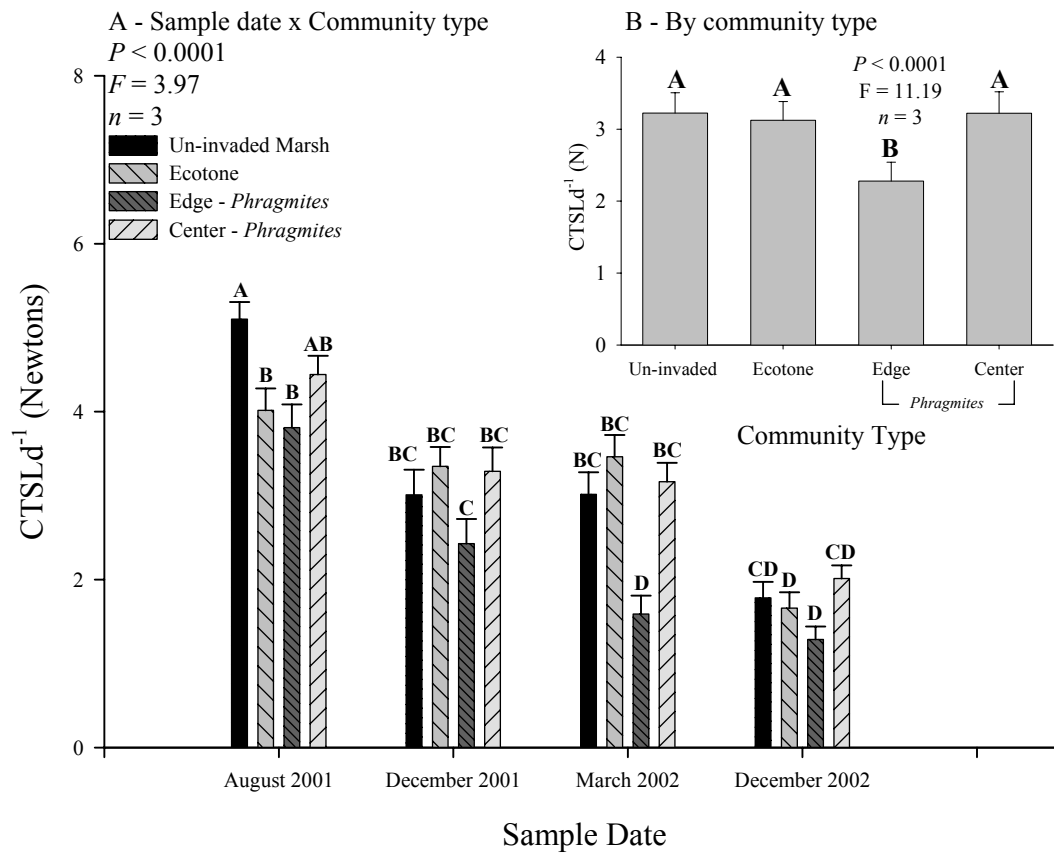


Figure 4-8. Daily cellulose decomposition (CTSLd⁻¹) by (A) community type and sample date, and by (B) community type. Error bars reflect SE.

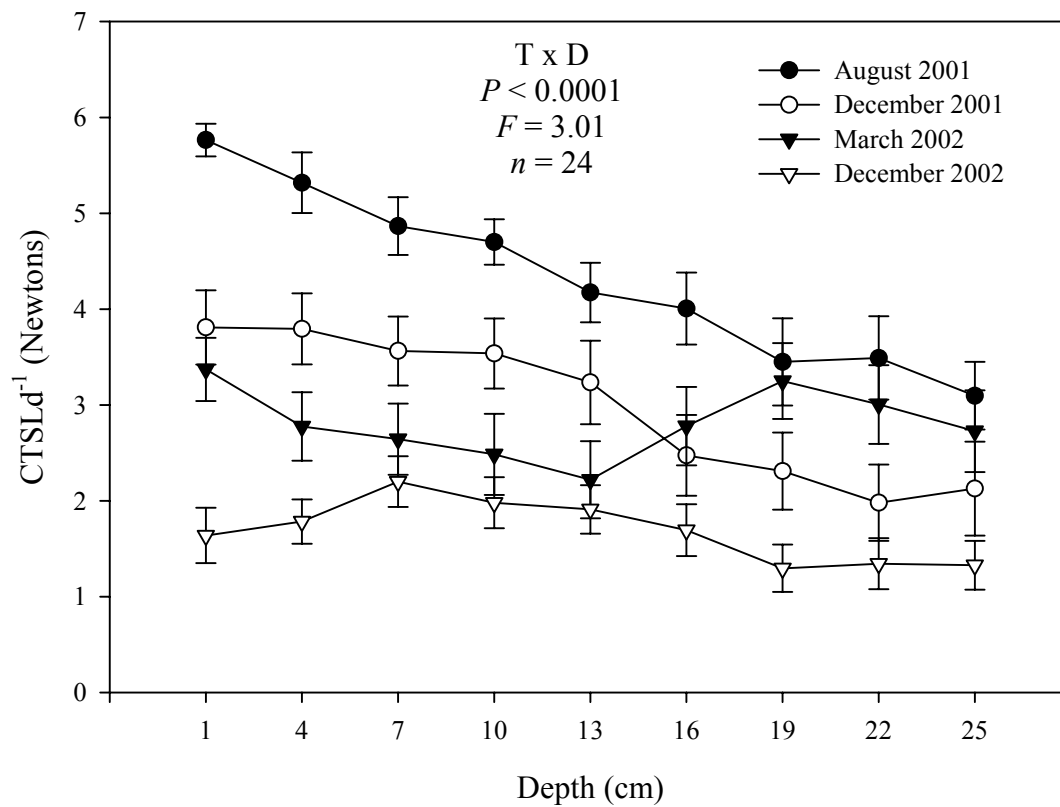


Figure 4-9. Daily cellulose decomposition (CTSLd⁻¹) by sample date and depth. Error bars reflect SE.

decomposition rates remained constant with increasing depth, with a slight increase in decomposition at 7 cm and decreased from that point as depth increased. The decomposition rates in March 2002 initially appeared to follow the same pattern, decreasing with depth; however, at 13-cm depth, decomposition rates abruptly increased at 16 and 19-cm depth, and then diminished from that point downward (Figure 4-9).

Temperature was the most important variable in predicting cellulose decomposition and explained 55% of the variation in the stepwise multiple regression model (Table 4-4). In addition, pH and water levels also were significant variables and contributed an additional 10 and 5%, respectively, to the model. No other environmental variables significantly affected decomposition rates at the $\alpha = 0.05\%$ level of significance.

Table 4-4. Variables selected in the stepwise multiple regression on the relationship between CTSLd^{-1} and sediment temperature, marsh elevation, porewater pH, water levels, depth Eh, porewater ammonium concentrations and salinity. Error terms of the final model had 31 degrees of freedom. For decomposition the model was: $\text{CTSLd}^{-1} = -9.64 + 0.18$ (sediment temperature) $+ 1.50$ (pH) $+ 0.06$ (water level). Only sediment temperature, porewater pH and water levels affected decomposition at $\alpha = 0.05$ level of significance.

