12-19-2008

Responses of a Louisiana oligohaline marsh plant community to nutrient loading and disturbance

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Responses of a Louisiana oligohaline marsh plant community to nutrient loading and disturbance

A Thesis

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
requirements for the degree of

Master of Science
in
Biological Sciences

by

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B.A. St. Ambrose University, 1999

December 2008

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ACKNOWLEDGEMENTS

I would like to thank my committee, Mark Hester, John Utley, Mike Poirrier and Denise Reed for their guidance and patience during this project. Dr. Mark Hester is the reason I chose to pursue this degree at the University of New Orleans. His flexibility and patience was tested many times while I was a graduate student in his lab and I will forever be grateful to him. Also, from the Coastal Plant Science Lab at UNO I need to thank Jonathon Willis, Ellery Mayence, Theryn Henkle and Raven Brasseux. Jonathon reminded me that things could always be worse. Ellery was always available to lend everyone a hand or build something. Honorary-Aunt Theryn was the first person to meet Lily in the hospital the day she was born and entertained her in lab. Raven was always encouraging and told me to never quit. A special thank you to Michael Rowe for without him I never would have finished. I also want to thank my fellow graduate students in the Department of Biological Sciences especially Dawn Allenbach, Rachel Wallace, Heather Hurston and Marjorie Linares for their friendship. I also want to thank the LSU-DOCS for their generosity following Hurricane Katrina. In particular, thanks to Irv Mendelssohn for use of his lab and equipment and Sean Graham for opening his home and giving me a place to stay. Of course, support from my family and friends have given me confidence to attempt all the adventures in my life. Even though she did not exactly help me "write" any part of my thesis, I was inspired by my wonderful daughter Lilith Aelita.

The Lake Pontchartrain Basin Foundation provided funding for this project.

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ABSTRACT

Aboveground plant community dynamics in the oligohaline marsh at Big Branch Marsh National Wildlife Refuge, Louisiana, USA, were assessed in response to nutrient loading (3 N x 3 P treatments) and disturbance (both planned lethal disturbance and stochastic tropical storm/hurricane disturbance). Sampling was conducted seasonally from April 2004 to September 2006. *Spartina patens* and *Schoenoplectus americanus* are co-dominant plant species in this marsh. Low N-loading additions resulted in increased *S. patens* cover. However, increased N loading did not result in a shift in plant community composition despite *S. americanus* consistently having higher leaf tissue N than *S. patens*. Our results indicate that *S. americanus* may be more resilient than *S. patens* to disturbances that do not increase marsh surface elevation. Hurricane Katrina deposited significant amounts of sediment into remaining plots (August 29, 2005). By 2006, this disturbance resulted in a significant increase in both species richness and *S. patens* cover.

Keywords: Gulf coast, Hurricanes, Multiple disturbance, Nitrogen, Phosphorus, *Schoenoplectus americanus*, *Spartina patens*

INTRODUCTION

Long-term sustainability of Louisiana's coastal wetlands is essential to maintain healthy ecosystem functioning and, more importantly, to protect inhabitants from future hurricanes. In St. Tammany Parish, Louisiana, urban encroachment on the north shore of Lake Pontchartrain has increased the nutrient load and imposed increasing demands on the few remaining intact wetlands. Recent efforts have been made to reduce wetland loss and restore health to Louisiana's coastal environment.

Coastal Plant Community Dynamics

Plant community composition is the result of multiple interactions between abiotic and biotic variables (MITSCH and GOSSELINK 2000, CRONK and FENNESSEY 2001, CRAIN et al. 2004, HESTER et al. 2005). Abiotic variables controlling coastal plant community dynamics include salinity, hydroperiod, nutrient availability and disturbance whereas biotic variables include herbivory and competition (DAY et al. 1989, CRAIN et al. 2004). Fluctuations of these variables result in a shift in species productivity and plant community composition.

Salinity

In estuarine environments, riverine freshwater input creates a salinity gradient. Plant communities occupying areas furthest inland are dominated by species intolerant to salt stress (ODUM 1988, DAY et al. 1989, MITSCH and GOSSELINK 2000, CRONK and FENNESSEY 2001). Conversely, as marine influence increases, the plant community is dominated by increasingly salt tolerant vegetation (DAY et al. 1989, MITSCH and GOSSELINK 2000, CRONK and FENNESSEY 2001). The dominant halophytic grasses along

the eastern Atlantic and Gulf Coast are *Spartina alterniflora* (salt marsh cordgrass) in the low marsh zone (MENDELSSOHN and MORRIS 2002) and a *Spartina patens* (marshhay cordgrass) mixed community in the high marsh zone (MITSCH and GOSSELINK 2000). However, emergent vegetation dominating lower salinity habitats varies geographically (MITSCH and GOSSELINK 2000, CRONK and FENNESSY 2001).

Hydroperiod

Within each of these salinity-based habitat types the plant community is further influenced by hydroperiod (SALISBURY and ROSS 1992, MITSCH and GOSSELINK 2000, CRONK and FENNESSEY 2001, SPALDING and HESTER 2007). Although the frequently flooded low marsh zone is dominated by species adapted to waterlogging stress, the infrequently flooded high marsh zone is dominated by competitive species (BERTNESS and ELLISON 1987, ODUM 1988, BERTNESS 1991, MITSCH and GOSSELINK 2000, EMERY et al. 2001, CRONK and FENNESSEY 2001, PENNINGS et al. 2005b). Efficient competition for limited nutrient resources by the high marsh species is thought to restrict the expansion of stress tolerant low marsh species into the high marsh zone (BERTNESS 1991, LEVINE et al. 1998, EMERY et al. 2001, PENNINGS et al. 2005b). Conversely, physiological constraints restrict distribution of high marsh species from the more frequently flooded low marsh zone (BERTNESS 1991, LEVINE et al. 1998, EMERY et al. 2001, PENNINGS et al. 2005b). Competition for limited nutrient resources results in a competitive hierarchy between plants species with the stress tolerant species often being poor competitors under non-stressful conditions (BERTNESS 1991, LEVINE et al. 1998, EMERY et al. 2001).

Nutrient Availability

Alterations to the global nutrient cycle can create eutrophic conditions and result in a reversal of the competitive hierarchy and reduction in plant species diversity in coastal habitats (MORRIS 1991, CRAFT et al. 1995, VITOUSEK et al. 1997, LEVINE et al. 1998, RICHARDSON et al. 1999, EMERY et al. 2001, BERTNESS et al. 2002, PENNINGS et al. 2002, PENNINGS et al. 2005a). Under ambient nutrient availability, plants with dense belowground biomass dominate the plant community by capturing limited nutrients. Nutrient enhanced conditions reduce belowground competition for limiting nutrients (TILMAN 1982). As nutrient availability increases, plants that allocate biomass to aboveground leaf production are favored and the distribution of stress tolerant low marsh species has been shown to increase (CRAFT et al. 1995, LEVINE et al. 1998, RICHARDSON et al. 1999, EMERY et al. 2001, BERTNESS et al. 2002, PENNINGS et al. 2002). This allows stress tolerant species to inhabit higher elevations than under ambient nutrient availability (CRAFT et al. 1995, LEVINE et al. 1998, RICHARDSON et al. 1999, EMERY et al. 2001, PENNINGS et al. 2002). As a result, competitive high marsh species may become less abundant under eutrophic conditions (BERTNESS et al. 2002, SILLIMAN and BERTNESS 2004).

The relative importance of essential plant nutrients depends on salinity-based habitat type. Phosphorus is primarily considered to be the limiting nutrient in freshwater marshes (CRAFT et al. 1995, NEWMAN et al. 1996, RICHARDSON et al. 1999, MACEK and REJMANKOVA 2007), whereas nitrogen availability limits primary productivity in salt marshes (VALIELA and TEAL 1974, SMART and BARKO 1980, LEVINE et al. 1998, EMERY et al. 2001, MITSCH and GOSSELINK 2000). In both of these environmental extremes, an

increase in the limiting nutrient results in increases in stem height, aboveground productivity and plant cover.

In freshwater habitats, phosphorus is often bound to oxidized iron compounds forming insoluble complexes that are unavailable for plant uptake (SUNDARESHWAR and MORRIS 1999). In the Florida Everglades, phosphorus enrichment has resulted in a shift in plant community composition and decline of species diversity (CRONK and FENNESSEY 2001). Under ambient nutrient availability, *Typha domingensis* (southern cattail) and *T. latifolia* (broad-leaved cattail) dominate the more stressful frequently flooded low marsh zone whereas *Cladium jamaicense* (sawgrass) dominates the less frequently flooded high marsh zone (CRAFT et al. 1995, NEWMAN et al. 1996, RICHARDSON et al. 1999, MACEK and REJMANKOVA 2007). However, increases in phosphorus availability have reduced competition for the limiting resource. The result is a shift in plant community composition favoring the expansion of *Typha* species into the high marsh and a decrease in *Cladium* abundance (CRAFT et al. 1995, NEWMAN et al. 1996, RICHARDSON et al. 1999, CRONK and FENNESSEY 2001, MACEK and REJMANKOVA 2007).

Phosphorus is generally not considered to be a limiting nutrient in salt marshes because anoxia and sulfide drive iron reduction leaving iron less capable of binding to phosphorus (PALUDAN and MORRIS 1999). Contrary to freshwater habitats, coastal salt marsh productivity is limited by nitrogen availability (VALIELA and TEAL 1974). The mechanisms used by halophytic vegetation to tolerate salinity stress, such as salt excretion and intracellular compartmentation (FLOWERS et al. 1977, MUNNS 2002), create a high biological demand for nitrogen which may further drive nitrogen limitation in

coastal salt marsh habitats (Valiela and Teal 1974, Bradley and Morris 1990, Koch et al. 1990).

Spartina alterniflora, the low salt marsh dominant along the Eastern and Gulf Coasts of the United States, is restricted to the stressful low marsh zone by interspecific competition with less flood tolerant high marsh species (Bertness 1991, Mendelssohn and Morris 2002). Similar to the response of cattail species to increases in phosphorus availability, nitrogen-loading results in consistent increases in *S. alterniflora* stem height and aboveground productivity (Patrick and DeLaune 1976, Mendelssohn 1979, Buresh et al. 1980) thereby extending the upper limit of its distribution previously set by nutrient competition (Levine et al. 1998, Emery et al. 2001, Gratton and Denno 2003, Pennings et al. 2005b). Similarly, *Spartina patens* also benefits from nitrogen additions (Hester et al. 1994a). However, response of the high marsh perennial *S. patens* to nutrient loading depends on biotic interactions and geographic location (Pennings et al. 2005b). In a Rhode Island salt marsh, *S. patens* increases stem height in response to nutrient loading in both dense monoculture stands and in mixed-species communities (Levine et al. 1998, Emery et al. 2001). When paired with another high marsh perennial *Juncus gerardii*, under elevated nutrient loading conditions *S. patens* consistently increases aboveground productivity and dominates the community (Levine et al. 1998, Emery et al. 2001). However, when paired with *S. alterniflora* and *Distichlis spicata,* elevated nutrient loading did not result in an increase in *S. patens* aboveground productivity while its ability to dominate decreased (Levine et al. 1998, Emery et al. 2001, Pennings et al. 2002, Pennings et al. 2005). Contrary to the results found in New England, a fertilization study in a Mississippi mixed salt marsh community (*Distichlis*-*S.*

patens-Schoenoplectus species) favored the salt tolerant *Distichlis*, had no effect on *S. patens* and resulted in a decrease in the *Schoenoplectus* species (PENNINGS et al. 2002). With the exception of the conclusive findings of *S. alterniflora*, it remains unclear whether or not salt marsh species show predictable responses to nutrient additions (PENNINGS et al. 2005a).

While it is widely accepted that phosphorus and nitrogen availability limits productivity in freshwater and salt marsh habitats, respectively, estuarine oligohaline marshes are thought to be co-limited by nitrogen and phosphorus availability (CRAIN 2007). Individual nutrient addition had minimal effect on aboveground productivity and species composition of an oligohaline marsh in southern Maine (CRAIN 2007). However, addition of both nitrogen and phosphorus resulted in an overall increase in aboveground plant community productivity, although *S. patens* decreased individually (CRAIN 2007). Compared to nutrient studies of freshwater and salt marshes, relatively few *in situ* studies of oligohaline marshes have been conducted due to the complexities of physical gradients influencing oligohaline plant communities (ODUM 1988, MERRILL and CORNWELL 2002).

Disturbance

Contrary to nutrient loading, disturbances typically result in an initial decrease in aboveground plant productivity (CHABRECK and PALMISANO 1973, BALDWIN and MENDELSSOHN 1998) while species diversity may increase due to the temporal co-existence of additional plant species in favorable microsites (PICKETT 1980, ROXBURGH et al. 2004). When a disturbance occurs, the plant community responds by re-allocating resources from aboveground productivity to maintenance of belowground roots and rhizomes for storage (BALDWIN and MENDELSSOHN 1998). The reduction in

aboveground productivity and cover creates an opportunity for new species to colonize the disturbed area (Levin and Paine 1974, Brewer et al. 1998). Disturbances can be caused by biotic factors such as herbivory (Hester et al. 1994b, Silliman and Newell 2003), or abiotic factors, including oil spills (Mendelssohn et al. 1990, Hester and Mendelssohn 2000, Pezeshki et al. 2000) and hurricanes (Chabreck and Palmisano 1973, Meeder 1987, Conner et al. 1989, Guntenspergen et al. 1995, Courtemanche et al. 1999, Greening et al. 2006, Mallin and Corbett 2006). Hurricanes are unique in that they may produce different effects resulting from a combination of prolonged flooding, deposition sediment or wrack debris, marsh folding or erosion of the marsh surface (Meeder 1987, Conner et al. 1989, Guntenspergen et al. 1995, Brewer et al. 1998, Courtemanche et al. 1999, Greening et al. 2006, Mallin and Corbett 2006). Regardless of disturbance type, a disturbance disrupts healthy function, such as nutrient cycling or productivity, and often results in a structural change of the plant community (Sousa 1984, Johnson and Miyanishi 2007).

Long-term impacts and recovery of the plant community depends on intensity and frequency of the disturbance (Sousa 1984, Baldwin and Mendelssohn 1998, Roxburgh et al. 2004). Recovery from a mild or intermediate disturbance can be as rapid as one to two growing seasons (Chabreck and Palmisano 1973) and occurs via regeneration from belowground roots and rhizomes or germination from the seed bank (Baldwin and Mendelssohn 1998). However, as the magnitude of disturbance intensity increases the recovery period becomes prolonged. In the case of a lethal disturbance, which kills both the aboveground and belowground productivity, the plant

community may not ever recover to pre-disturbance conditions (BALDWIN and MENDELSSOHN 1998).

Importance of Research

As part of the effort to restore the Lake Pontchartrain Basin, Big Branch Marsh PENLAND et al. 2002). The 15,000 acres refuge is the largest remaining undeveloped natural area along the northern shore of Lake Pontchartrain and encompasses habitat zones ranging from sandy beaches to upland pine systems (MCCARTY 2001). These habitats support countless wildlife including migratory birds and waterfowl, a variety of mammal species, as well as critical spawning grounds and nursery habitats for economically important fish species (PENLAND et al. 2002).

The inland habitats at Big Branch Marsh NWR are hydrologically connected to Lake Pontchartrain via several bayous and a network of tidal creeks (MCCARTY 2001). Along Bayou Lacombe, the oligohaline marsh community is co-dominated by *Spartina patens* (Ait.) Muhl. and *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller (formerly *Scirpus olneyi*) (MCCARTY 2001). Previous research on these co-dominants has focused on the interactive effects of salinity and flooding regime (BROOME et al. 1995). Neither species experiences a decrease in productivity at salinities less than 10 ppt, but they do have differential responses to flooding regime (BROOME et al. 1995). Although *S. americanus* is tolerant of flooding stress (ROSS and CHABRECK 1972, BROOME et al. 1995, HOWARD and MENDELSSOHN 2000), the hypoxic conditions associated with prolonged flooding inhibit *S. patens* root elongation (PEZESHKI and DELAUNE 1990). Therefore, distribution of *S. patens* is often restricted to the higher marsh zone as increased flooding depth reduces growth (BERTNESS 1991, BROOME et al.

1995, LEVINE et al. 1998, EMERY et al. 2001, SPALDING and HESTER 2007). In spite of these interspecific differences in flooding tolerance, *S. patens* and *S. americanus* are able to co-dominate the oligohaline community along Bayou Lacombe in Big Branch Marsh NWR.

The coastal wetlands of southeastern Louisiana are subjected to both elevated nutrients and disturbance. While it is generally accepted that nutrient loading should favor the more flood tolerant species, previous research has not evaluated the effects of nutrient loading on the oligohaline plant community co-dominated by *S. patens* and *S. americanus*. A critical data gap in nutrient-loading studies exists in a geographic location subjected to elevated nutrients. Therefore, in this study I sought to isolate the effects phosphorus and nitrogen loading on aboveground plant community dynamics in a co-dominated low salinity marsh at Big Branch Marsh NWR located in Southeastern Louisiana. To improve our understanding of the processes that influence plant community composition in the oligohaline marsh habitat we manipulated nutrient loading rates as well as simulated a lethal disturbance. The nutrient-loading component of this study allows us to further understand oligohaline marsh community responses to altered nutrient regimes in the Lake Pontchartrain Basin. Meanwhile, the lethal disturbance component confirms the importance of maintaining a healthy plant community in providing valuable functions such as nutrient cycling and storm protection.