Summary of Stepwise Selection				
Step	Variable Entered	Cumulative r^2	F	P
1	Sediment temperature	0.553	37.11	<0.0001
2	pH	0.6554	8.62	0.0064
3	Water level	0.7098	5.25	0.0297

Vegetative Measurements

For each species in this study, there was a significant vegetative community effect for biomass, stem density, stem height and *Phragmites* basal diameter (Table 4-5). Cumulative

biomass was significantly greater in the ecotone and in the edge of the mono-specific *Phragmites* than in un-invaded marsh (Figure 4-10). Biomass in the center of the *Phragmites* colony was not significantly different than that in any other community type. Species composition also changed significantly across community types (Figure 4-10). Un-invaded marsh was comprised of *Spartina*, *Distichlis* and *Schoenoplectus* whose combined weight was approximately 1600 g dwt m⁻² (Figure 4-10). The ecotone, comprised of both short graminoid species and *Phragmites*, weighed ~2200 g dwt m⁻². Biomass from the edge of mono-specific *Phragmites* weighed 2400 g dwt m⁻². Biomass in the center of the *Phragmites* colony was 2000 g dwt m⁻², and not different than un-invaded marsh.

When each species was analyzed separately, *Spartina*, *Distichlis* and *Schoenoplectus* biomass decreased from un-invaded marsh to the ecotone, and no plants were present within the mono-specific *Phragmites* stand (Table 4-5; Figures 4-11(a-c)). Both *Spartina* and *Distichlis* biomass decreased by more than half when growing with *Phragmites*, while *Schoenoplectus* decreased by a third. Likewise, *Phragmites* biomass was a third less in the ecotone when compared to biomass from the edge of the mono-specific *Phragmites* (Table 4-5; Figure 4-11(d)). *Phragmites* biomass in the center was not different than that in the ecotone or the mono-specific edge.

Stem densities also significantly decreased for both *Spartina* and *Distichlis* between un-invaded marsh and the ecotone (Table 4-5; Figures 4-12(a) and (b)). *Spartina* stem densities decreased by half in the ecotone, and were not present in *Phragmites*. Likewise, *Distichlis* densities decreased by two thirds from un-invaded marsh to the ecotone, and also were not present in *Phragmites*. In contrast, there was no difference between *Schoenoplectus* densities in either un-invaded marsh or in the ecotone, but also was not found in *Phragmites* (Table 4-5;

Table 4-5. ANOVA table of biomass, stem density, stem height and *Phragmites* basal diameter as analyzed using PROC MIXED by community type. Bold indicates statistical significance at $\alpha = 0.05$.

Vegetation		Biomass		Density		Height		Basal Diameter	
Source	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Cumulative	3	3.17	0.0384	-	-	-	-	-	-
<i>Spartina</i>	3	16.51	< 0.0001	29.23	< 0.0001	43.05	< 0.0001	-	-
<i>Distichlis</i>	3	38.74	< 0.0001	49.61	< 0.0001	322.14	< 0.0001	-	-
<i>Schoenoplectus</i>	3	12.78	< 0.0001	10.58	< 0.0001	177.23	< 0.0001	-	-
<i>Phragmites</i>	3	24.64	< 0.0001	110.35	< 0.0001	12.18	< 0.0001	36.84	< 0.0001

Note: Block was tested as a random effect.

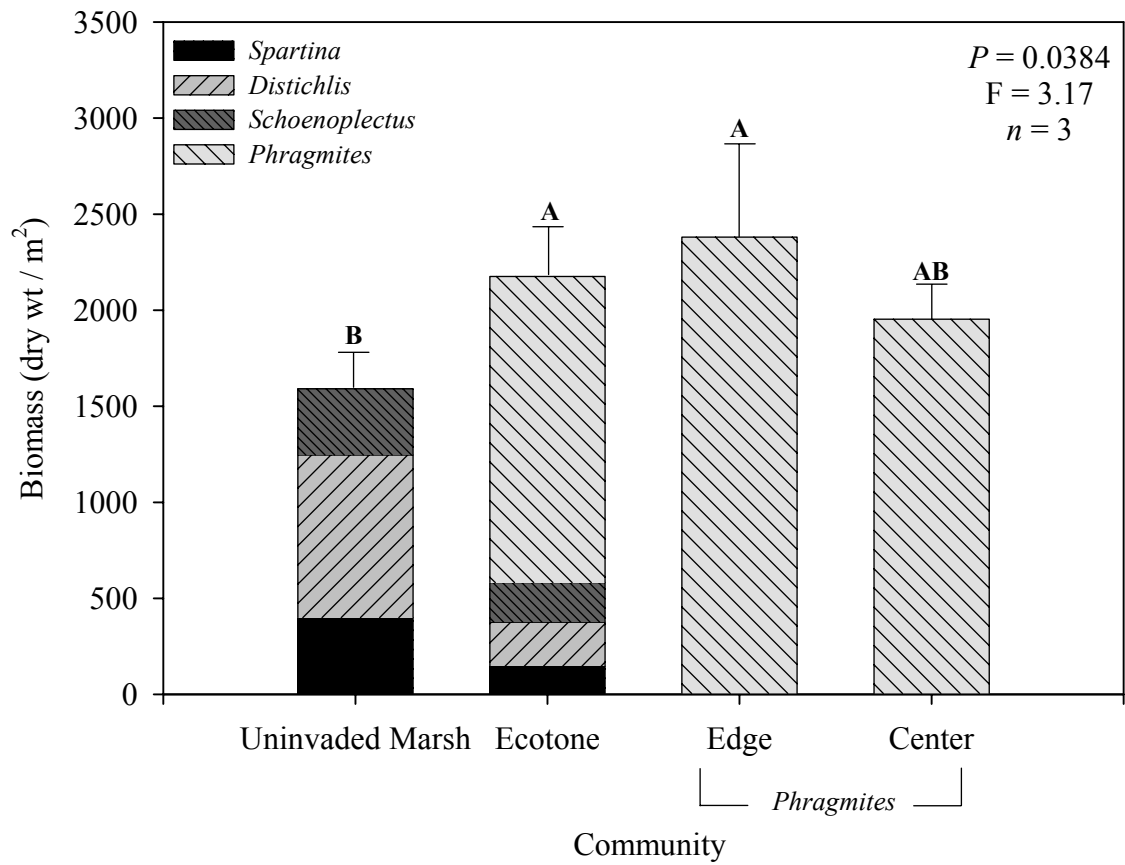


Figure 4-10. Total cumulative biomass by community type. Bars demonstrate the cumulative contribution of each type of vegetation to total biomass (dry weight / m²) and error bars reflect SE. Bars sharing letters are not significantly different.