Hypotheses

1. The oligohaline marsh aboveground plant community at Big Branch Marsh is co-limited by nitrogen and phosphorus availability. Application of individual nutrients will not result in an increase of the aboveground plant productivity.

However, when added together, phosphorus and nitrogen will result in a significant increase in mean stem height, aboveground primary productivity and plant community composition. In addition, nutrient loading will favor expansion of the more flood tolerant *S. americanus* over the less flood tolerant *S. patens* and lead to a decrease in species richness.

2. The lethal disturbance will result in significant decreases in stem height, productivity and species richness, and will display differential recovery by the two co-dominant plant species.
3. The recovery period from non-lethal, hurricane disturbance will occur faster than recovery from the lethal disturbance and will result in a temporal increase in species richness.

To test my hypotheses I conducted a nutrient loading experiment to identify nutrients limiting plant primary productivity and the consequences of increasing nutrient availability on the oligohaline marsh plant community composition. The lethal disturbance treatment was applied to remove both aboveground and belowground plant community entirely. Although the additional hurricane disturbance aspect of the study was unplanned it did provide a unique opportunity to further examine plant community response to multiple disturbances following nutrient treatment. Plant community response to each treatment was assessed during early-, mid- and late-growing season through biomass harvests and percent cover estimates.

Results from this study will provide data currently absent in coastal research. Past research on the effects of nutrient loading on coastal plant community dynamics has

focused on freshwater and salt marshes. Lack of data in the transitional marshes leaves a critical data gap across the landscape scale. In addition, the possibility of geographic variations in interspecific responses to nutrient loading needs to be further addressed. Another area of concern in Southeastern Louisiana is the effect of disturbance on coastal plant community. The widespread disturbances in Louisiana's coastal plant communities differ in severity of damage. Previous research on the impacts disturbance and recovery of the plant community in coastal Louisiana has focused on a single event per growing season (CHABRECK and PALMISANO 1973, MEEDER 1987, MENDELSSOHN et al. 1990, GUNTENSPERGEN et al. 1995, COURTEMANCHE et al. 1999, HESTER and MENDELSSOHN 2000). In addition to the lethal disturbance treatment, six tropical cyclone disturbances had a direct impact on the research site at Big Branch Marsh NWR during two consecutive growing seasons making this a multiple disturbance study. The exceptional frequency of tropical disturbances provided a unique opportunity to monitor plant community response to multiple disturbances.

MATERIALS AND METHODS

Study Site

The study site is an oligohaline marsh located at 30° 27.294° North Latitude by 89° 95.364° West latitude on the eastern bank of Bayou Lacombe in Big Branch NWR, St. Tammany Parish, Louisiana, United States. Site selection was based on location of healthy, representative plant community at similar elevations and equal distances from the bayou. The oligohaline marsh community is co-dominated by *S. patens* and *S. americanus*. Several minor species also occurred including *Aster subulatus* Michx.,

Echinochloa walteri (Pursh) Heller, *Eleocharis parvula* (R. & S.) Link, *Galium tinctorium* (L.) Scop., *Ipomoea sagittata* (Poir.), *Lythrum lineare* (L.), *Pluchea camphorata* (L.) D.C., *Polygnum* spp., *Ptilimniun costatum* (Ell.) Raf., *Sesbania macrocarpa*, *Solidago* sp. and *Vigna luteola* (Jacq.) Benth.

Experimental Design

The nutrient additions used in for this research project bracket the freshwater Mississippi River Diversion at Caernarvon (LANE et al. 1999) located south of New Orleans, Louisiana. Three levels of nitrogen (0, 20 and 40 g N m^{-2} yr^{-1}) and three levels of phosphorus (0, 15 and 30 g P m^{-2} yr^{-1}) were added in a completely cross-classified manner to create nine nutrient loading combinations. In addition, one lethal treatment (herbicide application) was used to simulate a lethal disturbance. Using a randomized block design, each of the ten treatments (3N*3P + Lethal) had five true replicates yielding a total of 50 experimental plots. Five plots were un-manipulated reference plots (undisturbed, no nutrient) while the remaining 45 plots were experimentally manipulated.

Experiment Establishment

Upon initiation of the experiment, a healthy representative stand of the dominant marsh vegetation was identified along the eastern banks of Bayou Lacombe. Set-up of the study site began in the fall of 2003 with the installation of the boardwalk. Side-by-side primary productivity (0.75 x 1m) and community composition (1m x 1m) experimental plots were established. A buffer area of approximately 0.25 m was allocated between the side-by-side plots as well as the area immediately adjacent the plots. The set-up was replicated in 5 blocks along Bayou Lacombe with Block 1 being situated most inland and Block 5 located closest to Lake Pontchartrain. After an initial

data collection to characterize baseline conditions during the spring of 2004 the nutrient loading regime and lethal disturbance treatments were implemented in the summer of 2004. Slow-release nitrogen (in the form of urea) and phosphorus (Humaphos) pellets were applied via broadcast dispersal during the first two years of the study (June 2004, March 2005 and June 2005). Nutrient treatments were not applied in 2006. The lethal herbicide treatment was applied using a backpack sprayer until leaves were lightly covered in June 2004 resulting in 100% mortality. The lethal treatment was re-applied in March 2006. The solution consisted of the herbicide Rodeo® diluted to 1.5% (KALLER 2003) with active ingredients Glycophosphate and N-(phosphonomethyl 1) glycine.

Data Collection

Complete sampling of edaphic and vegetative conditions was conducted seasonally (generally in the spring, summer and fall) throughout the experiment. Edaphic measurements and water samples were collected in the buffer area between the side-by-side productivity and community plots with representative elevation and plant community cover. Water samples were collected using an interstitial water sipper (MCKEE et al. 1988). The tubing, perforated to a depth of 15 cm, collects a homogenous water sample in the area of maximum root production.

Variables Measured: Edaphic Conditions

Soil Oxidation-Reduction Potential

Brightened platinum electrodes were inserted in the soil to depths of 1 and 15 cm (FAULKNER et al. 1989) and allowed to equilibrate for 20 minutes. Measurements were determined using a Corning® Model # 313 pH-mV meter with a KCl-filled calomel

reference electrode. Readings were corrected for the reference electrode potential by adding +244 mV.

Interstitial Water: Salinity, pH and Sulfide Concentration

To quantify interstitial salinity, water samples collected in the field using the interstitial water sipper (MCKEE et al. 1988) and were stored in sealed Nalgene bottles and returned to lab for analysis. Readings were taken at room temperature within 24 hours of collection with YSI® Model # 30 Salinity Conductivity Meter. To quantify interstitial pH, an additional water sample was collected using the interstitial water sipper and analyzed in the field using a Corning® Model # 313 pH-mV meter. The meter was calibrated with pH 4 and pH 10 buffer solutions between each measurement. A third water sample was collected with the interstitial water sipper for sulfide analysis. Prior to collection, sulfide anti-oxidant buffer (SAOB) reagent was purged of oxygen by bubbling nitrogen gas for 20 minutes to create an anaerobic environment. Upon collection, the interstitial water sample was combined with an equal quantity of SAOB reagent and stored upright in scintillation vials and returned to the lab for further analysis. In the lab, standard dilutions were created using deoxygenated deionized water and the remaining SAOB reagent (also deoxygenated). Serial dilutions were established at concentrations of 0.1, 1.0, 10, 100 and 1000 ppm. Readings were taken using a Corning® Model # 313 mV meter within 24 hours of collection.

Interstitial Nutrients and Elements

Approximately 250-mL of interstitial water was collected with the interstitial water sipper (MCKEE et al. 1988) and stored in acid-washed Nalgene bottles under refrigerated conditions until filtered. Within 24 hours of collection, the samples were

suction-filtered using 0.45 micron filters and transferred into clean, acid-washed scintillation vials. Each sample was analyzed for both element and nutrient content. For elemental analysis, samples were preserved with 2 drops of trace metal grade nitric acid and were refrigerated until ICP Optical Emission Spectrometer analysis (P reported for this study) at Louisiana State University (LSU) Agriculture Center's Soil Testing and Plant Analysis Lab. Samples analyzed for nutrients (NO_2^-, NO_3^- and NH_4^+) were frozen until analysis by automated N analyzer at LSU and Southeastern Louisiana University.

Elevation

Representative plot surface elevations were surveyed with a laser level and stadia rod and tied-in to SET station elevations in the community composition plots. During the first two years of the study elevation was recorded each fall in October 2004 (post-Hurricane Ivan) and October 2005 (post-Hurricane Katrina). During year three, elevation was recorded for each sample period (March, June and September 2006).

Soil Core Analysis: Bulk Density and Organic Matter Content

Soil cores were collected from a representative area located between the adjacent productivity and community composition plots and stored in pre-weighed plastic bags. Upon return to the laboratory the wet weights of soil core samples were recorded. Samples were then dried at 65 °C for one week and re-weighed to calculate percent moisture and bulk density. Soil organic matter content was determined after homogenizing by the loss on ignition method by heating in the muffle furnace at 550 °C for five hours until combustion was complete.

Variables Measured: Vegetative Conditions

Leaf Tissue Nutrient Concentrations: Elements and Nutrients

Additional plant tissue was collected from the various treatment plot areas, rinsed lightly with deionized water to remove debris, dried at 65 °C for one week and homogenized in a Wiley Mill® through a size 20 mesh plate. For elemental analysis, tissues were digested in trace metal grade nitric acid at 110 °C and 130 °C in a block digester (A.I. Scientific AIM500). Samples were stored in acid-washed scintillation vials and delivered to LSU Agriculture Center's Soil Testing and Plant Analysis Lab for elemental analysis (P reported) using ICP Optical Emission Spectrometer. LSU Wetland Biogeochemistry Institute Analytical Service performed CHN analysis.

Mean Stem Height and Aboveground Primary Productivity

Aboveground plant productivity was determined during years one and two of the study by sequentially harvesting a 0.25 m x 0.25 m area from the 1 m x 0.75 m aboveground productivity plot. All plant biomass samples were sorted by species and categorized as either live or dead. Stem heights were measured for the live co-dominants *S. patens* and *S. americanus*. Samples were then dried at 65 °C for one week and weighed. During year one of the study aboveground biomass was collected on 24 April 2004 and 18 October 2004. Hurricane Ivan (16 September 2004) and Tropical Storm Matthew (10 October 2004) both significantly raised Lake Pontchartrain water levels, resulting in prolonged flooding of the marsh surface in addition to deposition of wrack on our experimental plots. As previous research has shown wrack deposition results in a decrease in aboveground productivity, wrack deposition was removed from the experimental plots to prevent obfuscation of treatment effects. During year two of the

study, aboveground biomass was collected on 16 March 2005, 23 June 2005 and 7 October 2005 (post-Hurricanes Cindy, Katrina and Rita) of 2005. As the study site was severely impacted by the three hurricanes at the end of year two it was impossible to collect biomass during year three of the study because many of the plot markers were either removed by the storm surge or buried by debris.

Plant Community Composition and Species Richness

Aboveground plant community composition was determined non-destructively via ocular estimation (BARBOUR et al. 1999). Species richness was quantified as the total number of species present in the community composition plots. The permanent 1 x 1 m quadrants were observed to determine seasonal and interannual changes in aboveground plant community composition and species richness during all three years of the study. Wrack deposition from Hurricane Ivan, Tropical Storm Ivan and Tropical Storm Matthew was removed from the plots in October 2004 to prevent further obfuscation of treatment effects. Following Hurricanes Katrina and Rita (29 August and 23 September 2005), wrack and small sods (marsh balls) were removed, but the hurricane effects of sediment deposition and large sods were left intact.

Statistical Analysis

Data were analyzed as a randomized block design using KaleidaGraph version 4.0 at a significance level of p=0.05 to interpret results of statistical tests. To reduce heterogeneity of variance, aboveground primary productivity data were ln(x+1) transformed prior to analysis then de-transformed for presentation (BALDWIN and MENDELSSOHN 1998, EMERY et al. 2001, CRAIN 2007). The interactive effects of P- and N-loading on leaf tissue nutrient content, stem height, biomass, cover and species

richness were analyzed using a two-way ANOVA. The main effects of individual P- or N-loading on vegetative conditions were analyzed using one-way ANOVA followed by the Bonferroni post-hoc test to isolate significant differences between the ambient, low and high nutrient loading treatments. The Student t-Test was used to analyze intraspecific differences between two disturbance treatments (no disturbance and lethal disturbance). However, the interspecific differences between the *S. patens*, *S. americanus* and other species were analyzed using ANOVA followed by Bonferroni post-hoc test. On 29 August 2005 the sample size (n) decreased from 50 to 39 due to interior pond formation and plot destruction resulting from Hurricane Katrina's storm surge.

RESULTS

Soil Physicochemical Characterization

Interstitial salinity levels were generally low and fluctuated between 1.9 ppt and 6.8 ppt during 2004 and 2005, but were higher (5.7 - 8.2 ppt) in 2006 (Table 1). The 2006 data was also characterized by a decrease in pH, and an increase in soil redox potentials and bulk density (Table 1). Three months after the initial nutrient-loading application, the high N-loading treatment resulted in a significant increase in interstitial NH_4^+-N from 11.3 *u*Molar under ambient nitrogen availability to 52.6 *u*Molar under the high N-loading treatment (Table 2). The lethal treatment (herbicide), which resulted in 100% mortality of both the aboveground and belowground plant community, also resulted in significant increase in interstitial NH_4^+-N. From October 2004 to June 2005, the lethal treatment resulted in an increase in interstitial NH_4^+-N ranging from 3.5 to 10.8 times greater than under ambient N-availability (p<0.01).

Interaction of Nitrogen and Phosphorus Loading

Analysis of the interactive effects of P- and N-loading treatments of vegetative responses of the co-dominant species *S. patens* and *S. americanus* from October 2004 through June 2005 (prior to Hurricane Katrina's landfall on 29 August 2005) was not significant. Therefore, the main effects of P- or N-loading are interpreted for this interval.

Responses to Phosphorus Loading Treatments

Leaf Tissue [P]

Three months after the initial nutrient application, in October 2004, the P-loading treatments did not result in an increase in leaf tissue phosphorus concentration [P] for either *S. patens* (p=0.56, F=0.6, Appendix 1a) or *S. americanus* (p=0.35, F=1.1, Appendix 1b). However, in March 2005 the high P-loading treatment resulted in an increase in leaf tissue [P] of 0.5 mg/kg for *S. patens* (p=0.02. F=5.2). Conversely, the P-loading treatments did not result in an increase of leaf tissue [P] for *S. americanus* by March 2005 (p=0.9, F=0.1). Although the significant effects of P-loading treatments on intraspecific leaf tissue [P] were limited to March 2005, *S. americanus* maintained a higher leaf tissue [P] than *S. patens* in both October 2004 and March 2005. In October 2004, under the low P-loading treatment, *S. americanus* leaf tissue [P] was 34.4% higher than *S. patens* leaf tissue [P] (p=0.01, Figure 1a). Subsequently, in March 2005, *S. americanus* had 53.1-60.3% higher leaf tissue [P] than *S. patens* under all three P-loading treatments (p=0.002, F=493, Figure 1b).

Table 1. Summary of edaphic conditions including salinity, pH, redox potential (depths of 1 and 15 cm), sulfides, soil bulk density, and soil organic matter content. Values represent the mean followed by standard error in parentheses.