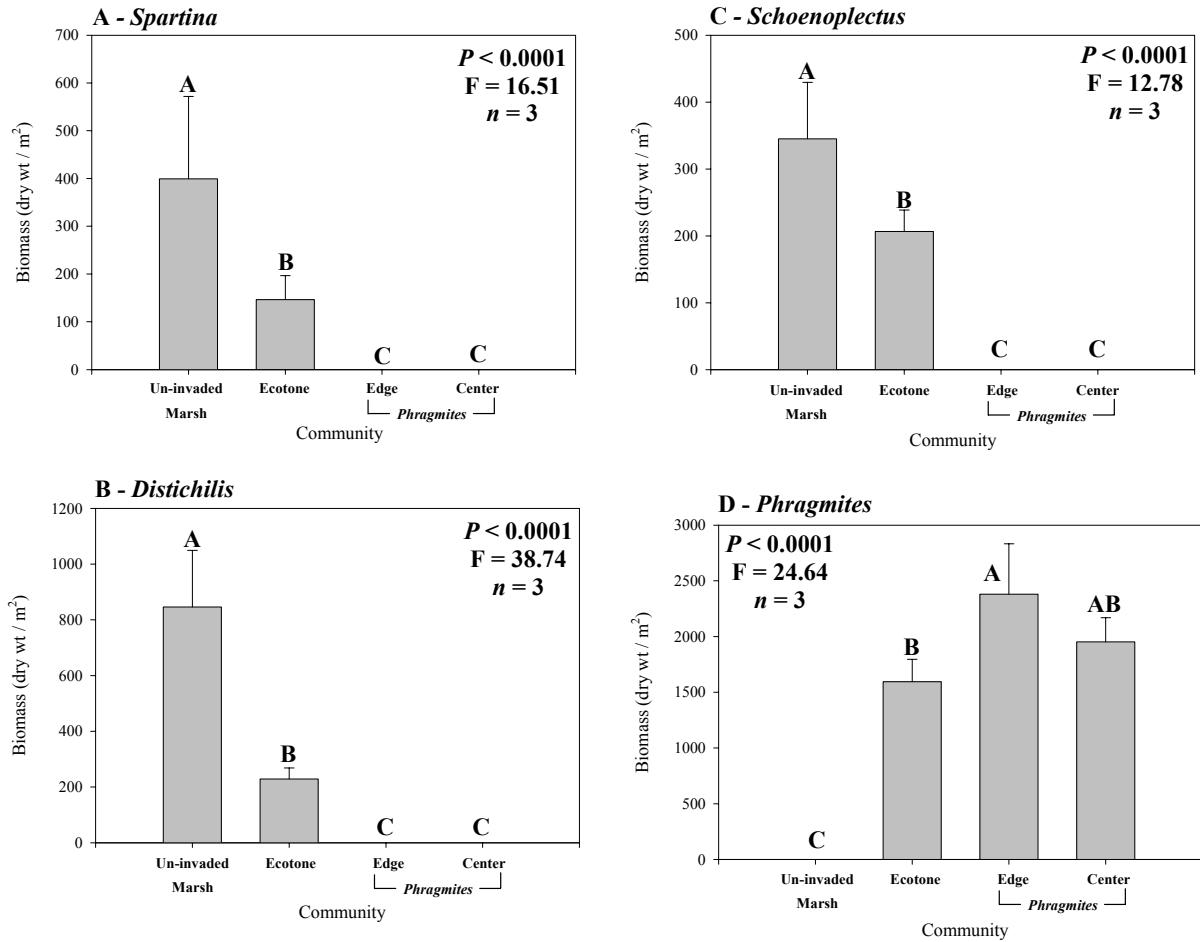


Figure 4-11(a-d). Total individual biomass of *Phragmites*, *Spartina*, *Distichlis* and *Schoenoplectus* by community type. Error bars reflect SE and bars that share letters are not significantly different.

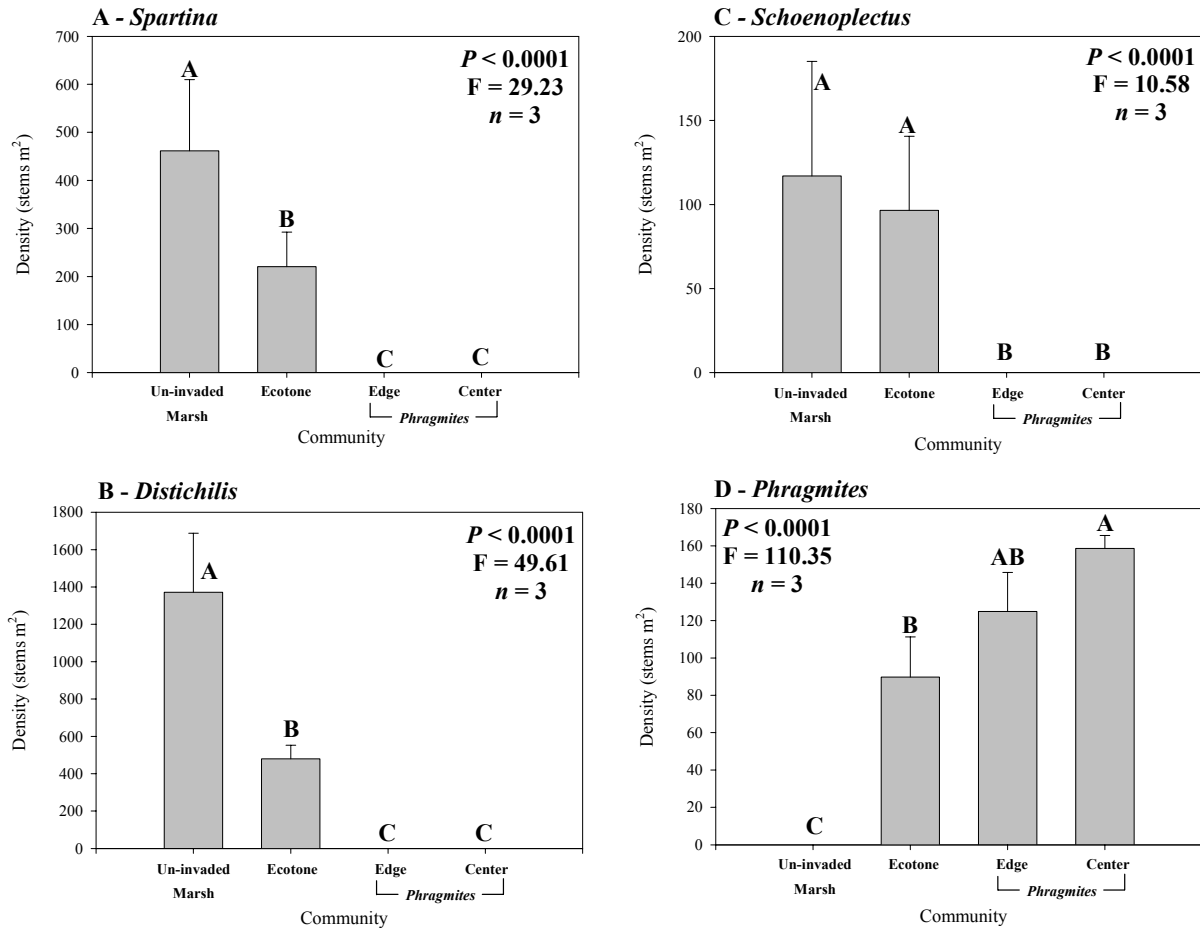


Figure 4-12(a-d). Total individual density (m⁻²) of *Phragmites*, *Spartina*, *Distichlis* and *Schoenoplectus* by community type. Error bars reflect SE and bars that share letters are not significantly different.

Figure 4-12(c)). *Phragmites* stem densities steadily increased from 0 in un-invaded marsh to approximately 80 stems m⁻² in the ecotone (Table 4-5; Figure 4-12(d)). Although *Phragmites* stem density in the edge of the mono-specific stand was not significantly different than in the ecotone or the center, densities in the center of the colony were twice that in the ecotone.

Stem height was greater in the ecotone for each short graminoid species than in un-invaded marsh (Table 4-5; Figures 4-13(a-c)). No stems of any short graminoid species were present in the mono-specific *Phragmites* stand. Surprisingly, *Phragmites* stem height was not different between the ecotone and the edge of the mono-specific *Phragmites* (Table 4-5; Figure 4-13(d)). However, *Phragmites* height was lower in the center, or oldest part of the colony. The same trend appeared in *Phragmites* basal diameter, and also yielded lower diameters in the oldest section of the colony (Table 4-5; Figure 4-14).

Interstitial Measurements

Ammonium Concentrations and Nitrogen Mineralization Rates

Ammonium concentrations were lowest in March 2002 when compared to concentrations measured in August 2001, December 2001 and December 2002 (Table 4-6). The concentrations measured on those dates were not different from each other (Table 4-6). Nitrogen mineralization rates, however, were greater in March 2002 when compared to other sample dates (Tables 4-6, 4-7 and 4-8). Mineralization rates were lower in December 2001 than in both August 2001 and March 2002, while rates measured in December 2002 were only lower than March 2002 (Table 4-8).

Sulfide, Salinity and pH

Both porewater sulfide and salinity demonstrated significant time effects over the course of the study, while the change in pH over time was dependent on the community (Table 4-6).

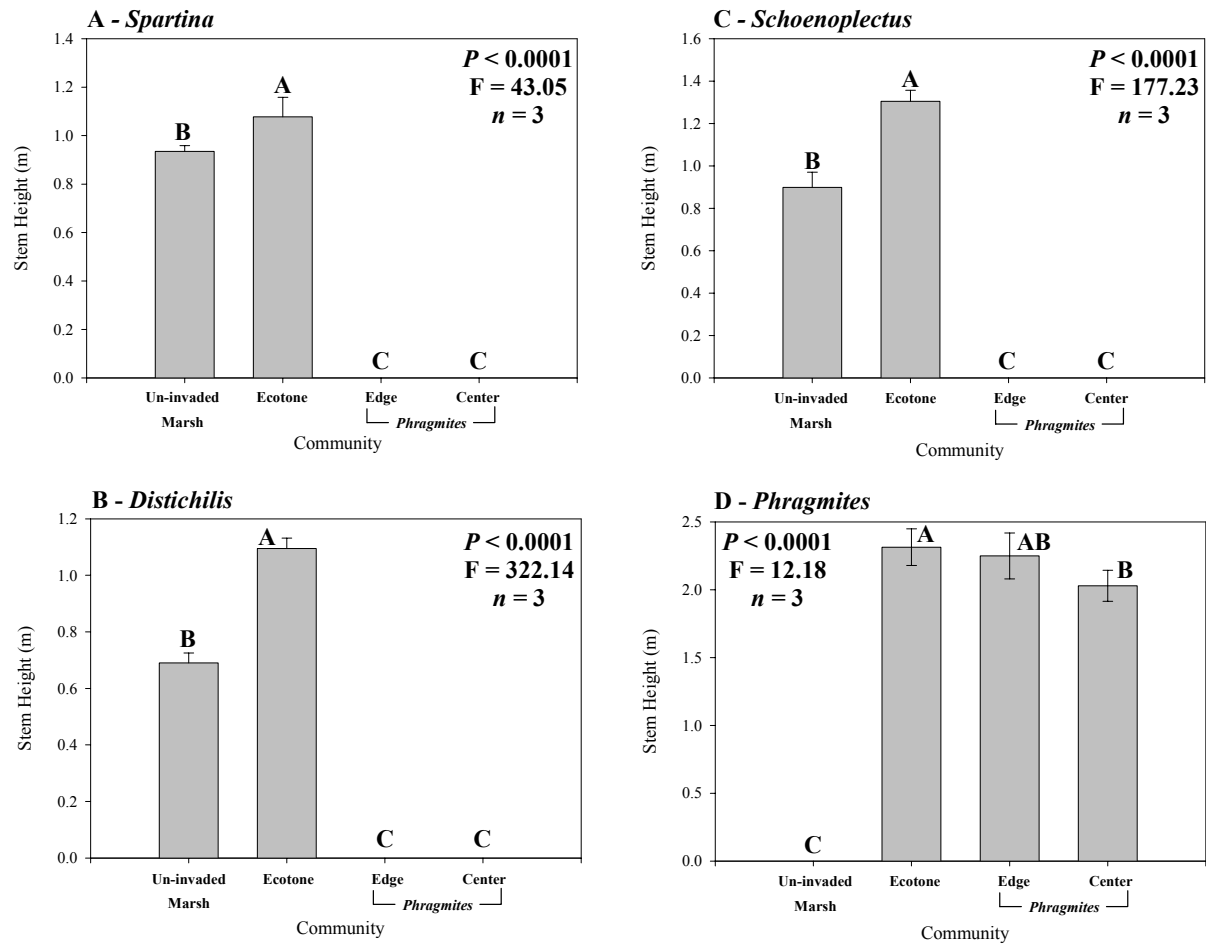


Figure 4-13(a-d). Average stem height (m) of *Phragmites*, *Spartina*, *Distichlis* and *Schoenoplectus* by community type. Error bars reflect SE and bars that share letters are not significantly different.

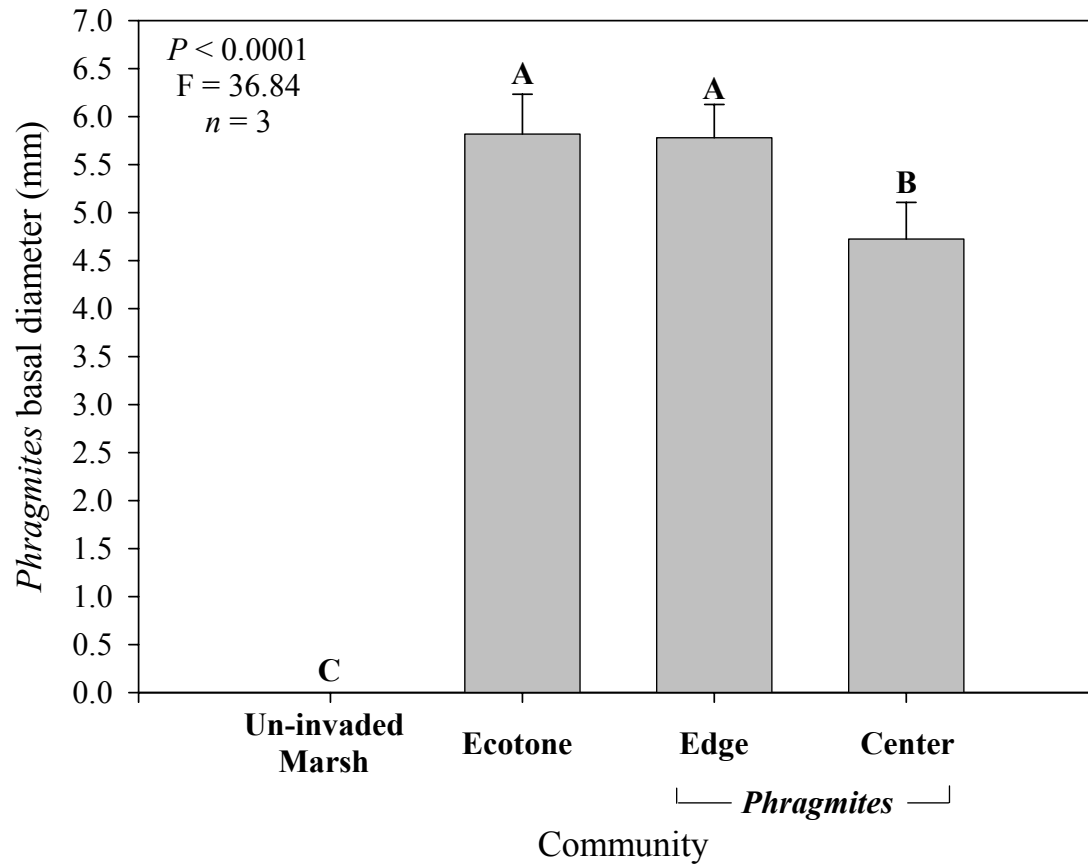


Figure 4-14. Basal diameter (mm) of *Phragmites* stems by community type. Error bars reflect SE and bars that share letters are not significantly different.