Date	Soil Salinity (ppt)	pH	Eh 1 (mV)	Eh 15 (mV)	S^{-2} (ppm)	n
Apr-04	3.6 (0.03)	6.5 (0.04)	128 (27)	93 (31)	15 (1.8)	(50)
Oct-04	6.8 (0.16)	6.4 (0.03)	-130 (8)	-89 (7)	30 (2.4)	(50)
Mar-05	1.9 (0.06)	6.3 (0.02)	81 (11)	2 (7)	10 (1.1)	(50)
Jun-05	3.3 (0.06)	6.5 (0.03)	74 (11)	-84 (9)	30 (2.3)	(50)
Oct-05	2.1 (0.16)	6.4 (0.02)	50 (12)	4 (7)	69 (5.2)	(40)
Mar-06	5.7 (0.16)	5.8 (0.10)	346 (26)	130 (33)	9 (2.1)	(40)
Jun-06	8.2 (0.21)	5.9 (0.07)	251 (26)	77 (23)	47 (5.8)	(40)
Sep-06	7.6 (0.20)	5.8 (0.11)	86 (10)	26 (13)	33 (5.7)	(40)

Date	BD ($g\ cm^{-3}$)	Soil OM (%)	Relative Elevation - Range (m)	Relative Elevation – Mean (m)	n
Apr-04	0.063 (0.003)	52.6 (1.2)			(50)
Oct-04	-	-	0 – 0.21	0.11	(50)
Mar-05	-	-			(50)
Jun-05	0.062 (0.003)	51.7 (1.2)			(50)
Oct-05	0.072 (0.004)	52.2 (0.7)	0.20 – 0.51	0.38	(40)
Mar-06	0.088 (0.004)	50.6 (0.8)			(40)
Jun-06	0.093 (0.004)	-			(40)
Sep-06	-	-			(40)

Table 2. Summary of interstitial nitrogen and phosphorus levels. Values represent mean (SE) for porewater (a) Nitrogen (NH_4^+-N and NO_3^--N) and (b) Phosphorus under the three N-loading (0, 20 and 40 g N m^{-2} yr^-) and P-loading treatments (0, 15 and 30 g P m^{-2} yr^{-1}) plus the lethal disturbance treatment. Within each sample period, means having different superscripted letters are significantly different based on Bonferroni multiple comparisons.

a. NH_4^+-N

Date	Ambient	Low N	High N	Lethal
Apr-04	22 (6.3)	37.9 (14.6)	29.2 (9.5)	44.5 (9.2)
Oct-04	11.3 (3.7) ^{c}	29.1 (6.4) ^{bc}	52.6 (13.3) ^{ab}	85.7 (26.1) ^{a}
Mar-05	33.2 (14.5) ^{b}	14.4 (4.2) ^{b}	17.4 (4.5) ^{b}	117.5 (24.5) ^{a}
Jun-05	14.1 (2.5) ^{b}	23.5 (11.6) ^{b}	20.2 (8.3) ^{b}	152.6 (35.2) ^{a}
Mar-06	0.4 (0.2)	0.6 (0.2)	0.3 (0.1)	0.8 (0.48)
Jun-06	0.1 (0.02)	0.1 (0.05)	0.1 (0.03)	0.03 (0.014)

b. NO_3^--N

Date	Ambient	Low N	High N	Lethal
Apr-04	4.7 (0.7)	4.1 (0.5)	27.1 (13.3)	2.9 (1.4)
Oct-04	2.8 (1.0)	3.1 (1.4)	1.8 (0.9)	3.3 (2.8)
Mar-05	1.5 (0.3)	2.4 (0.8)	1.3 (0.2)	1.2 (0.3)
Jun-05	0.6 (0.2)	0.4 (0.04)	0.6 (0.1)	0.56 (0.1)
Mar-06	0.03 (0.005)	0.03 (0.004)	0.02 (0.002)	0.03 (0.01)
Jun-06	0.01 (0.003)	0.02 (0.003)	0.02 (0.004)	0.01 (0.01)

c. P

Date	Ambient	Low P	High P	Lethal
Apr-04	0.51 (0.01)	0.49 (0.02)	0.52 (0.01)	0.46 (0.03)
Mar-05	0.48 (0.02)	0.47 (0.02)	0.49 (0.02)	0.38 (0.03)
Oct-05	2.34 (0.07)	2.3 (0.1)	2.58 (0.11)	2.49 (0.11)
Mar-06	1.07 (0.02)	1.06 (0.01)	1.06 (0.01)	1.15 (0.09)
Jun-06	2.04 (0.03)	2.08 (0.05)	2.07 (0.05)	2.06 (0.03)

Mean Stem Height

In March 2005, the high P-loading treatment resulted in an 11.5 cm increase on *S. patens* mean stem height increase above the low P-loading treatment (p=0.025, Appendix 2a). However, *S. patens* mean stem height under the high P-loading treatment (49.9 cm) was not significantly taller than the other two treatments (p=0.053, F=5). On the contrary, the P-loading treatments did not result in an increase in *S. americanus* mean stem height during any sample period (p=0.09, F=3.8, Appendix 2b). Interspecific responses of mean stem height to P-loading fluctuated seasonally. In October 2004, under the ambient P-loading treatment *S. americanus* mean stem height was 15.1 cm taller than *S. patens* (p=0.008, F=9.7, Figure 2a). However, under the low and high P-loading treatments *S. americanus* and *S. patens* mean stem heights were equal (Figures 2b and 2c). In March 2005, *S. patens* was significantly taller than *S. americanus* under the ambient (p=0.034, F=5.5, Figure 2a), low (p=0.014, F=7.8, Figure 2b) and high (p<0.0001, F=31.2, Figure 2c) P-loading treatments. In contrast, in June 2005, *S. americanus* was significantly taller than *Spartina* under the ambient (p=0.0005, F=21.9, Figure 2a) and high (p=0.0002, F=33.4, Figure 2c) P-loading treatments. Five weeks after Hurricane Katrina, in October 2005, *S. americanus* was 19.9 cm taller than *S. patens* under the low P-loading treatment (p=0.002, F=21.9, Figure 2b).

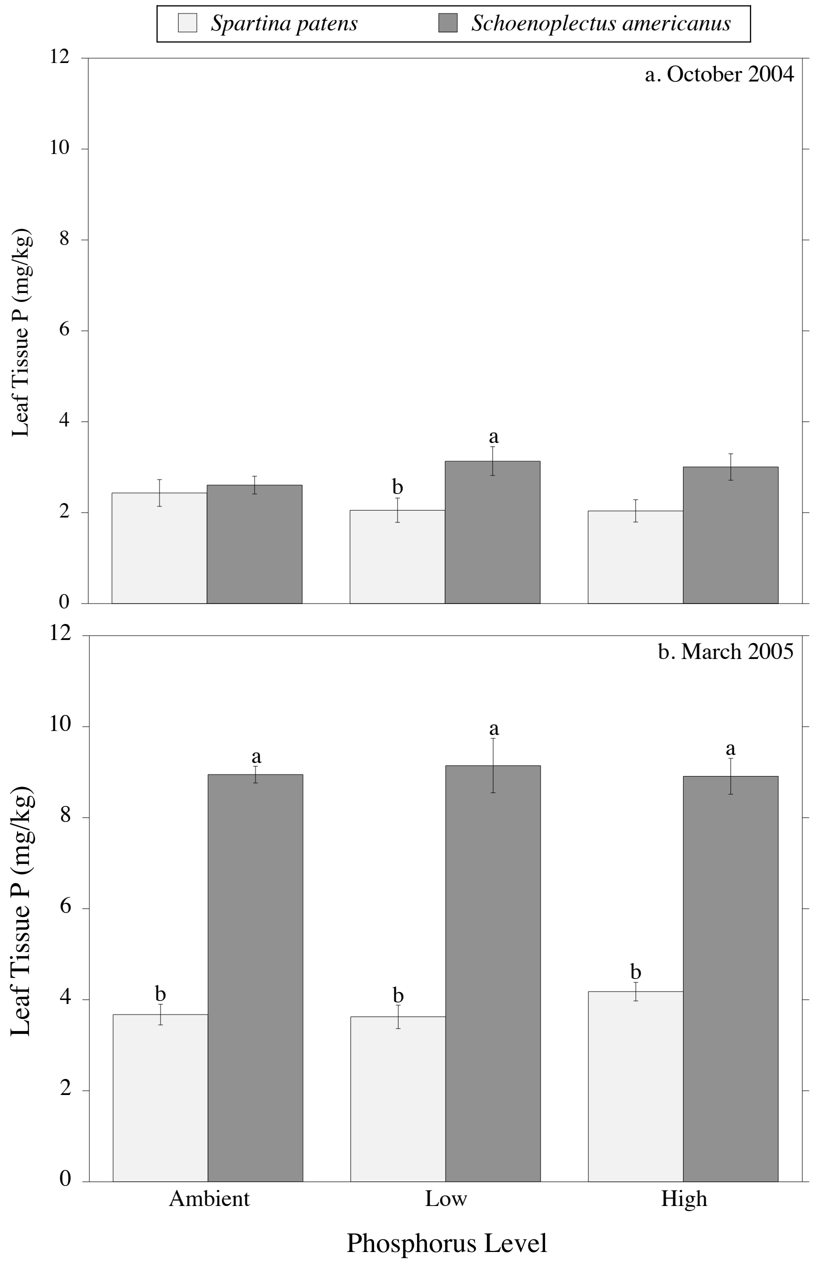

Figure 1. Interspecific differences in leaf tissue phosphorus concentration under increasing P-loading treatments. Bars represent mean ± standard error of leaf tissue [P] for *Spartina patens* and *Schoenoplectus americanus* for the two sample periods of (a) October 2004 and (b) March 2005. Within each sample period, different letters represent significant interspecific differences in leaf tissue [P] based on Bonferroni multiple comparisons. Sample size depended on available plant tissue and varied during the two sample periods (see Appendix 1a and 1b).

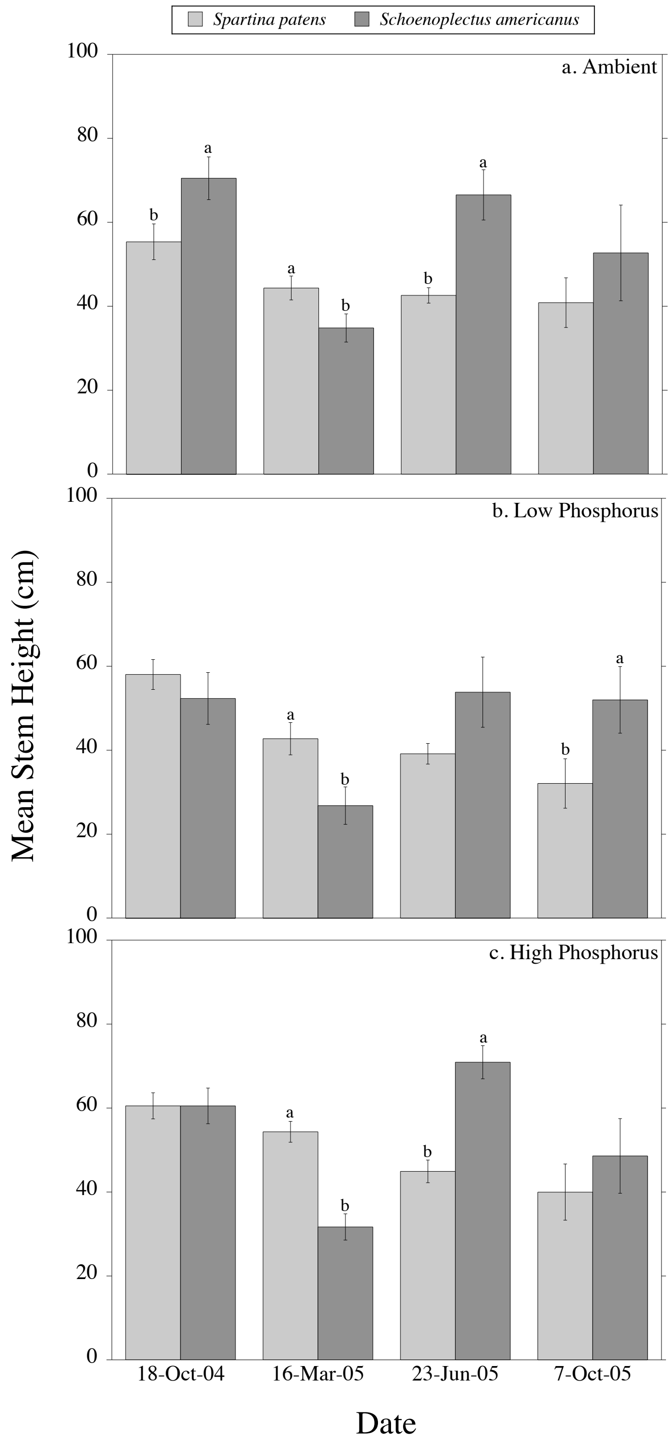

Figure 2. Result of P-loading treatment on interspecific differences in stem height. Bars represent mean $\pm$ standard error mean stem height (cm) for *Spartina patens* and *Schoenoplectus americanus* under the (a) ambient, (b) low and (c) high P-loading treatments. Different superscripted letters denote significant interspecific differences within P-loading treatments based on Bonferroni multiple comparisons. Sample size decreased on 29 August 2005 (see Appendix 2).

Primary Productivity

The significant effects of P-loading treatments on *S. patens* aboveground productivity were isolated to March 2005 when *S. patens* total biomass increased by 32.7% from 1,018 g m^{-2} under the low P-loading treatment to 1,512 g m^{-2} under the high P-loading treatment (p=0.048, Appendix 3c). The significant effects of P-loading treatments on *S. americanus* productivity were also isolated to Year 2 of the study. In March 2005, the low P-loading treatment had less *S. americanus* live (p=0.05), dead (p=0.005) and total biomass (p=0.03) than plots receiving the high P-loading treatment (Appendix 4). In June 2005, low P-loading resulted in a decrease in *S. americanus* total biomass relative to the ambient P-loading treatment (p=0.04). Although P-loading did not result in a significant increase in *S. patens* live biomass, *S. patens* experienced significantly greater live biomass than *S. americanus* under all P-loading treatments in April 2004 and March 2005 (Figure 3).

Plant Community Composition

Phosphorus-loading treatments resulted in a slight increase in *S. patens* live cover (p=0.03, F=4.8) but did not affect either *S. patens* dead (p=0.69, F=0.4) or total cover (p=0.36, F=1.1, Appendix 5). In October 2004 the high P-loading treatment resulted in an increase in *S. americanus* live cover above the ambient P-loading treatment (p=0.002, Appendix 6a). The P-loading treatments did not result in an apparent shift in plant community composition. Initially, it appeared that *S. americanus* would dominate under the high P-loading treatments. In October 2004, *S. americanus* experienced 11.7% more live cover than *S. patens* under the high P-loading treatment (p=0.007, Figure 4c). However, in June 2005 *S. americanus* had 10% more live cover than *S. patens* under the

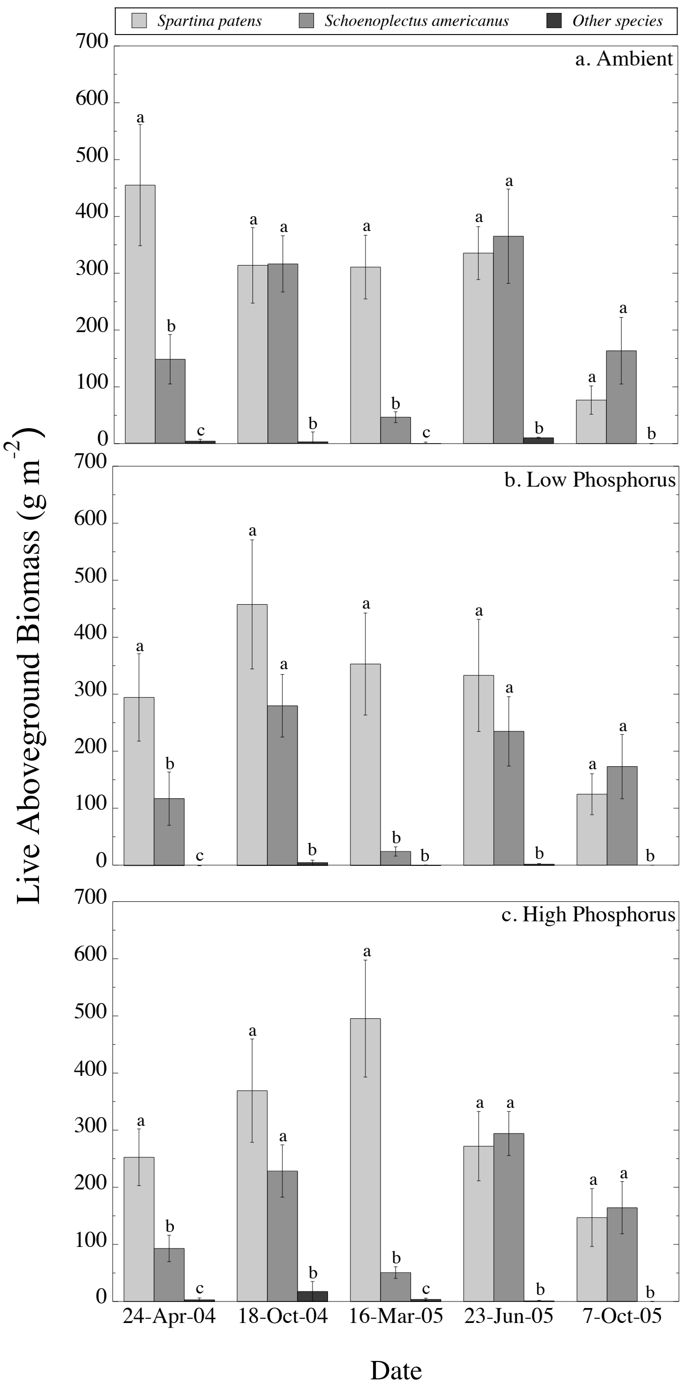

Figure 3. Interspecific differences in live standing crop under increasing P-loading treatments. Bars represent mean ± standard error of live aboveground biomass (g m^{-2}) for *Spartina patens*, *Schoenoplectus americanus* and all other species present under the (a) ambient, (b) low and (c) high P-loading treatments. Different superscripted letters denote significant interspecific differences within P-loading treatments based on Bonferroni multiple comparisons. Sample size decreased on 29 August 2005 (see Appendix 3 and 4).

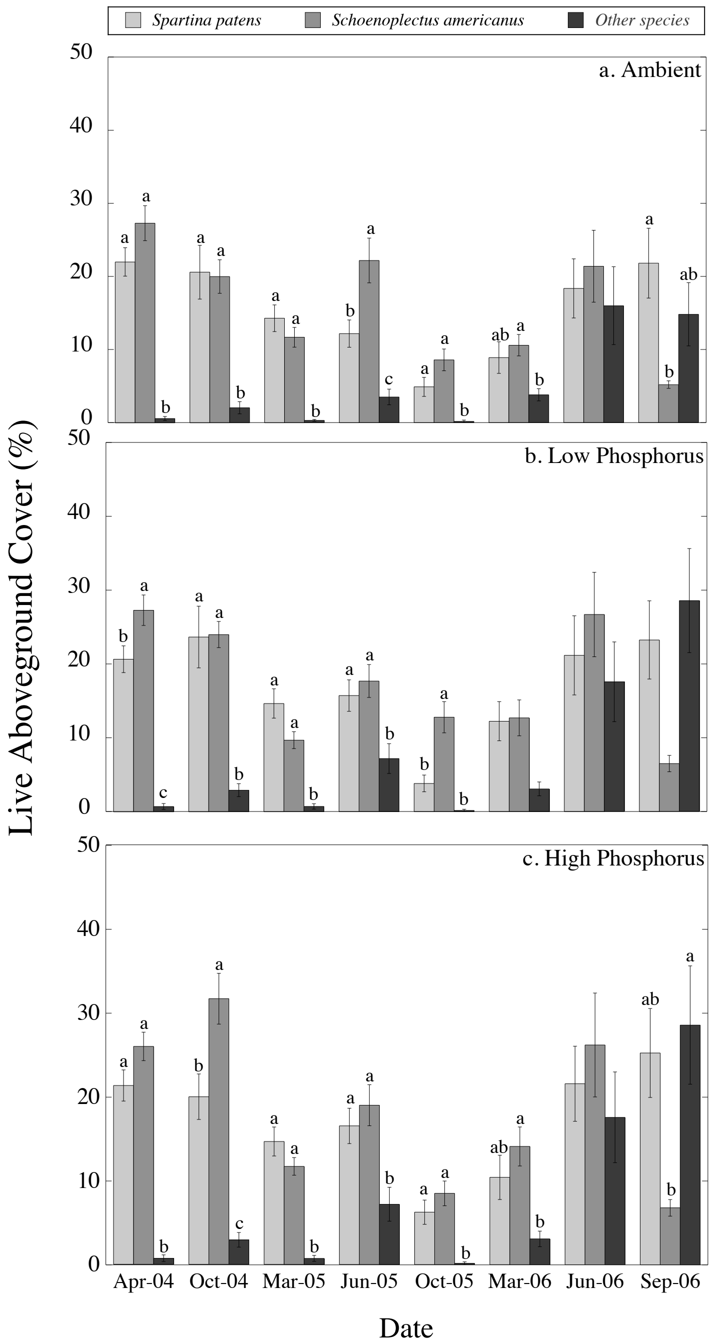

Figure 4. Interspecific differences in live plant community composition under increasing P-loading treatments. Bars represent mean ± standard error of live cover (% m^{-2}) for *Spartina patens*, *Schoenoplectus americanus* and all other species present under the (a) ambient, (b) low and (c) high P-loading treatments. Different superscripted letters denote significant interspecific differences within P-loading treatments based on Bonferroni multiple comparisons. Sample size decreased on 29 August 2005 (see Appendix 5 and 6).

ambient P-loading treatment (*p*=0.02, Figure 4a). Then, in October 2005 *S. americanus* had 9% more live cover than *S. patens* under the low P-loading treatment (*p*=0.005, Figure 4b). However, in September 2006 *S. patens* had greater live cover than *S. americanus* under all three P-loading treatments (*p*=0.001).

Species Richness

Phosphorus-loading treatments only significantly affected species richness during one sample period. In October 2004, species richness increased from 2.4 species m^{-2} under the low P-loading treatment to 2.9 species m^{-2} under the high P-loading treatment (*p*=0.03, Appendix 7). However, overall the P-loading treatments did not significantly affect species richness (*p*=0.8).

Responses to Nitrogen Loading Treatments

Leaf Tissue [N]

Contrary to the initial effect of phosphorus, in October 2004 the nitrogen-loading treatments resulted in a significant increase in leaf tissue nitrogen concentration [N] for both *S. patens* (*p*=0.001, F=8.6, Appendix 8a) and *S. americanus* (*p*=0.015, F=4.6, Appendix 8b). Although only the high N-loading treatment resulted in a significant increase in leaf tissue [N] for both species, *S. americanus* maintained greater leaf tissue [N] under all three N-loading treatments (Figure 5). *S. americanus* assimilated 30.7% (*p*=0.0004), 24.7% (*p*=0.003) and 28.2% (*p*<0.0001) more nitrogen into leaf tissue than *S. patens* under the ambient, low and high N-loading treatments, respectively.

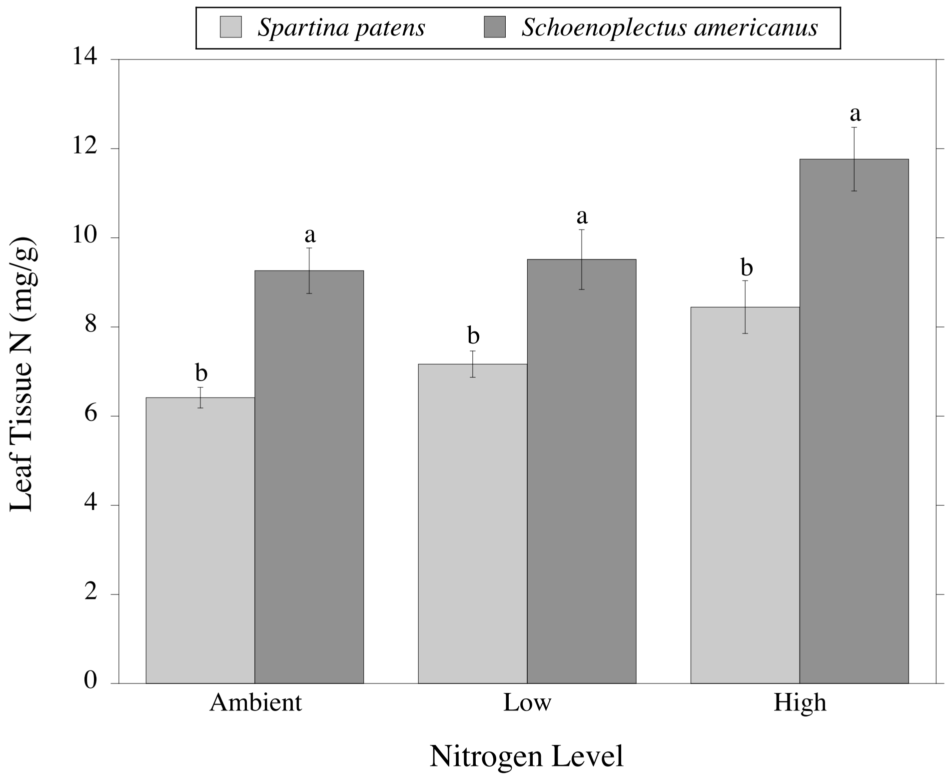

Figure 5. Interspecific differences in leaf tissue nitrogen concentration [N] under increasing N-loading treatments for *Spartina patens* and *Schoenoplectus americanus*. Bars represent mean $\pm$ standard error for plant tissue collected in October 2004 (n=15 except *Schoenoplectus* ambient N-loading when n=14, see Appendix 8). Different superscripted letters denote significant interspecific differences within N-loading treatments based on Bonferroni multiple comparisons.

Mean Stem Height

In October 2004, the low N-loading treatment resulted in a 12.4 cm increase in *S. patens* mean stem height compared to the ambient N-loading treatment (p=0.043, Appendix 9a). However, the N-loading treatments did not increase *S. patens* stem heights during March (p=0.59, F=0.53), June (p=0.48, F=0.75) or October 2005 (p=0.71, F=0.34). The N-loading treatments did not result in a significant increase *S. americanus* mean stem height (p=0.97, F=0.03, Appendix 9b). The N-loading treatments did not favor interspecific increase in mean stem heights. Instead, interspecific differences in mean stem height fluctuated seasonally. In March 2005, *S. patens* mean stem heights were taller than *S. americanus* under all N-loading treatments ($p<0.05$, Figure 6). On the contrary, in June 2005, *S. americanus* mean stem heights were taller than *S. patens* under all N-loading treatments.

Primary Productivity

The N-loading treatments did not affect *S. patens* live (p=0.15, F=2.6), dead (p=0.07, F=4.3) or total biomass production (p=0.09, F=3.8, Appendix 10). However, in June 2005 the N-loading treatment resulted in a 55.9% increase in *S. americanus* live biomass from 185.6 g m^{-2} under the ambient to 456 g m^{-2} under the high N-loading treatment (p=0.023, Appendix 11a). The N-loading treatments did not affect *S. americanus* dead (p=0.18, F=2.3) or total biomass (p=0.63, F=0.5 Appendix 11b,c). Although the N-loading treatments did not result in an increase in *S. patens* live biomass, *S. patens* produced 59-93% more live biomass than *S. americanus* in April 2004 and March 2005 under all three N-loading treatments ($p<0.05$, Figure 7).

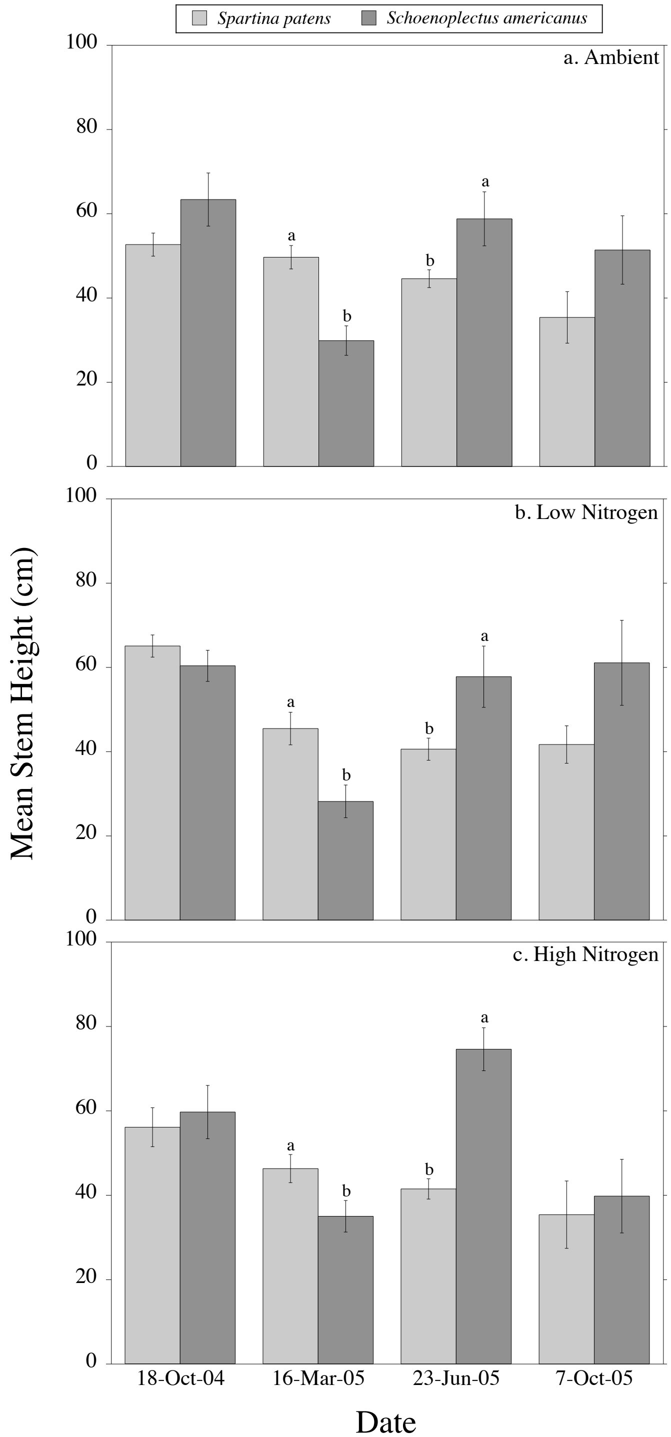

Figure 6. Result of N-loading treatments on interspecific differences in mean stem height. Bars represent means ± standard error for *Spartina patens* and *Schoenoplectus americanus* mean stem height (cm) under the (a) ambient, (b) low and (c) high N-loading treatments. Sample size decrease on 29 August 2005 (see Appendix 9). Different superscripted letters denote significant interspecific differences within N-loading treatments based on Bonferroni multiple comparisons.

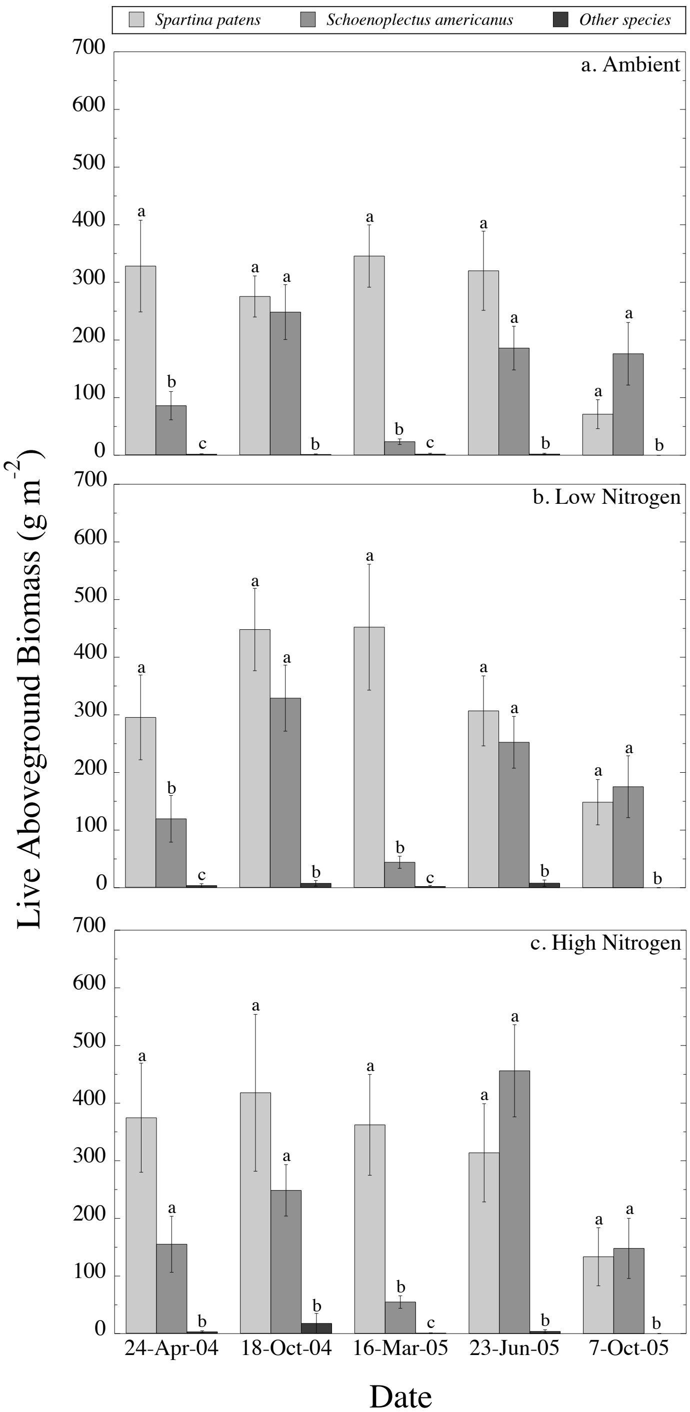

Figure 7. Result of N-loading treatments on interspecific differences in live standing crop. Bars represent means ± standard error of live standing crop (g m^{-2}) for *Spartina patens*, *Schoenoplectus americanus* and all other species present under the (a) ambient, (b) low and (c) high N-loading treatments. Different superscripted letters denote significant interspecific differences within N-loading treatments based on Bonferroni multiple comparisons. Sample size decreased on 29 August 2005 (see Appendix 10a and 11a).

Plant Community Composition

The N-loading treatments resulted in significant increases in *S. patens* live ($p<0.0001$, F=31.9) and total cover ($p<0.0001$, F=27.7, Appendix 12). Contrary to the consistent response of *S. patens* cover, the effects of N-loading treatments on *S. americanus* cover fluctuated between sample periods. In June 2005, the high N-loading treatment resulted in an increase in *S. americanus* live (p=0.033) and total cover (p=0.03, Appendix 13) although this was not sustained. The N-loading treatments did not favor either *S. patens* or *S. americanus*. Under ambient nitrogen availability, *S. americanus* had greater live cover than *S. patens* in October 2005 (p=0.001) and March 2006 (p=0.001, Figure 8a). Although the low N-loading treatment consistently increased *S. patens* live cover (see Appendix 12a), low N-loading only resulted in an increase in *S. patens* over *S. americanus* in March 2005 (p=0.005, Figure 8b). Similarly, under the high N-loading treatment, *S. americanus* displayed greater live cover than *S. patens* only in October 2005 (p=0.032, Figure 8c).

Species Richness

The greatest species richness occurred in plots receiving the low N-loading treatment during two sample periods. One year after the initial treatment application, in June 2005, the low N-loading treatment resulted in a 28.3% increase in species richness over the ambient N-loading treatment (p=0.013, Appendix 14). In October 2005 (Post-Hurricane Katrina), the low N-loading treatment resulted in a 24% increase in species richness over plots receiving the high N-loading treatment (p=0.042).