Table 4-6. ANOVA table of ammonium concentrations, daily nitrogen mineralization rates, sulfide concentrations, porewater salinity and pH analyzed using PROC MIXED with time as a repeated measure. Bold indicates statistical significance at $\alpha = 0.05$.

Environmental Variables		Ammonium (μM)		Nitrogen mineralization ($\mu\text{M day}^{-1}$)		Sulfide (μM)		Salinity (ppt)		pH	
Source	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Community (C)	3	1.02	0.4462	0.51	0.6863	0.88	0.4518	0.82	0.5283	4.91	0.047
Time (T)	3	15.1	<0.0001	19.36	<0.0001	2.77	0.0445	42.15	<0.0001	27.66	<0.0001
C x T	9	1.83	0.077	1.47	0.1745	0.86	0.5616	1.75	0.0848	4.01	0.0002

Note: Community refers to un-invaded marsh, ecotone, edge of mono-specific *Phragmites* and center of mono-specific *Phragmites* colony. Block was tested as a random effect.

Table 4-7. ANOVA table of surface and depth Eh measurements, water levels and sediment temperature analyzed using PROC MIXED with time as a repeated measure. Block was tested as a random effect for this analysis. Bold indicates statistical significance at $\alpha = 0.05$.

Environmental Variables		Eh (mV-Surface)		Eh (mV-Depth)		Water Levels (cm)		Sediment Temperature ($^{\circ}\text{C}$)	
Source	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Community (C)	3	0.6	0.6394	0.42	0.7448	0.15	0.9246	0.57	0.6540
Time (T)	3	5.25	0.0066	0.98	0.4173	148.53	<0.0001	284.89	<0.0001
C x T	9	0.65	0.7461	0.35	0.9474	1.48	0.1735	0.75	0.6645

Note: Community refers to un-invaded marsh, ecotone, edge of mono-specific *Phragmites* and center of mono-specific *Phragmites* colony. Block was tested as a random effect.

Table 4-8. Means of environmental measurements on each sample date. Means are \pm standard error and measurements that share letters are not significantly different.

Variables	n	August 2001	December 2001	March 2002	December 2002	<i>P</i>
Ammonium (μM)	24	8.0833 ± 0.8100 (a)	8.3433 ± 0.4131 (a)	4.1633 ± 0.5779 (b)	9.5225 ± 2.5956 (a)	< 0.0001
N-mineralization ($\mu\text{M d}^{-1}$)	24	1.8125 ± 0.2185 (b)	0.7745 ± 0.1445 (c)	2.7474 ± 0.2793 (a)	1.2180 ± 0.1698 (bc)	< 0.0001
Sulfide (μM)	36	$2.489\text{e-}5 \pm 1.379\text{e-}5$ (ab)	$2.253\text{e-}5 \pm 3.970\text{e-}6$ (a)	$3.610\text{e-}7 \pm 1.650\text{e-}7$ (c)	$7.810\text{e-}6 \pm 1.050\text{e-}6$ (b)	0.0445
Salinity (ppt)	36	15.3889 ± 0.7141 (a)	11.6389 ± 0.5243 (c)	9.5556 ± 0.6600 (d)	13.9722 ± 0.2745 (b)	< 0.0001
pH	36	5.70 ± 0.093 (d)	6.33 ± 0.038 (a)	6.21 ± 0.062 (ab)	5.96 ± 0.049 (c)	< 0.0001
Surface Eh (mV)	108	234.35 ± 34.39 (a)	-38.62 ± 9.83 (b)	149.91 ± 20.58 (a)	19.86 ± 12.75 (b)	0.0066
Water levels (cm)	24	8.1708 ± 0.8646 (a)	7.0792 ± 0.9590 (a)	-2.7292 ± 0.7691 (b)	7.6522 ± 0.8029 (a)	< 0.0001
Sediment Temp ($^{\circ}\text{C}$)	24	26.21 ± 0.1201 (a)	16.75 ± 0.0796 (b)	17.08 ± 0.4812 (b)	11.917 ± 0.3803 (c)	< 0.0001

Sulfide concentrations in December 2001 were significantly higher than those in both March and December 2002 (Table 4-8). Concentrations measured in August 2001 were only significantly greater than those in March 2002, and not statistically different from concentrations in December 2001 or 2002.

Porewater salinities were highest in August 2001 and different between each sample date (Table 4-8). Salinity in December 2002 was lower than in July 2001 and higher than in December 2001. Salinities were lowest in March 2002.

Although pH only fluctuated between 6.48 and 7.34 throughout the study, there was a significant time x community interaction (Table 4-6). Mono-specific *Phragmites* at the edge and in the center of each colony had lower porewater pH than un-invaded marsh and the ecotone in March 2002 (Figure 4-15; Table 4-6). In contrast, only mono-specific *Phragmites* at the edge demonstrated a lower pH when compared to un-invaded marsh, the ecotone and the mono-specific *Phragmites* in the center in August 2001. There were no differences in porewater pH between community type in either December 2001 or December 2002. Although sulfide levels were different between sample periods, concentrations failed to reach a biologically significant level (i.e., growth limiting) at any time during the study (Table 4-6).

Sediment Eh, Water Levels and Temperature

Although surface Eh did significantly vary during the study, Eh did not differ with community types (Table 4-7 and 4-8). Surface Eh in both December 2001 and 2002 was significantly lower than in July 2001 and March 2002 (Table 4-8). There was no effect of either time or community type on redox at 15-cm depth (Table 4-7). When compared between surface and depth across all community types and sample dates, surface Eh ($88 \text{ mV} \pm 11$) was higher than at 15-cm depth ($61 \text{ mV} \pm 6$; $p = 0.0384$; $F = 4.30$; $n = 432$). Hence, soils within the un-invaded marsh, ecotone and

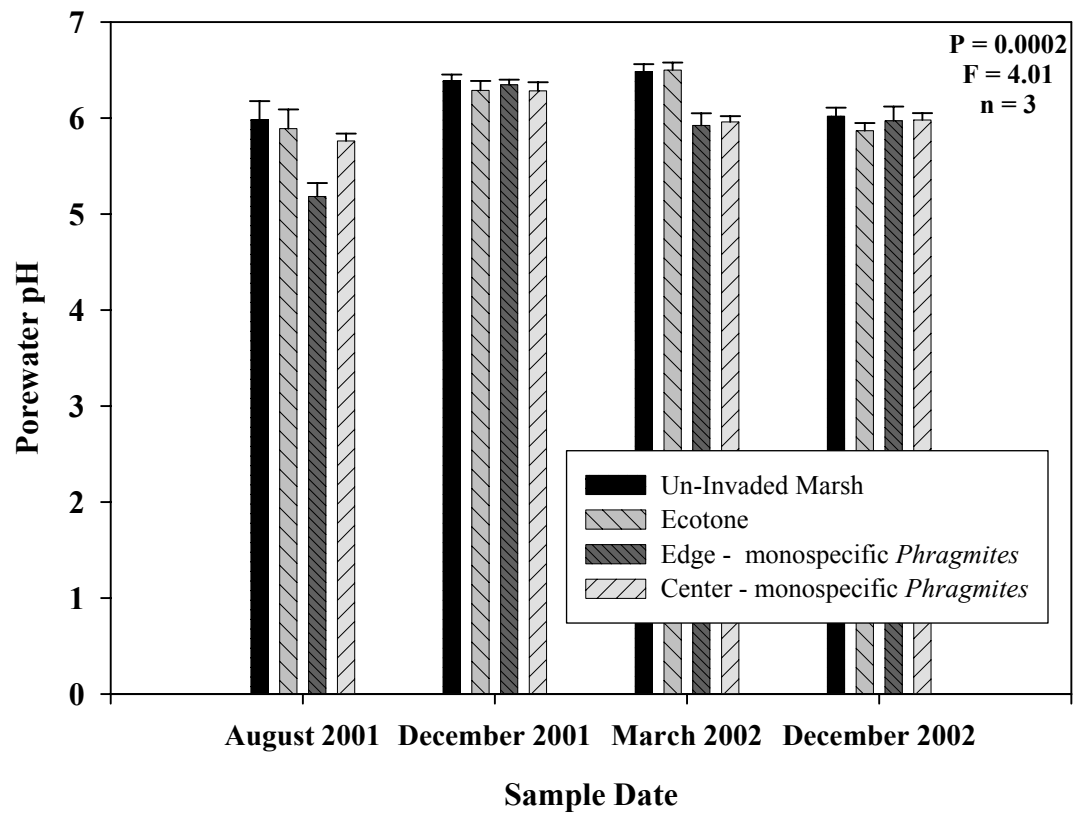


Figure 4-15. Porewater pH interaction between sample date and community type. Error bars reflect SE.

in the edge and center of *Phragmites* colonies were moderately reduced to reduced (Patrick 1972).

Water level was lowest only in March of 2003 (Tables 4-7 and 4-8). In July and December 2001 and December 2002 however, water levels remained between 6 and 8 cm above the marsh. Water levels did not differ between vegetative communities.

Likewise, sediment temperature did not differ between community types, but did change over time (Table 4-7). Sediment temperature was highest in July 2001 when compared to other sample dates while December 2002 was lowest (Table 4-8). Sediment temperatures in December 2001 and March 2002 were not different from each other although they were lower than July 2001 and higher than December 2002.

Discussion

Phragmites clearly demonstrated its role as an ecosystem engineer by increasing true elevation, peat accumulation and organic matter concentration of the marsh sediment when compared to un-invaded brackish marsh in Southwestern Louisiana. As a result of increased organic accumulation, soil bulk density within *Phragmites* stands was lower relative to un-invaded marsh as was soil decomposition rates. *Phragmites* productivity in the edge of the mono-specific *Phragmites* also exceeded that in the un-invaded marsh, and is likely responsible for the greater accumulation of organic material and positive elevation gain. Yet *Phragmites* invasion had little effect on interstitial variables when compared to un-invaded natural marsh. Although interstitial variables were within the range reported in other studies, it is likely that marsh management practices in the study area muted potential differences that might have existed otherwise between vegetative communities.

Phragmites as an Ecosystem Engineer

The ecological distinctiveness of an invading species, relative to the species that exist in a community, is an important factor determining the nature and the degree of the ecological impact (Cox 1999, Ehrenfeld 2001). *Phragmites* often grows to heights in excess of 3 m while the native short graminoid species in brackish marshes seldom exceed 1 m, and therefore invasions are readily apparent. Unlike short graminoid species, *Phragmites* stems can remain standing for up to 4 years after senescence (Haslam 1972). Once they fall, stems decompose slowly and accumulate as organic matter (Windham 2001). Belowground, *Phragmites* rhizomes grow to depths of 1 m and can be twice as productive as short graminoid species, which exhibit an effective rooting zone of only 30 cm (Mitsch and Gosselink 1993, Burdick et al. 2001, Windham 2001). *Phragmites* roots adventitiously from nodes along the stem when subjected to high water levels, further contributing to organic matter accumulation at the sediment surface. With such obvious differences between the growth morphology of *Phragmites* and short graminoid species in un-invaded marshes, it is no surprise that ecosystem processes change as a result of *Phragmites* invasion.

Soil Development and Elevation

One primary ecosystem process affected by *Phragmites* invasion was soil development and elevation change. The increased productivity of *Phragmites* relative to un-invaded marsh had profound effects on litter and organic matter accumulation (Figure 4-4). Marsh sediments beneath *Phragmites* had greater organic matter concentration, lower bulk density and much thicker peat than in un-invaded marsh (Figures 4-4(a), 4-6 and 4-7). Other studies have shown both increased litter accumulation rates and positive correlations between sedimentation rates and *Phragmites* dominated communities (Windham 2001, Leonard et al. 2002, Rooth et al.

2003). In the present study, the low bulk densities and high percentage of organic matter in the center of the mono-specific *Phragmites* community (~40 yr), combined with the thickest peat layer, demonstrates that *Phragmites* accumulates more organic matter than short graminoid species in un-invaded marshes. Peat thickness was also based on the size of the *Phragmites* colony. Colony 1, with a diameter of 145 m, had the thickest peat compared to colonies 2 and 3, with 100 and 90 m diameters, respectively (Figure 4-4(b)). Peat thickness in the larger colony was 5-cm thicker than that in the smaller colonies. Therefore it seems apparent that a larger stand of *Phragmites* will have better developed and greater depth of peat than smaller stands.

The most striking evidence for *Phragmites* role as an ecosystem engineer was its effect on marsh elevation (Figure 4-3(a)). Marsh surface elevation in *Phragmites* was nearly 10 cm higher than that in un-invaded marsh, 6 cm higher than the ecotone and nearly 3 cm greater than at the edge of mono-specific *Phragmites*. In addition, the elevation in the ecotone, which was comprised of 50% *Phragmites*, was 4 cm greater than un-invaded marsh. Based on the estimated ages for the three colonies (Chapter 2), I calculated the annual increase in elevation relative to the un-invaded marsh. When calculated as a per year rate, the elevation increases in the center mono-specific *Phragmites* (~40 yrs old) is approximately 0.28 cm yr^{-1} , the edge of the mono-specific *Phragmites* (~7 yrs old) was 1.02 cm yr^{-1} and 1.31 cm yr^{-1} in the ecotone (~3 yrs old). The average elevation increase in the un-invaded marshes in RWR are 0.23 cm yr^{-1} (Phillips 2002). These rates indicate that initial increases in elevation occur rapidly once *Phragmites* invades and slows as *Phragmites* matures.

In addition to colony age, inorganic sediment input can also affect marsh elevation. The brackish marsh in Price Lake Unit is hydrologically restricted from coastal waters by low hurricane levees and fixed-crest weirs (Wicker 1983). As a result, managed marshes do not

typically receive inorganic sediment input (Cahoon 1994, Bryant and Chabreck 1998, Perez and Cahoon 2004). Nutrient supply has been positively correlated with sediment supply (DeLaune 1979, Miller 1983). Therefore, a reduction in inorganic sediment supply could result in lower plant productivity and slow organic matter formation, ultimately decreasing organic matter accretion rates and marsh elevation (DeLaune and Patrick 1979, Nyman et al. 1993). However, *Phragmites* is likely to remain highly productive and continue contributing to marsh surface elevation even in the absence of nutrients supplied with inorganic sediment. *Phragmites* active root zone extends at least 70 cm deeper into marsh sediments than that of short graminoid species (~30 cm, Mitsch and Gosselink 1993), and can likely acquire nutrients that are unavailable to short graminoid species. Thus, it seems unlikely that low nutrient levels as a result of decreased inorganic sediment supply will affect *Phragmites* productivity or reduce organic matter accumulation in *Phragmites*-dominated marshes.