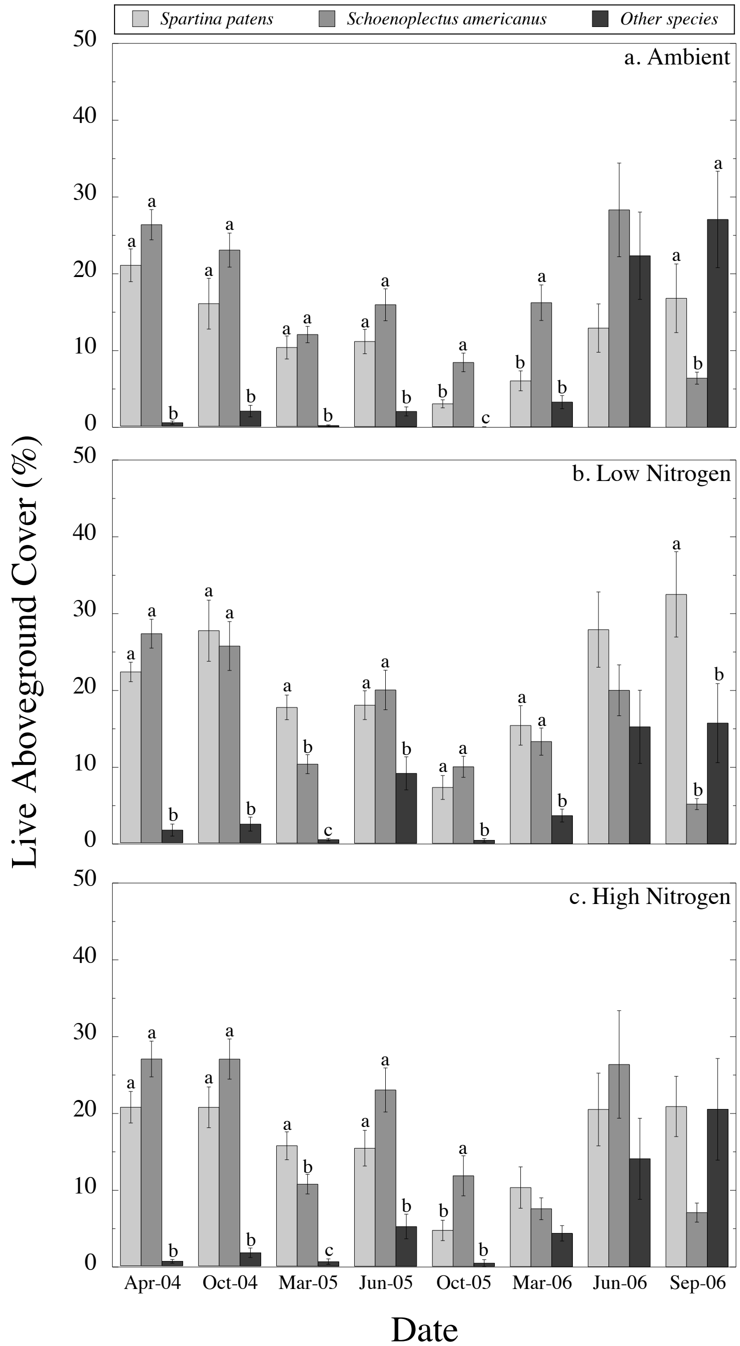

Figure 8. Result of increasing N-loading treatments on interspecific differences in aboveground plant community composition. Bars represent means ± standard error of *Spartina patens*, *Schoenoplectus americanus* and all other species live cover (% m^{-2}) under the (a) ambient, (b) low and (c) high N-loading treatments. Different superscripted letters denote significant interspecific differences within N-loading treatments based on Bonferroni multiple comparisons. Sample size decreased on 29 August 2005 (see Appendix 12 and 13).

Responses to Lethal Disturbance

Mean Stem Height

The lethal disturbance treatment (herbicide) resulted in a decrease in mean stem height of both *S. patens* and *S. americanus*. Initially, *S. patens* experienced a delayed decrease in mean stem height. Three months after lethal treatment application, the lethal disturbance resulted in a 44.4% decrease in *S. patens* mean stem height from 50.2 cm under the non-disturbance treatment to 27.9 cm under the lethal disturbance (p=0.24, Appendix 15a). During the second growing following, the response of *S. patens* stem height to the lethal disturbance was significant and showed no signs of recovery. In March 2005, the lethal disturbance resulted in a 92.5% decrease in *S. patens* mean stem height from 48.0 cm under the non-disturbance treatment to 3.6 cm under the lethal disturbance (p=0.001). Subsequently, the lethal disturbance resulted in a 100% decrease in *S. patens* mean stem height in both June (p=0.0005) and October 2005 (p=0.03).

Contrary to the delayed response experienced by *S. patens*, *S. americanus* response to lethal disturbance was immediately evident three months after lethal treatment application (Appendix 15b). However, recovery from the lethal disturbance was evident within one year of the initial application. By June 2005, *S. americanus* mean stem height in the lethal treatment plots increased to 32.3 cm which was no longer significantly different from reference treatment height. Whereas the lethal disturbance treatment resulted in a decrease in mean stem height for both *S. patens* and *S. americanus*, the interspecific differences in mean stem height fluctuated seasonally in the non-disturbance reference plots (Figure 9).

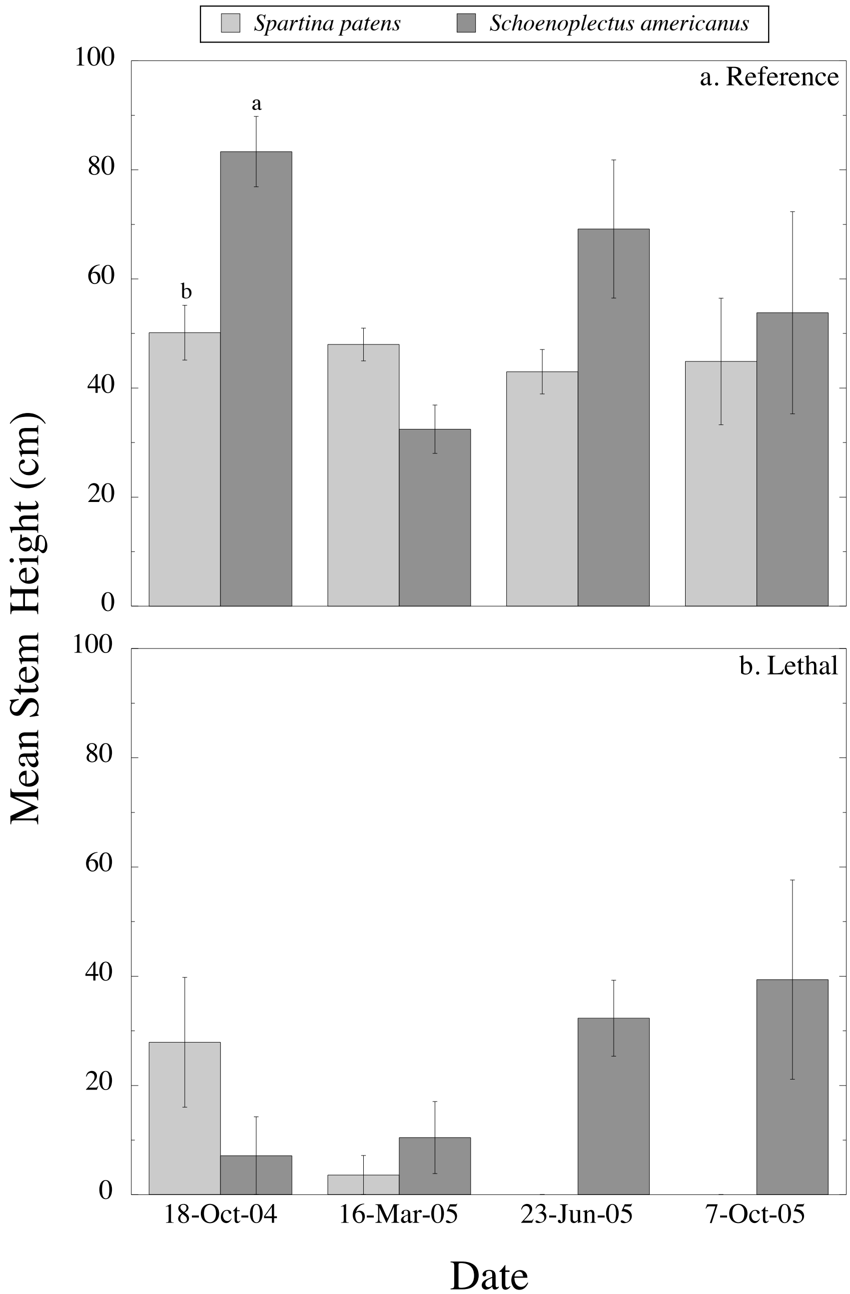

Figure 9. Interspecific responses in mean stem height to disturbance treatments. Bars represent means ± standard error of *Spartina patens* and *Schoenoplectus americanus* mean stem height (cm) under the (a) non-disturbance reference and (b) lethal disturbance treatments. Different superscripted letters denote significant interspecific differences within disturbance treatments based on Bonferroni multiple comparisons. Sample size decreased on 29 August 2005 (see Appendix 15).

Primary Productivity

The lethal treatment resulted in a significant decrease of *S. patens* live productivity from pre-disturbance conditions (p=0.0034, F=7.2, Appendix 16a). Prior to the lethal treatment application, in April 2004, *S. patens* produced 401.6 g m^{-2} of live biomass in the lethal plots. Three months after the lethal treatment application (October 2004) *S. patens* live biomass decreased significantly by 87% to 30.4 g m^{-2} (p=0.03). Compared to the non-disturbance reference plots, the lethal disturbance treatment resulted in a significant decrease in *S. patens* live biomass during all four sample periods following treatment application with a 100% decrease in *S. patens* live biomass evident throughout 2005. Similar to the response of *S. patens*, the lethal disturbance treatment also resulted in a significant decrease in *S. americanus* live biomass production with a 100% decrease evident by October 2004 (p=0.004, Appendix 17a). Contrary to the prolonged negative effects of the lethal treatment on *S. patens* live biomass, *S. americanus* showed signs of recovery by June 2005. One year after the lethal treatment application, in June 2005 *S. americanus* live biomass showed signs of growth and increased productivity to 108.8 g m^{-2}. Although 46.5% less than 203.2 g m^{-2} of *S. americanus* live biomass in the non-disturbance treatment, the difference was not significantly different (p=0.19). Similar to the seasonal fluctuations in mean stem height, *S. patens* and *S. americanus* also experienced seasonal fluctuations in live biomass production under the non-disturbance reference treatment (Figure 10).

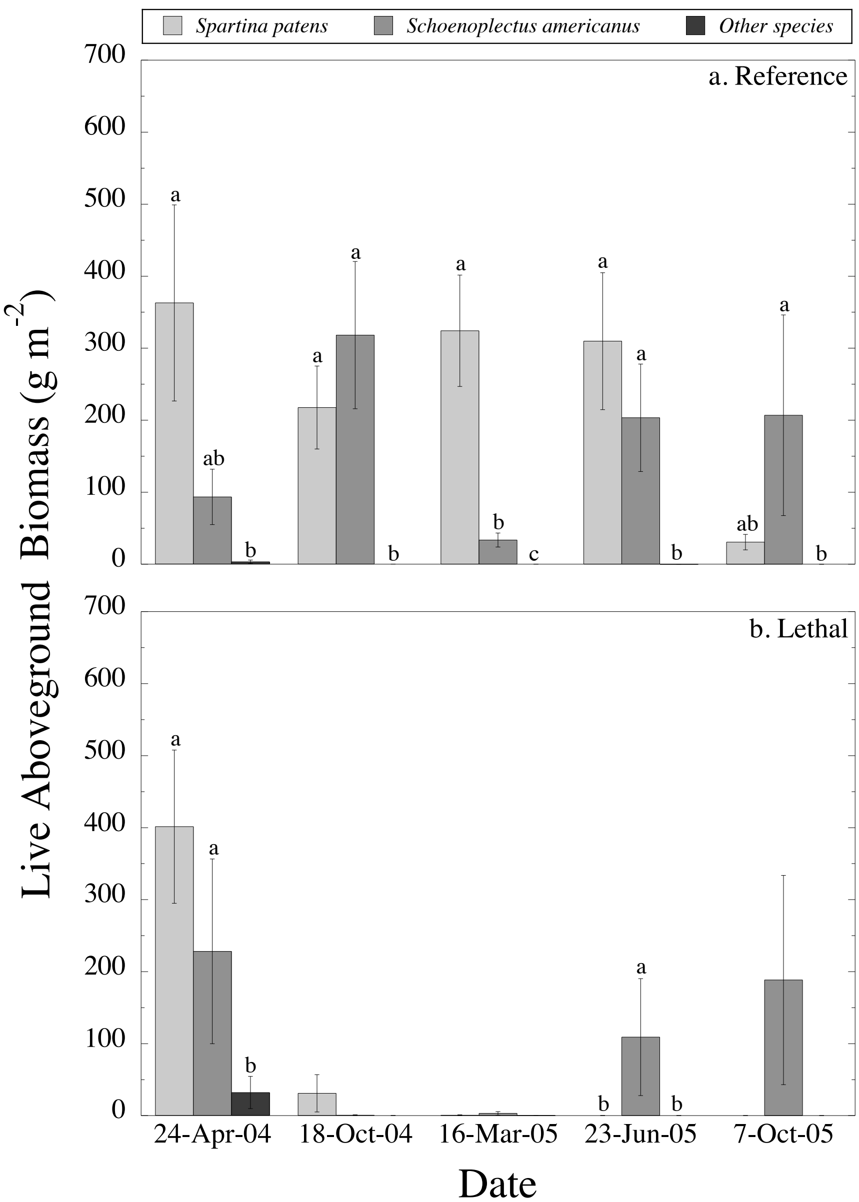

Figure 10. Interspecific differences in response of live standing crop to disturbance treatments. Bars represent means + standard error of *Spartina patens*, *Schoenoplectus americanus* and all other species live aboveground biomass (g m^{-2}) under the (a) reference (no disturbance) and (b) lethal disturbance treatments. Different superscripted letters denote significant interspecific differences within disturbance treatments based on Bonferroni multiple comparisons. Sample size decreased on 29 August 2005 (see Appendices 16a and 17a).

Plant Community Composition

The lethal disturbance treatment resulted in a significant decrease in live cover for both *S. patens* (*p*=0.002, Appendix 18) and *S. americanus* (*p*=0.002, Appendix 19). In October 2004, three months after treatment application, the lethal treatment resulted in a 99.9% decrease in *S. patens* (*p*=0.05) and a 99.1% decrease in *S. americanus* live cover (*p*=0.03). Neither of the co-dominant species dominated the plots receiving the lethal treatment except in March 2006, when *S. americanus* live cover at 2.3% m^{-2} was significantly greater than *S. patens* (*p*=0.037, Figure 11a). Neither species showed signs of recovery to pre-disturbance conditions in either 2005 or 2006. In addition, neither species dominated the plant community under the non-disturbance reference treatment (Figure 11b). However, *Eleocharis parvula* dominated the lethal disturbance plots by June 2006 (p=0.03, Figure 11b).

Species Richness

Species richness of the plant community composition plots did not exhibit consistent responses to the lethal disturbance treatment. The only significant response occurred in September 2006 when the lethal treatment resulted in a 67.1% decrease in species richness from 3.8 species per plot (including *Andropogon* sp., *Aster subulatus*, *Lythrum lineare*, *S. americanus*, *S. patens*, *Sesbania macrocarpa* and *Vigna luteola*) in the non-disturbance treatment to 1.3 species per plot (mainly *Eleocharis parvula* with small amounts of *A. subulatus*, *S. americanus* and *S. patens*) under the lethal disturbance treatment (*p*=0.02, Appendix 20).

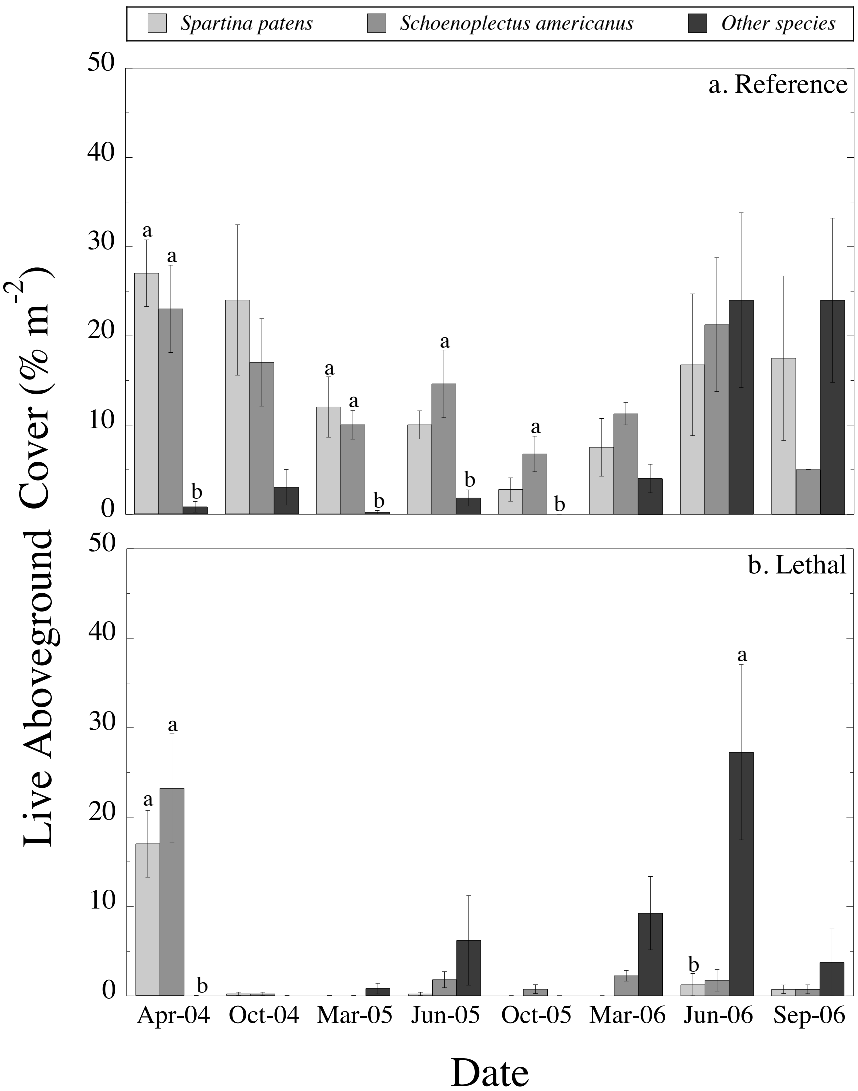

Figure 11. Interspecific differences in live aboveground plant community in response to disturbance treatments. Bars represent means + standard error of *Spartina patens*, *Schoenoplectus americanus* and all other species live cover (% m^{-2}) under the (a) reference (no-disturbance) and (b) lethal disturbance treatments. Different superscripted letters denote significant interspecific differences within disturbance treatments based on Bonferroni multiple comparisons. Sample size decreased on 29 August 2005 (see Appendices 18 and 19).

Responses of the Plant Community to Multiple Disturbances

During the first two years of the study, six tropical disturbances impacted the coastal wetlands along the Northern Gulf of Mexico (Appendix 21). Of those six tropical disturbances, four hurricanes and one tropical storm resulted in a combination of prolonged flooding, wrack deposition and eventual erosion of the vegetated marsh surface of the research site at Big Branch Marsh NWR. Contrary to the homogeneity of the lethal disturbance treatment, individual hurricanes did not result in uniform disturbance of the permanent research plots.

Atlantic Hurricane Season of 2004

In 2004, Hurricane Ivan and Tropical Storm Matthew produced flooded conditions and resulted in the deposition of wrack on some of the experimental plots (Figure 12). Whereas P-loading treatments did not result in an increase in *S. patens* live biomass in October 2004, *S. americanus* experienced an increase in live biomass from pre-treatment conditions under all three P-loading treatments (p=0.009, F=107). Interestingly, P-loading did not significantly affect cover of either species (Figures 13a and 13b). Both species experienced an increase in live standing crop from the pre-treatment conditions under the low N-loading treatment. *S. patens* live biomass increased from 290 g m^{-2} in April 2004 to 448 g m^{-2} in October 2004 (p=0.037). *S. americanus* experienced an increase in live biomass from 85 to 248 g m^{-2} under the ambient (p=0.017) and from 118 to 328 g m^{-2} under the low N-loading treatments (p=0.002). However, the N-loading treatments did not result in an increase in live cover from April to October 2004 for either species (Figures 13c and 13d).

Figure 12. Wrack deposition from Hurricane Ivan and Tropical Storm Matthew. In 2004 the wrack deposition was not uniform on experimental plots. The plant and other debris were removed from experimental plots to prevent obfuscation of nutrient loading treatments.

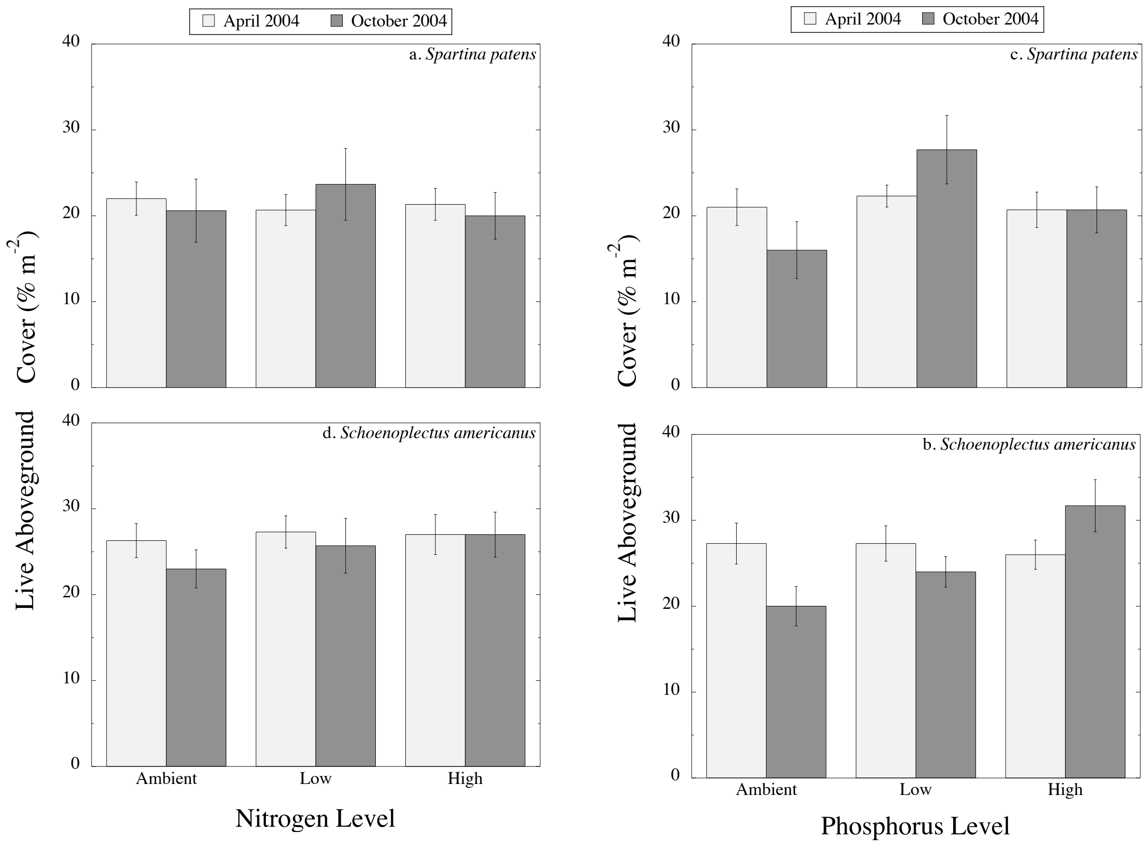

Figure 13. Pre- and post-Hurricane Ivan and T.S. Matthew live cover under increasing nutrient-loading treatments. Bars represent means ± standard error of live aboveground cover (% m^{-2}) for *Spartina patens* (a, c) and *Schoenoplectus americanus* (b, d) under increasing P- and N-loading treatments. Different superscripted letters denote significant intraspecific differences between April and October 2004 within P-loading treatment based on Bonferroni multiple comparisons.

Atlantic Hurricane Season of 2005

The most infamous disturbance impacting the research site, Hurricane Katrina, occurred on 29 August 2005. Hurricane Katrina's storm surge eroded the large portions of marsh surface and resulted in the formation numerous interior ponds at Big Branch Marsh NWR (Figure 14). Twenty-two percent of the permanent research plots were also enveloped in the 10-acre interior pond formed adjacent to the research site (Figure 15) and the remaining research plots received considerable deposition. Entire sods of vegetated marsh surface and *S. patens* "marsh balls" of various size were strewn across the research plots (Figure 16). Deposition on the remaining plots averaged 27 cm on the community composition plots (see Table 1).

Following Hurricane Katrina, both *S. patens* and *S. americanus* experienced decreases in live productivity and cover under nutrient loading treatments from the pre-Hurricane conditions of June 2005. *S. patens* experienced a significant decrease in live biomass under the ambient P-loading treatment ($p<0.0001$) whereas *S. americanus* live biomass decreased significantly under both the ambient ($p=0.045$) and high P-loading treatments ($p=0.032$). Although *S. patens* only experienced a decrease in live biomass under the ambient P-loading treatment, *S. patens* live cover experienced a significant decrease in live cover under all P-loading treatments ($p=0.02$, $F=53$, Figure 17a). *S. americanus* live cover experienced a significant decrease from June to October 2005 under the ambient ($p=0.002$) and high P-loading treatments ($p=0.002$, Figure 17b). The co-dominant species experienced similar decreases in live biomass and cover following Hurricane Katrina under the N-loading treatments. *S. patens* experienced significant decrease in live biomass under the ambient N-loading treatment ($p=0.002$) whereas

Figure 14. Interior pond formation along Bayou Lacombe at Big Branch Marsh NWR. The (a) pre-Katrina image shows the vegetated marsh surface along Bayou Lacombe (courtesy of **www.lacoast.gov**) whereas (b) shows the numerous interior ponds present after Hurricane Katrina (courtesy of **www.ngs.noaa.gov**).

Figure 15. Interior pond adjacent to experimental plots. Following Hurricane Katrina, a ten-acre interior pond was present adjacent to the permanent research plots (above). The ten permanent research plots belonging to Block 4 were enveloped in the pond (below) therefore were not included in the analyses after 29 August 2005.

Figure 16. Hurricane Deposition. (a) Small sods of *S. patens* “marsh balls” were removed from plots, however (b) the larger sods of vegetated marsh surface were left in place.

S. americanus live biomass decreased significantly under the high N-loading treatment (p=0.001). From June to October 2005, both *S. patens* (p=0.001, Figure 17c) and *S. americanus* (p=0.008, Figure 17d) experienced significant decreases in live cover under all three N-loading treatments.

Recovery of the Plant Community from Multiple Disturbances

Contrary to the plots receiving the lethal treatment application (see Figure 11a), all other experimental plots showed signs of recovery in 2006 from the multiple hurricane disturbances of 2005. By September 2006, there was an increase in species richness (Table 3), and *S. patens* displayed significantly greater live cover than *S. americanus* (Figure 18). Further, a significant positive relationship (p= 0.0001; R^2 = 0.351) was detected between marsh surface relative elevation post-Hurricane Katrina (October 2005) and plant community species richness (number of species per plot) the following year (June 2006; Figure 19). Similarly, a significant positive effect of change in elevation was found in regard to the change in plot species richness (P= 0.0327, R^2 =0.1174; Figure 20), indicating that additional species were recruiting into the higher elevation sites post Hurricane Katrina. Opportunistic species, such *Sesbania macrocarpa*, and *Solidago sempervirens,* were among those new species recruiting into the disturbed, higher elevation sites (Table 3). Although no significant linear effect of change in elevation was found in regard to vegetative cover of either *S. patens* (p=0.492, R^2= 0.013) or *S. americanus* (p= 0.380, R^2 = 0.021) individually during this same period (Appendix 22), elevation increase during this time interval was associated with a linear increase in vegetative cover of all other species (p= 0.053, R^2 =0.192).

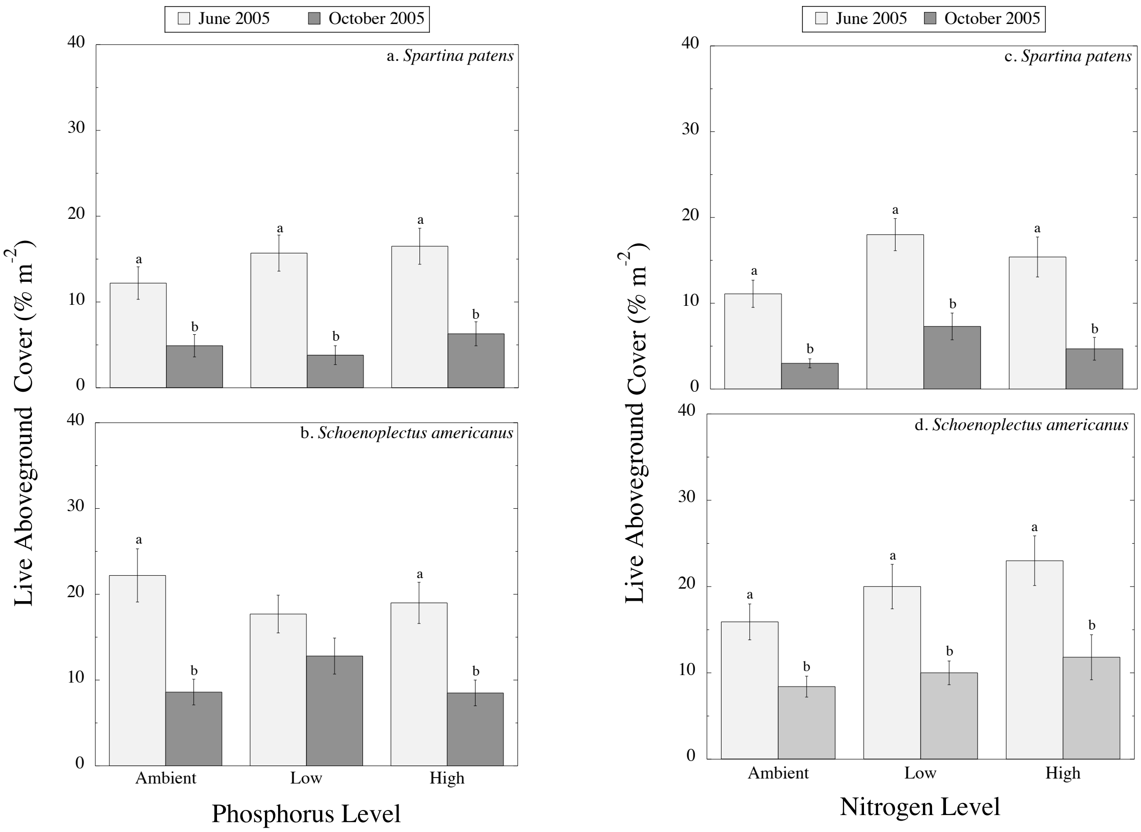

Figure 17. Pre- and post-Hurricane (Cindy, Katrina and Rita) live cover under increasing nutrient-loading treatments. Bars represent means $\pm$ standard error of live cover (% m^{-2}) for *Spartina patens* (a, c) and *Schoenoplectus americanus* (b, d) under increasing P- and N-loading treatments. Different superscripted letters denote significant intraspecific differences between June and October 2005 within P-loading treatment. Sample size decreased on 29 August 2005 (see Appendices 3, 4, 5 and 6).

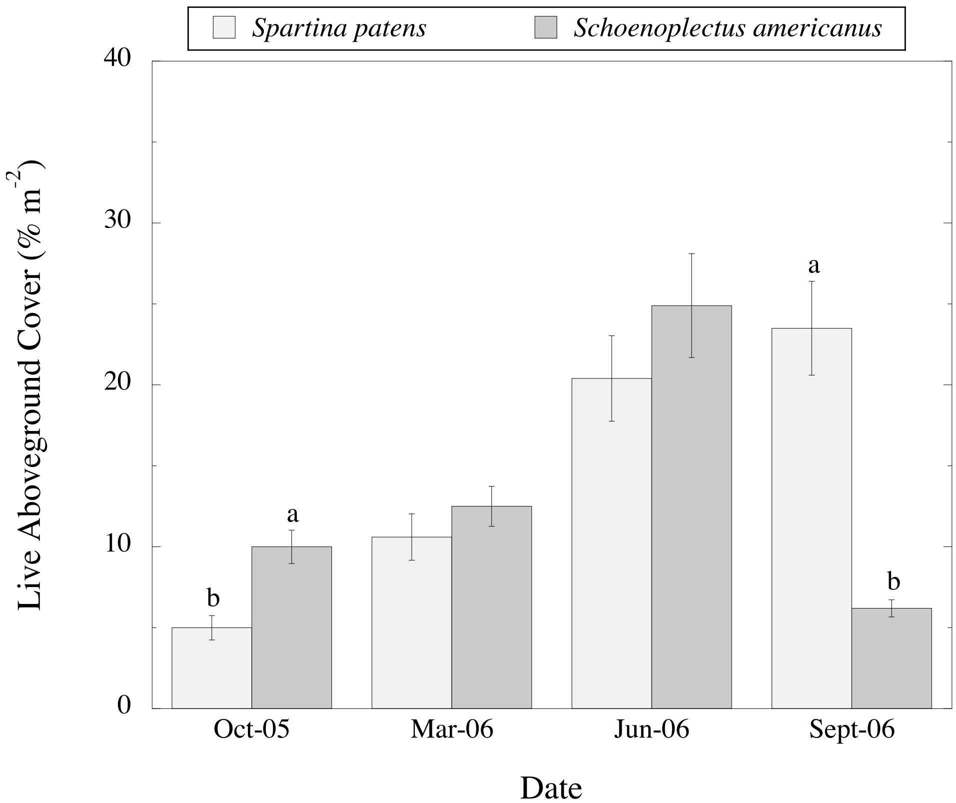

Figure 18. Recovery of aboveground cover from multiple hurricane disturbances. Bars represent means ± standard error of *Spartina patens* and *Schoenoplectus americanus* live aboveground cover (% m^{-2}) for all remaining plots (post-Hurricane Katrina) that had received the nutrient-loading treatments during the first two years of the study (n=34). Nutrient-loading treatments were not applied in 2006.