In the absence of inorganic sediment supply, the surface elevation of managed marshes is generally built up by the deposition of peat and maintained by shallow permanent flooding (Hatton 1983, Wicker et al. 1983, Flynn et al. 1995). Therefore, the biomass production of the plant communities will affect the rate of elevation gain and water level will limit maximum elevation. Within the center mono-specific *Phragmites* community, peat thickness was 11 cm greater than in un-invaded marsh (Figure 4-4), and resulted in an elevation gain of almost 10 cm over un-invaded marsh (Figure 4-3). Although elevation gain occurred in the center mono-specific *Phragmites* at a rate of approximately 0.28 cm yr^{-1} , the approximate rate of elevation increase in edge of the mono-specific *Phragmites* (~7 yrs old) was 1.02 cm yr^{-1} . In an un-invaded managed marsh at RWR, Phillips (2002) reported average elevation increases of 0.17 cm yr^{-1} , while other studies in un-invaded managed marshes have recorded similar elevation

increases of 0.34 cm yr^{-1} (Perez and Cahoon 2004). It is apparent that *Phragmites* invasion accumulates more peat than un-invaded marsh and results in more rapid elevation gain than the un-invaded marsh. In addition, permanent flooding of the marsh surface will likely maintain elevation gain. The study area is passively managed to prevent excessive drainage of the marsh and marsh ponds during periods of sustained low tides (Wicker et al. 1983). As a result, permanent flooding prevents the collapse of organic soils by oxidation/decomposition and can prevent soil shrinkage, and thereby help maintain marsh surface elevation (Nyman and DeLaune 1991, Perez and Cahoon 2004).

MARSH PLANT BIOMASS

Of all the species in this study, *Phragmites* produced the most biomass. Even in the ecotone, *Phragmites* biomass was 25-30 % greater than in the un-invaded marsh (Figures 4-11(a-d)). Cumulative biomass in the ecotone was approximately $2200 \text{ g dry wt m}^{-2}$, almost 600 g more than the un-invaded marsh (Figure 4-10). When considered separately from the other species, *Phragmites* biomass in the ecotone was equivalent to the combined biomass of short graminoid species in the un-invaded marsh, and reached the greatest biomass in the mono-specific edge ($\sim 800 \text{ g m}^{-2}$ more than in un-invaded marsh). Surprisingly, *Phragmites* biomass in the center of the colony (~ 40 yrs old) was not greater than biomass in the un-invaded marsh. Although *Phragmites* biomass in the mono-specific center of the colonies was similar to that which Windham and Lathrop (1999) found in mature *Phragmites* stands in Southern New Jersey ($\sim 2000 \text{ g m}^{-2}$), biomass from their adjacent un-invaded marsh was much less than in the un-invaded marsh in this study ($\sim 200 \text{ g m}^{-2}$ compared to $\sim 1600 \text{ g m}^{-2}$). There was a corresponding increase in stem density with increasing age of the *Phragmites* (Figure 4-12(d)), yet both stem height and basal diameter decreased with age (Figure 4-13(d) and 4-14). *Phragmites* dry weight

was positively correlated with basal diameter and height (Stanton, unpublished data). Therefore, lower aboveground biomass in the center mono-specific *Phragmites* in conjunction with smaller basal diameter is not surprising when compared to mono-specific *Phragmites* at the edge of the colony.

Even though dead *Phragmites* leaves and stems were found incorporated into the peat in the mono-specific *Phragmites* community types, belowground productivity likely has a greater affect on organic matter accumulation and elevation gains than does litter-fall. For example, aboveground biomass in the oldest *Phragmites* stands was not statistically greater than aboveground biomass from the un-invaded marsh (Figure 4-10). Although *Phragmites* litter may decompose slower relative to the short graminoid species in the un-invaded marsh, no differences in decomposition rates were found between un-invaded marsh and the ecotone (Figure 4-8(b)). Furthermore, the significant increase in elevation observed in the ecotone relative to the un-invaded marsh would suggest a mechanism other than aboveground litter accumulation since *Phragmites* has only been present in portion of the marsh for approximately 3 years (Figure 4-3(a), Chapter 2). Although not measured in this study, Windham (2001) reported that *Phragmites* belowground biomass was nearly twice as much as *Spartina patens* (1368 g m^{-2} vs. 757.37 g m^{-2}). Furthermore, the distribution of *Phragmites* belowground tissue extended at least 40 cm below that of *S. patens* and produced 200 g m^{-2} at the 40-50 cm depth interval (Windham 2001). This suggests that belowground productivity may have a greater impact on net marsh surface elevation than the deposition of organic material from aboveground production (Paille 1991), which is true for other high organic wetlands (Turner et al. 2001, McKee 2004).

There were strongly significant community effects on cotton decomposition rates in this study. Soil decomposition rates can affect peat accumulation and organic matter concentrations. Therefore, decomposition rates can affect marsh communities dependent on peat accumulation for positive elevation gain. Decomposition rates were measured using the cotton strip technique, (Maltby 1988). Although plant litter is composed of a complex mixture of different carbohydrates, including cellulose, lignin, and tannins, cotton strips are comprised primarily cellulose. The simplified structure of cotton strip is useful in measuring general cellulolytic microbial activity, making comparisons between experimental treatments more uniform and repeatable (Mendelssohn et al. 1999, Larson 2004). The mono-specific *Phragmites* community at the edge of the colony had a strong impact on decomposition rates (Table 4-3; Figures 4-8 and 4-9) and clearly demonstrated the lowest cellulose decomposition rates when compared to other community types (Figure 4-8(b)). However, the effect of community type on cellulose decomposition was dependent on sample time. This response, however, was affected by sediment temperatures as a result of changing seasons (Table 4-4). Although pH and water levels were also correlated with decomposition, each contributed 10 and 5% to the model while temperature accounted for 55%. Because temperature increases metabolic activity, decomposition rates increase with increasing sediment temperatures (French 1988). The lowest decomposition rates correlated with the lowest sediment temperatures (December 2002) and vice versa (August 2001). In addition, plant litter quality can also influence decomposition rates (Windham 2001). When compared to *Spartina patens*, carbon to nitrogen ratios in *Phragmites* fresh litter is almost two times greater. Thus, poor quality litter produced by *Phragmites* relative to un-invaded marsh could result in slower decomposition rates (Windham 2001).

Decomposition rates also decreased as depth increased (Figure 4-9). Other studies have observed this trend, and suggest that increased decomposition rates at the surface indicate greater oxygen availability (Mendelssohn et al. 1999, Larson 2004, Mendelssohn and Slocum 2004), while decreases in decomposition at increasing depths have been attributed to more reducing conditions at depth (Maltby 1988) or lower soil fertility at increasing depths (Schipper and Reddy 1995). When decomposition rates were examined by sample date and depth, the decomposition profile in March actually increased at 16 and 19-cm depth. Since decomposition is a result of microbial activity, this increase in decomposition at that depth may have been stimulated by a combination of both increased oxidation of the rhizosphere, or exudates from increased root activity during spring growth stimulating microbial activity (Howarth and Hobbie 1982, Lawson 1988, Larson 2004). The low water levels during that time period may have accelerated decomposition. However, the drained portion of the soil profile did not correspond to the depth where increased decomposition was measured.