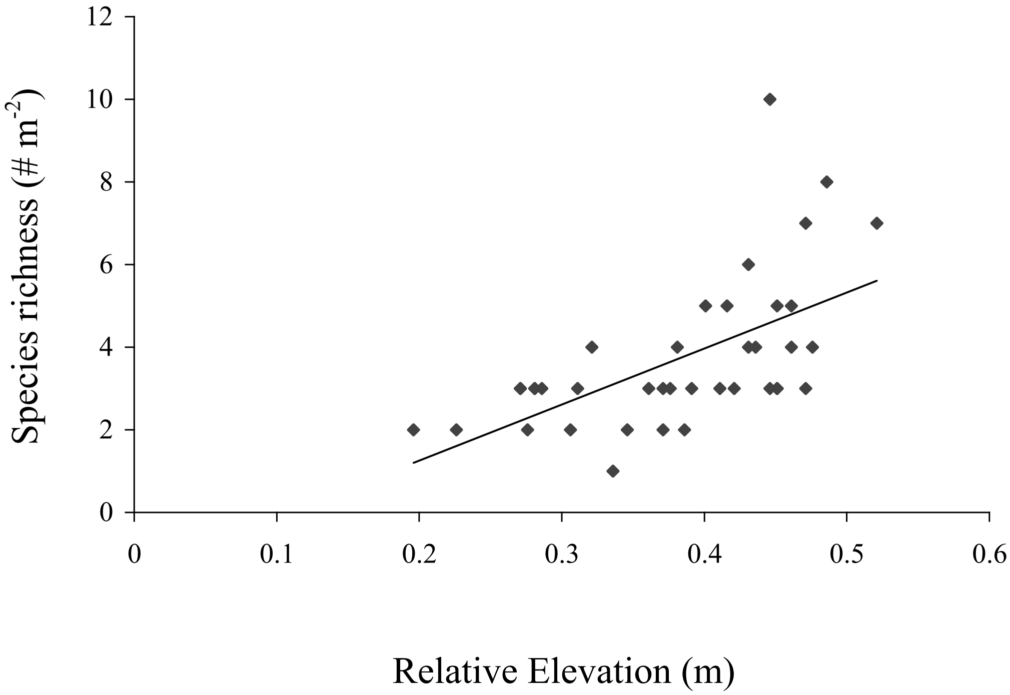

Figure 19. The significant positive relationship (p=0.0001; R^2 = 0.351) between marsh surface relative elevation post Hurricane Katrina (October 2005) and plant community species richness (number of species per plot) the following year (June 2006).

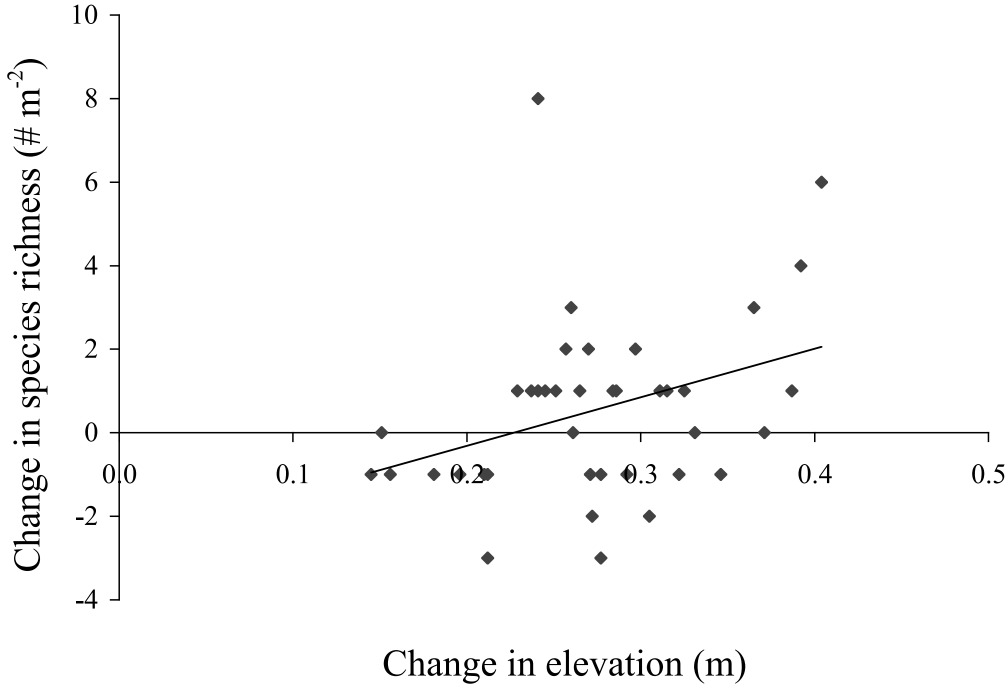

Figure 20. The effect of change in marsh surface relative elevation prior to (October 2004) and after Hurricane Katrina (October 2005) on the change in plant community species richness (number of species per plot) from October 2004 to September 2006 (p=0.033; R^2 = 0.117).

Table 3. Summary of emergent species present in the plant community composition plots. Mark indicates presence in 1m x 1m aboveground plant community composition plots during indicated sample period.

Scientific Name	Apr-04	Oct-04	Mar-05	Jun-05	Oct-05	Mar-06	Jun-06	Sep-06
Amaranth spp.				X		X	X	X
Andropogon spp.							X	
Aster subulatus	X	X	X	X	X	X	X	X
Bacopa spp.								X
Cyperus spp.				X		X	X	X
Echinochloa walteri							X	X
Eleocharis parvula				X		X	X	X
Galium tinctorium	X			X		X		X
Hibiscus grandifloras							X	
Ipomoea sagittata	X	X		X		X	X	X
Lythrum lineare	X		X	X	X	X	X	X
Pluchea camphorata								X
Polygonum spp.				X		X	X	X
Ptilimnium costatum						X		X
S. americanus	X	X	X	X	X	X	X	X
Sesbania macrocarpa							X	X
Solidago sempervirens						X		X
S. patens	X	X	X	X	X	X	X	X
Vigna luteola				X		X	X	X

DISCUSSION

Previous research has reported that oligohaline marsh plant communities may be co-limited by nitrogen and phosphorus (Crain 2007). Results from this study did not support our hypothesis that phosphorus and nitrogen availability co-limit the oligohaline plant community at Big Branch Marsh NWR in Southeastern Louisiana. Contrary to the hypothesis, individual nutrient additions resulted in significant responses of aboveground vegetative conditions. However, responses to individual nutrient addition treatments were not always uniformly expressed in the aboveground productivity (clip) plots and community composition (non-clipped) plots. Although these two types of sub-plots were located within one meter of each other (each within the larger treatment plots), small-scale heterogeneity with the marsh was present and may have been due to nutria activity and other stochastic events. Therefore, we believe that the aboveground community composition (% cover) plots are the best of the pair to use for interpretation of vegetative change over time since the same (1m x 1m) area was always censured, whereas the same exact area was never clipped more than once in the productivity plots.

Previous research on the responses of aboveground plant community to P-loading treatments have found that an increase in phosphorus availability results in an increase in leaf tissue [P], stem height and productivity for the flood tolerant *Typha* species (CRAFT et. al 1995, NEWMAN et al. 1996, MACEK and REJMANKOVA 2007). In March 2005, the high P-loading treatment resulted in significant increases in *S. patens* leaf tissue [P] (Appendix 1a) and mean stem height (Appendix 2a). However, the P-loading treatments did not result in an increase in *S. patens* productivity (Appendix 3) or cover (Appendix 5) during any time period. Similarly, the P-loading treatments did not increase in *S.*

americanus leaf tissue [P] (Appendix 1b) or mean stem height (Appendix 2b) but did result in an increase live cover in October 2004 (Appendix 6) and live biomass in March 2005 (Appendix 4). Although *S. americanus* is the more flood tolerant of the two species (BROOME et al. 1995) it did not experience preferential growth under the P-loading treatments.

Previous research on the responses of the aboveground plant community to N-loading treatments have reported that an increase in nitrogen availability results in an increase in stem height, productivity and an expansion of the low marsh species into the high marsh zone (LEVINE et al. 1998, EMERY et al. 2001, PENNINGS et al. 2005b). In October 2004 the high N-loading treatment resulted in an increase in leaf tissue [N] for both *S. patens* and *S. americanus* (Appendix 9). However, the high N-loading treatment did not result in parallel increases in mean stem height, biomass or cover for either species. Instead, the low N-loading treatment resulted in significant increases in *S. patens* mean stem height and cover. Whereas the increase in mean stem height occurred only once, the increase in *S. patens* live cover under the low N-loading treatment continued the duration of the experiment. Although *S. americanus* is more flood tolerant than *S. patens* (BROOME et al. 1995) the N-loading treatment did not result in a consistent increase in *S. americanus* cover and biomass. One possibility for the lack of increase in *S. americanus* may be nutria herbivory as the experimental plots were not enclosed.

Contrary to the hypothesis, the nutrient loading did not result in a shift in plant community composition favoring the more flood tolerant *S. americanus*. The significant interspecific differences in vegetative conditions reflected seasonal fluctuations between the co-dominant species such that early emergence favored *S. patens* in the spring

whereas *S. americanus* dominated the latter portion of the growing season regardless of nutrient-loading treatments (Figures 2, 3, 4, 6, 7, and 8). It was also expected that an increase in site fertility would result in a decrease in species richness (BERTNESS 2002, KEDDY 1990). However, the nutrient loading treatments did not result in a significant decrease in species richness. On the contrary, species richness was greatest in October 2004 under the high P-loading treatment and in June and October 2005 species richness was greatest under the low N-loading treatment. However, at the end of the study there were no significant differences.

Results from the disturbance aspect of this study did support the hypothesis that disturbance results in a significant reduction in aboveground vegetative cover and biomass. The lethal treatment resulted in significant decreases in mean stem height (see Figure 9, Appendix 15), standing crop (see Figure 10, Appendices 16 and 17) and cover for both *S. patens* and *S. americanus* (see Figure 11, Appendices 18 and 19). However, within one year of the herbicide application, both *S. americanus* stem height and productivity (Figures 9 and 10) and *Eleocharis parvula* cover showed significant signs of recovery from the lethal disturbance treatment, which indicates these two species are very resilient to disturbance. This recovery contradicts findings from a nearby marsh on Lake Pontchartrain's north shore where the plant community showed little signs of resiliency from lethal disturbance treatment (BALDWIN and MENDELSSOHN 1998); however, *Sagittaria lancifolia* and *S. patens* were the dominant species at this other site with *S. americanus* absent. However, another *Eleocharis* species, *Eleocharis fallax*, showed signs of recovery from the lethal disturbance (BALDWIN and MENDELSSOHN 1998). The practice of marsh burning, also a type of disturbance, is recognized for favoring regrowth

and dominance of *S. americanus* over *S. patens*, and is often used a management strategy, especially in regard to increasing numbers and visibility of fur-bearing animals for harvest (Chabreck 1975).

Subsequently, the multiple hurricane disturbances in 2005 also resulted in a decrease prevalence of *S. patens* and *S. americanus*. Hurricane Katrina's storm surge formed countless *S. patens* "marsh balls" that were strewn across the landscape. Marsh balls were physically scoured and removed from a previously vegetated marsh surfaces and relocated to adjacent bodies of water, structures and, in some instances, landed on experimental plots along Bayou Lacombe in Big Branch Marsh (see Figure 16a). Excessive rainfall from Hurricanes Katrina and Rita north of the research site likely reduced salinity levels and salinity levels did not exceed lethal levels for either of the co-dominant species in October 2005. Contrary to *S. americanus* recovery from the lethal disturbance, *S. patens* experienced preferential recovery from the 2005 Atlantic Hurricane Season. In September 2006, one year after Hurricanes Cindy, Katrina and Rita, *S. patens* dominated the plant community under all nutrient-loading treatments (see Figure 18). The most probable explanation is that less the flood tolerant *S. patens* (BROOME et al. 1995) benefited from the average of 27 cm of hurricane-deposited sediment that resulted in less frequently flooded elevations (see Table 1). The sediment deposition also resulted in an increase in soil bulk density, oxidation-reduction potentials, and decreased interstitial pH (see Table 1). As deposition increased elevation, the duration of flooding decreased resulting in more oxidized conditions, as evident in the higher redox potentials in 2006. Under the more oxidized conditions there is an

accelerated rate of decomposition of the newly deposited organic matter in the hurricane sod deposits which likely resulted in the decrease in interstitial pH.

The increase in elevation that resulted from sediment deposition post-Hurricane Katrina resulted in an increase in species richness and total cover by 2006. As elevation increased, flooding stress was decreased, which would favor the recruitment of less flood-tolerant species and the creation of relatively open colonization sites for opportunistic species recruitment. For example, at lower elevation site species such as *Eleocharis parvula* increased in prevalence, whereas at the higher elevation sites, less flood-tolerant, opportunistic species such as *Solidago sempervirens* and *Sesbania macrocarpa* increased in prevalence. Interestingly, small positive changes in elevation actually resulted in a decrease in species richness, but as the elevation further increased, species richness increased significantly (Figure 20). This indicates that small amounts of sediment addition favored the previously existing co-dominants of the community (*S. patens* and *S. americanus*), and that it wasn't until significant sediment deposition occurred (change in relative elevation of greater than + 22 cm) that recruitment of new species into less flooded, disturbed areas with favorable open microsites for colonization was favored (PICKET 1980, SOUSA 1984, PETERSON and BALDWIN 2004, ROXBURGH et al. 2004).

CONCLUSION

Results from the nutrient-loading aspect of this study support findings that individual plant species do not show predictable responses to nutrient additions and that responses to nutrient-loading treatments may depend on geographic location. In addition,

prolonged flooding, deposition (wrack, sediments and sods of varying size) and erosion made the task of isolating nutrient treatments challenging. The effects of nutrient loading on vegetative conditions were likely masked by the above normal frequency and intensity of two consecutive years of relatively high tropic storm and hurricane activity in the area. The incongruities between intraspecific and interspecific responses to nutrient loading treatments are likely a reflection of the heterogeneity of the multiple hurricanes impacting the region during the first two years of the study. Although *S. patens* dominated the plant community by the end of the third year following an elevation increase from hurricane-deposited sediments, as compaction of sediments occurs *S. americanus* will likely resume co-dominant status. Similarly, the increase in species richness following disturbance and elevation increase due to storm-related sediment deposition will likely diminish over time. Our results, in conjunction with other literature, suggest that *S. americanus* is more resilient to disturbance as may occur with marsh burning and other disturbances that do not translate into an increase in marsh surface elevation. In subsiding, oligohaline to mesohaline marshes of this type, we anticipate that *S. americanus* will again increase in dominance over *S. patens* as frequency, depth and duration of flooding increases over time.

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Appendix 1. Result of phosphorus loading treatments on leaf tissue phosphorus concentration. Values are the mean ± standard error of leaf tissue phosphorus [P] concentration (mg/kg) for (a) *Spartina patens* and (b) *Schoenoplectus americanus* under the ambient (O), low (P) and high (PP) phosphorus loading treatments followed by sample size (n) in parentheses. Within each species sample period, means having different superscripted letters are significantly different.

		Phosphorus Loading Treatment		
Species	Date	O	P	PP
a. *Spartina*				
	18-Oct-04	$2.44^{A} \pm 0.30$ (15)	$2.06^{A} \pm 0.27$ (14)	$2.41^{A} \pm 0.25$ (15)
	16-Mar-05	$3.67^{B} \pm 0.23$ (10)	$3.63^{B} \pm 0.26$ (10)	$4.18^{A} \pm 0.20$ (10)
b. *Schoenoplectus*				
	18-Oct-04	$2.61^{A} \pm 0.20$ (15)	$3.14^{A} \pm 0.32$ (13)	$3.01^{A} \pm 0.29$ (14)
	16-Mar-05	$8.95^{A} \pm 0.18$ (8)	$9.15^{A} \pm 0.60$ (9)	$8.91^{A} \pm 0.39$ (9)

Appendix 2. The results of P-loading treatments on mean stem height following treatment application. Values represent the mean ± standard error of (a) *Spartina patens* and (b) *Schoenoplectus americanus* mean stem height (cm) under the ambient (O), low (P) and high (PP) phosphorus-loading treatments followed by sample size (n) in parenthesis. Within each species sample period, means having different superscripted letters are significantly different.

		Phosphorus Loading Treatment		
Species	Date	O	P	PP
a. *Spartina*				
	18-Oct-04	55.4^{A} ± 4.27 (15)	58.1^{A} ± 3.57 (15)	60.5^{A} ± 3.12 (15)
	16-Mar-05	44.4^{AB} ± 2.84 (15)	42.8^{B} ± 3.85 (15)	54.3^{A} ± 2.48 (15)
	23-Jun-05	42.6^{A} ± 1.83 (15)	39.2^{A} ± 2.46 (15)	44.9^{A} ± 2.69 (15)
	7-Oct-05	40.9^{A} ± 5.92 (11)	32.1^{A} ± 5.89 (12)	40.0^{A} ± 6.69 (12)
	Mean	45.8^{A} ± 3.27	43.0^{A} ± 5.48	49.9^{A} ± 4.62
b. *Schoenoplectus*				
	18-Oct-04	70.5^{A} ± 5.10 (15)	52.4^{A} ± 6.18 (15)	60.5^{A} ± 4.24 (15)
	16-Mar-05	34.9^{A} ± 3.35 (15)	26.8^{A} ± 4.46 (15)	31.7^{A} ± 3.12 (15)
	23-Jun-05	66.5^{A} ± 5.98 (15)	53.8^{A} ± 8.37 (15)	70.9^{A} ± 3.95 (15)
	7-Oct-05	52.7^{A} ± 11.4 (11)	52.0^{A} ± 7.94 (12)	48.6^{A} ± 8.89 (12)
	Mean	56.2^{A} ± 8.04	46.3^{A} ± 6.5	52.9^{A} ± 8.4

Appendix 3. The results of P-loading treatments on *Spartina patens* live standing crop following treatment application. Data were ln(x+1) transformed prior to analysis to reduce heterogeneity of variance then de-transformed for presentation. Values represent mean ± standard error of *Spartina patens* (a) live, (b) dead and (c) total biomass (g 0.25 m^{-2}) in the ambient (O), low (P) and high (PP) phosphorus-loading treatments followed by sample size (n) in parentheses. Within each productivity type's sample period, means having different superscripted letters are significantly different.