Interstitial Chemical Status

Porewater pH was the only interstitial variable affected by *Phragmites* invasion (Table 4-6). However, this response was also dependent on time (Table 4-6). Although pH was lower in the mono-specific *Phragmites* edge and center community in March 2002 relative to the uninvaded marsh and the ecotone, those differences were not biologically significant. Only in August 2001 was the difference in pH between the edge mono-specific *Phragmites* and the other community types biologically significant (Figure 4-15). *Phragmites* invasion had no effect on other interstitial variables relative to un-invaded natural marsh. Although other studies have shown *Phragmites* to have significant effects on sulfide and ammonium concentrations, nitrogen mineralization rates, porewater pH and salinities, sediment redox potential (Eh – both surface

and depth), water table level, and sediment temperatures (Chambers 1997, Windham and Lathrop 1999), these effects were not evident in this study (Tables 4-6, 4-7 and 4-8). The only differences found between interstitial measurements were between sample dates (Table 4-3) with the exception of pH, where an interaction between community type and sample date was present (Figure 4-3). Porewater ammonium concentrations were lowest in March 2001, and likely due to increased uptake resulting from the onset of spring growth. Ammonium concentrations measured in this study for *Phragmites* ranged from 4.16 to 9.52 μM and are nearly identical to those measured in a *Phragmites* community in a Connecticut salt marsh (Chambers 1997). Conversely, nitrogen mineralization rates were highest in March 2001, and were within the ranges reported in a *Phragmites* community in a Mid-Atlantic brackish marsh (Windham and Ehrenfeld 2003). Sulfide concentrations were different between sample dates, but did not reach a biologically significant level at any time. Likewise, porewater salinities differed among sample dates, but did not reach a biologically inhibiting level for either *Phragmites* or the other species in this study.

Although interstitial variables were within the range reported in other studies, it is likely that marsh management practices in the study area muted potential differences between vegetative communities. Marsh management stabilized water levels throughout the study area, and as a result, water levels were not different between sample periods except on one date (Table 4-8). Furthermore, low porewater salinities reflect decreased tidal exchange with saline coastal waters.

The Cascading Effects of *Phragmites* Invasion

The increased *Phragmites* biomass through taller culms and a deeper active rooting zone make *Phragmites* a dominant competitor when invading short graminoid marshes (Figures 4-11

and 4-13(a-d)). Its taller growth form increases light capture efficiency for photosynthesis, while a deeper and larger rhizome network captures belowground resources not available to shallow-rooted graminoid species. Short graminoid species exhaust belowground resources when competing with *Phragmites* by increasing stem height, resulting in lower stem densities and less biomass when compared to un-invaded marsh (Figures 4-11(a-c), 4-12(a-c) and 4-13(a-c)). Ultimately, short graminoid species exhaust belowground reserves and perish, giving way to a mono-culture of *Phragmites* (Figure 4-10).

The shift in community structure from un-invaded short graminoid marsh to mono-specific *Phragmites* has an obvious impact on marsh surface elevation. *Phragmites* biomass is among the highest recorded in coastal marshes, with aboveground biomass of 2000 g m^{-2} not uncommon in invaded marshes and with this study reporting nearly 2500 g m^{-2} . *Phragmites* belowground productivity is twice that reported for *Spartina patens* communities (Windham 2001, Windham and Ehrenfeld 2003). This is reflected in immediate elevation gains of nearly 4 cm over un-invaded marsh in less than 5 years, and elevation gains of 10 cm are evident after nearly 40 years (Figure 4-3). In addition to the belowground contribution to elevation gain, standing culms can increase inorganic sedimentation rates (Rooth and Stevenson 2000), further raising marsh surface elevation. Although the transition of un-invaded short graminoid marshes to *Phragmites* mono-cultures immediately affects the physical nature of brackish marshes, the vastly greater productivity is likely to have a greater affect on faunal abundance and utilization as well as energy flow through the ecosystem.

Since coastal marshes serve as important habitats for shorebirds and commercial species (Mitsch and Gosselink 1993), modification resulting from *Phragmites* invasions could change faunal use pattern and community structure. Several studies have found contrasting affects of

Phragmites invasion on larval and juvenile utilization relative to un-invaded marsh (Fell et al. 1998, Able and Hagan 2000, Angradi et al. 2001, Meyer et al. 2001, Jivoff and Able 2003, Raichel et al. 2003). *Phragmites*-dominated marshes were not favored by blue crabs and some species of larval fish (Able and Hagan 2000, Jivoff and Able 2003, Raichel et al. 2003). In contrast, both Meyer et. al (2001) and Fell et. al (1998) found nekton usage between *Spartina alterniflora* and *Phragmites*-dominated marsh was indistinguishable. Furthermore, studies examining shorebird success found that Virginia rail abundances declined with the invasion of *Phragmites* (Benoit and Askins 1999), while invasion has had no effect on nesting success (Parsons 2003). These contrasting results suggest that the effect of *Phragmites* invasion will not be consistent over all aspects of coastal marsh ecology and will require a case by case approach to be fully understood.

Although *Phragmites* often forms monocultures and reduces wildlife usage in some cases relative to un-invaded marsh, increasing marsh elevations will likely increase the longevity of deteriorating coastal marshes. This finding holds particular relevance for coastal Louisiana. Due to myriad of factors including sediment starvation, compaction and subsidence, salt water intrusion and sea-level rise, annual Louisiana wetlands losses are exceeding 65 km², the greatest wetland loss rates in North America (Pezeshki et al. 1987, Penland et al. 1989, Flynn et al. 1995, Grace and Ford 1996, Webb and Mendelssohn 1996). Thus, the increasing prevalence of *Phragmites* in coastal Louisiana may contribute to positive marsh elevation gain and potentially slow local rates of wetland loss due to sea-level rise.

Conclusion

Phragmites has clearly demonstrated its role as an ecosystem engineer while invading this Louisiana brackish marsh. Marsh surface elevation is increased immediately with

Phragmites invasion, and rates of elevation gain were at their peak within 7 years. Although the aboveground productivity shown in *Phragmites* communities is far above that produced by short graminoid species, it is likely that belowground production has a greater impact on net marsh surface elevation than the deposition of organic material from aboveground production. The contribution of *Phragmites* belowground production to marsh soil development and surface elevation has not been quantified. Additional studies examining these relationships would not only benefit marsh managers, but also further increase understanding of invading species and the ensuing impacts on ecosystem processes.

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VITA

Lee Ellis Stanton was born in Graceville, Florida, on November 8, 1970. He is the son of Rual Kenneth Stanton and Dee Ellis Stanton of Chipley, Florida, and graduated from Chipley High School in 1988. He attended the Livingston University (LU) where he received both a trustee's scholarship and photography scholarship. In 1993, Lee graduated with a Bachelor of Science in biology from LU and enrolled in the graduate program at The University of South Alabama (USA) where he pursued a master's degree in biology. Although enrolled in the Graduate School at USA in Mobile, Alabama, Lee resided at the Dauphin Island Sea Lab (Dauphin Island, Alabama), where he completed the majority of his coursework and conducted research examining the role of competition and facilitation in structuring salt marsh plant zonation. During his graduate program, he received a University of South Alabama Graduate Fellowship and was also awarded a Mississippi-Alabama Sea Grant in his second year to fund his master's research. Lee received his Master of Science Degree in biology in 1998. Three days after his thesis defense, he moved to Baton Rouge where he had been accepted into the doctoral program in the Department of Oceanography and Coastal Sciences at Louisiana State University (LSU). There he became very interested in invasive wetland plant species and their ecology and pursued research examining the establishment of invasive species, their rate of spread and subsequent impacts on native wetland environments. During his tenure at LSU, Lee was awarded the annual Rockefeller Wildlife Research Scholarship for two consecutive years, was inducted into Phi Kappa Phi Honor Society, and received the prestigious Joseph Lipsey, Sr., Memorial Scholarship Award for Excellence in Marine Science and Research.