		Phosphorus Loading Treatment		
Type	Date	O	P	PP
a. Live Biomass				
	18-Oct-04	19.6^{A} ± 4.2 (15)	28.6^{A} ± 7.1 (15)	23.1^{A} ± 5.6 (15)
	16-Mar-05	19.4^{A} ± 3.5 (15)	22.1^{A} ± 5.6 (15)	31.0^{A} ± 6.4 (15)
	23-Jun-05	21.0^{A} ± 2.9 (15)	20.8^{A} ± 6.1 (15)	17.0^{A} ± 3.8 (15)
	7-Oct-05	4.8^{A} ± 1.6 (11)	7.8^{A} ± 2.2 (12)	9.2^{A} ± 3.2 (12)
	Mean	16.2^{A} ± 3.8	19.8^{A} ± 4.4	20.1^{A} ± 4.6
b. Dead Biomass				
	18-Oct-04	49.9^{A} ± 12.6 (15)	61.3^{A} ± 9.6 (15)	48.6^{A} ± 6.9 (15)
	16-Mar-05	57.0^{A} ± 8.9 (15)	41.5^{A} ± 10.0 (15)	63.5^{A} ± 8.6 (15)
	23-Jun-05	45.6^{A} ± 5.8 (15)	32.4^{A} ± 7.0 (15)	27.3^{A} ± 5.7 (15)
	7-Oct-05	15.7^{A} ± 6.0 (11)	30.3^{A} ± 12.3 (12)	17.5^{A} ± 6.5 (12)
	Mean	42.0^{A} ± 9.1	41.4^{A} ± 7.1	39.2^{A} ± 10.4
c. Total Biomass				
	18-Oct-04	69.5^{A} ± 15.4 (15)	89.9^{A} ± 12.9 (15)	71.7^{A} ± 10.3 (15)
	16-Mar-05	76.4^{AB} ± 11.1 (15)	63.6^{B} ± 14.2 (15)	94.5^{A} ± 12.0 (15)
	23-Jun-05	66.6^{A} ± 7.5 (15)	53.2^{A} ± 12.7 (15)	44.4^{A} ± 8.5 (15)
	7-Oct-05	20.5^{A} ± 6.4 (11)	38.1^{A} ± 14.2 (12)	26.7^{A} ± 9.3 (12)
	Mean	58.2^{A} ± 12.8	61.2^{A} ± 10.9	59.3^{A} ± 14.9

Appendix 4. The results of P-loading treatments on *Schoenoplectus americanus* live standing drop following treatment application. Data were ln(x+1) transformed prior to analysis to reduce heterogeneity of variance then de-transformed for presentation. Values represent mean ± standard error of *Schoenoplectus americanus* (a) live, (b) dead and (c) total biomass (g 0.25 m^{-2}) in the ambient (O), low (P) and high (PP) phosphorus-loading treatments followed by sample size (n) in parentheses. Within each productivity type's sample period, means having different superscripted letters are significantly different.

		Phosphorus Loading Treatment		
Type	Date	O	P	PP
a. Live	Biomass			
	18-Oct-04	19.8^{A} ± 3.1 (15)	17.5^{A} ± 3.4 (15)	14.3^{A} ± 2.9 (15)
	16-Mar-05	2.9^{AB} ± 0.6 (15)	1.5^{B} ± 0.5 (15)	3.2^{A} ± 0.6 (15)
	23-Jun-05	22.8^{A} ± 5.2 (15)	14.7^{A} ± 3.8 (15)	18.4^{A} ± 2.4 (15)
	7-Oct-05	10.2^{A} ± 3.7 (11)	10.8^{A} ± 3.5 (12)	10.3^{A} ± 2.9 (12)
	Mean	13.9^{A} ± 4.6	11.1^{A} ± 3.5	11.5^{A} ± 3.2
b. Dead	Biomass			
	18-Oct-04	32.6^{A} ± 8.3 (15)	23.4^{A} ± 3.5 (15)	26.8^{A} ± 3.7 (15)
	16-Mar-05	21.8^{AB} ± 3.6 (15)	16.5^{B} ± 3.4 (15)	32.0^{A} ± 5.1 (15)
	23-Jun-05	21.8^{A} ± 3.1 (15)	16.1^{A} ± 2.4 (15)	21.6^{A} ± 4.5 (15)
	7-Oct-05	19.0^{A} ± 3.8 (11)	19.9^{A} ± 4.9 (12)	25.6^{A} ± 5.0 (12)
	Mean	23.8^{A} ± 3.0	19.0^{A} ± 1.7	26.5^{A} ± 2.1
c. Total	Biomass			
	18-Oct-04	52.3^{A} ± 7.8 (15)	40.9^{A} ± 4.7 (15)	41.1^{A} ± 5.1 (15)
	16-Mar-05	24.7^{AB} ± 3.9 (15)	18.0^{B} ± 3.6 (15)	35.1^{A} ± 4.9 (15)
	23-Jun-05	44.6^{A} ± 5.6 (15)	30.8^{B} ± 4.1 (15)	40.0^{AB} ± 4.2 (15)
	7-Oct-05	29.2^{A} ± 6.1 (11)	30.7^{A} ± 7.0 (12)	35.8^{A} ± 7.2 (12)
	Mean	37.7^{A} ± 6.5	30.1^{A} ± 4.7	38.0^{A} ± 1.5

Appendix 5. The results of P-loading treatments on the *Spartina patens* aboveground cover following treatment application. Values represent mean ± standard error of percent (%) cover data for (a) live, (b) dead and (c) total cover (% m^{-2}) in the ambient (O), low (P) and high (PP) phosphorus-loading treatments followed by sample size (n) in parentheses. Within each cover type sample period, means having different superscripted letters are significantly different.

Type	Date	Phosphorus Loading Treatment O	P	PP
a. Live Cover				
	18-Oct-04	20.6^{A} ± 3.7 (15)	23.7^{A} ± 4.2 (15)	20.0^{A} ± 2.7 (15)
	16-Mar-05	14.3^{A} ± 1.8 (15)	14.7^{A} ± 2.0 (15)	14.7^{A} ± 1.7 (15)
	23-Jun-05	12.2^{A} ± 1.9 (15)	15.7^{A} ± 2.1 (15)	16.5^{A} ± 2.1 (15)
	7-Oct-05	4.9^{A} ± 1.3 (11)	3.8^{A} ± 1.1 (12)	6.3^{A} ± 1.4 (12)
	28-Mar-06	8.9^{A} ± 2.2 (11)	12.3^{A} ± 2.7 (12)	10.4^{A} ± 2.6 (12)
	22-Jun-06	18.4^{A} ± 4.0 (11)	21.2^{A} ± 5.4 (12)	21.6^{A} ± 4.5 (12)
	22-Sep-06	21.8^{A} ± 4.8 (11)	23.3^{A} ± 5.3 (12)	25.3^{A} ± 5.3 (12)
	Mean	14.4^{A} ± 2.4	16.4^{A} ± 2.7	16.4^{A} ± 2.5
b. Dead Cover				
	18-Oct-04	13.3^{A} ± 1.6 (15)	11.0^{A} ± 1.7 (15)	10.3^{A} ± 1.9 (15)
	16-Mar-05	11.7^{A} ± 1.4 (15)	13.0^{A} ± 1.4 (15)	14.3^{A} ± 1.5 (15)
	23-Jun-05	7.9^{AB} ± 1.1 (15)	9.5^{A} ± 1.0 (15)	6.9^{B} ± 0.7 (15)
	7-Oct-05	11.8^{A} ± 2.9 (11)	8.8^{A} ± 2.4 (12)	10.8^{A} ± 2.0 (12)
	28-Mar-06	7.1^{A} ± 1.3 (11)	8.4^{A} ± 1.4 (12)	7.1^{A} ± 1.1 (12)
	22-Jun-06	0.0^{A} ± 0.0 (11)	0.0^{A} ± 0.0 (12)	0.0^{A} ± 0.0 (12)
	22-Sep-06	3.2^{A} ± 1.2 (11)	2.5^{A} ± 0.8 (12)	1.3^{A} ± 0.7 (12)
	Mean	7.9^{A} ± 1.9	7.6^{A} ± 1.8	7.2^{A} ± 2.0
c. Total Cover				
	18-Oct-04	34.0^{A} ± 4.2 (15)	34.7^{A} ± 4.3 (15)	30.3^{A} ± 2.5 (15)
	16-Mar-05	26.0^{A} ± 2.5 (15)	27.7^{A} ± 3.0 (15)	29.0^{A} ± 2.7 (15)
	23-Jun-05	20.1^{A} ± 2.1 (15)	25.3^{A} ± 2.0 (15)	23.5^{A} ± 2.1 (15)
	7-Oct-05	16.7^{A} ± 3.0 (11)	12.7^{A} ± 3.0 (12)	17.0^{A} ± 2.9 (12)
	28-Mar-06	16.0^{A} ± 2.6 (11)	20.7^{A} ± 3.4 (12)	17.5^{A} ± 3.1 (12)
	22-Jun-06	18.4^{A} ± 4.0 (11)	21.2^{A} ± 5.4 (12)	21.6^{A} ± 4.5 (12)
	22-Sep-06	25.0^{A} ± 5.3 (11)	25.8^{A} ± 5.8 (12)	26.5^{A} ± 5.6 (12)
	Mean	22.3^{A} ± 2.4	24.0^{A} ± 2.6	23.6^{A} ± 2.0

Appendix 6. The results of P-loading treatments on the *Schoenoplectus americanus* aboveground cover following treatment application. Values represent mean ± standard error of percent (%) cover data for (a) live, (b) dead and (c) total cover (% m^{-2}) in the ambient (O), low (P) and high phosphorus-loading treatments followed by sample size (n) in parentheses. Within sample period, means having different superscripted letters are significantly different.

		Phosphorus Loading Treatment		
Type	Date	O	P	PP
a. Live Cover				
	18-Oct-04	20.0 ^{B} ± 2.3 (15)	24.0 ^{AB} ± 1.8 (15)	31.7 ^{A} ± 3.0 (15)
	16-Mar-05	11.7 ^{A} ± 1.4 (15)	9.7 ^{A} ± 1.1 (15)	11.7 ^{A} ± 1.1 (15)
	23-Jun-05	22.2 ^{A} ± 3.1 (15)	17.7 ^{A} ± 2.2 (15)	19.0 ^{A} ± 2.4 (15)
	7-Oct-05	8.6 ^{A} ± 1.5 (11)	12.8 ^{A} ± 2.1 (12)	8.5 ^{A} ± 1.5 (12)
	28-Mar-06	10.6 ^{A} ± 1.5 (11)	12.7 ^{A} ± 2.4 (12)	14.1 ^{A} ± 2.3 (12)
	22-Jun-06	21.4 ^{A} ± 4.9 (11)	26.7 ^{A} ± 5.7 (12)	26.2 ^{A} ± 6.2 (12)
	22-Sep-06	5.2 ^{A} ± 0.5 (11)	6.5 ^{A} ± 1.1 (12)	6.8 ^{A} ± 1.0 (12)
	Mean	14.2 ^{A} ± 2.6	15.7 ^{A} ± 2.8	16.9 ^{A} ± 3.5
b. Dead Cover				
	18-Oct-04	17.0 ^{A} ± 1.5 (15)	17.0 ^{A} ± 2.2 (15)	17.3 ^{A} ± 2.7 (15)
	16-Mar-05	14.0 ^{B} ± 1.2 (15)	16.0 ^{AB} ± 1.3 (15)	18.7 ^{A} ± 1.1 (15)
	23-Jun-05	6.8 ^{A} ± 1.0 (15)	6.4 ^{A} ± 1.0 (15)	7.6 ^{A} ± 0.8 (15)
	7-Oct-05	16.1 ^{A} ± 3.3 (11)	17.5 ^{A} ± 3.7 (12)	11.2 ^{A} ± 1.9 (12)
	28-Mar-06	6.8 ^{A} ± 0.8 (11)	6.8 ^{A} ± 1.1 (12)	6.0 ^{A} ± 0.7 (12)
	22-Jun-06	0.0 ^{A} ± 0.0 (11)	0.0 ^{A} ± 0.0 (12)	0.0 ^{A} ± 0.0 (12)
	22-Sep-06	9.2 ^{A} ± 1.6 (11)	10.3 ^{A} ± 2.0 (12)	9.2 ^{A} ± 1.6 (12)
	Mean	10.0 ^{A} ± 2.3	10.6 ^{A} ± 2.5	10.0 ^{A} ± 2.5
c. Total Cover				
	18-Oct-04	37.0 ^{B} ± 2.1 (15)	41.0 ^{AB} ± 2.8 (15)	49.0 ^{A} ± 3.4 (15)
	16-Mar-05	25.7 ^{A} ± 2.1 (15)	25.7 ^{A} ± 2.2 (15)	30.3 ^{A} ± 1.5 (15)
	23-Jun-05	29.0 ^{A} ± 3.3 (15)	24.1 ^{A} ± 3.0 (15)	26.6 ^{A} ± 3.0 (15)
	7-Oct-05	23.8 ^{A} ± 4.1 (11)	30.3 ^{A} ± 5.4 (12)	19.8 ^{A} ± 2.5 (12)
	28-Mar-06	17.4 ^{A} ± 1.3 (11)	19.4 ^{A} ± 3.3 (12)	20.1 ^{A} ± 2.5 (12)
	22-Jun-06	21.4 ^{A} ± 4.9 (11)	26.7 ^{A} ± 5.7 (12)	26.2 ^{A} ± 6.2 (12)
	22-Sep-06	14.4 ^{A} ± 1.4 (11)	16.8 ^{A} ± 2.2 (12)	16.1 ^{A} ± 2.0 (12)
	Mean	24.1 ^{A} ± 2.8	26.3 ^{A} ± 3.0	26.9 ^{A} ± 4.1

Appendix 7. The results of P-loading treatments on species richness. Values represent mean ± standard error of species present (#) in the plant community composition plots under the ambient (O), low (P) and high (PP) phosphorus-loading treatments followed by sample size (n) in parenthesis. Within each sample period, means having superscripted letters are significantly different.

	Phosphorus Loading Treatment		
Date	O	P	PP
24-Apr-04	2.3^{A} ± 0.1 (15)	2.7^{A} ± 0.2 (15)	2.5^{A} ± 0.2 (15)
18-Oct-04	2.5^{AB} ± 0.2 (15)	2.4^{B} ± 0.2 (15)	2.9^{A} ± 0.2 (15)
16-Mar-05	2.4^{A} ± 0.2 (15)	2.4^{A} ± 0.1 (15)	2.4^{A} ± 0.2 (15)
23-Jun-05	3.4^{A} ± 0.3 (15)	3.3^{A} ± 0.4 (15)	3.3^{A} ± 0.3 (15)
7-Oct-05	2.2^{A} ± 0.1 (11)	2.4^{A} ± 0.2 (12)	2.6^{A} ± 0.2 (12)
28-Mar-06	3.6^{A} ± 0.4 (11)	4.0^{A} ± 0.3 (12)	3.6^{A} ± 0.4 (12)
22-Jun-06	4.6^{A} ± 0.8 (11)	3.8^{A} ± 0.6 (12)	3.8^{A} ± 0.6 (12)
22-Sep-06	3.6^{A} ± 0.4 (11)	4.2^{A} ± 0.4 (12)	4.2^{A} ± 0.4 (12)
Mean	3.1^{A} ± 0.3	3.2^{A} ± 0.3	3.1^{A} ± 0.2

Appendix 8. Result of N-loading treatments on leaf tissue nitrogen concentration. Values are the mean $\pm$ standard error of leaf tissue nitrogen [N] concentration (mg/g) for (a) *Spartina patens* and (b) *Schoenoplectus americanus* under the ambient (O), low (N) and high (NN) nitrogen-loading treatments followed by sample size (n) in parentheses. Within each species sample period, means having different superscripted letters are significantly different.

		Nitrogen Loading Treatment		
Species	Date	O	N	NN
a. *Spartina*	**18-Oct-04**	$6.41^{B} \pm 0.23$ (15)	$7.17^{B} \pm 0.30$ (15)	$8.45^{A} \pm 0.59$ (15)
b. *Schoenoplectus*	**18-Oct-04**	$9.26^{B} \pm 0.51$ (14)	$9.51^{B} + 0.67$ (15)	$11.77^{A} \pm 0.71$ (15)

Appendix 9. The results of N-loading treatments on mean stem height following treatment application. Values represent the mean ± standard error of (a) *Spartina patens* and (b) *Schoenoplectus americanus* mean stem height (cm) under the ambient (O), low (N) and high (NN) nitrogen-loading treatments followed by sample size (n) in parenthesis. Within each species sample period, means having different superscripted letters are significantly different.

		Nitrogen Loading Treatment		
Species	Date	O	N	NN
a. *Spartina*				
	18-Oct-04	52.7^{B} ± 2.73 (15)	65.1^{A} ± 2.63 (15)	56.1^{AB} ± 4.62 (15)
	16-Mar-05	49.7^{A} ± 2.78 (15)	45.5^{A} ± 3.87 (15)	46.3^{A} ± 3.35 (15)
	23-Jun-05	44.6^{A} ± 2.11 (15)	40.6^{A} ± 2.63 (15)	41.5^{A} ± 2.41 (15)
	7-Oct-05	35.4^{A} ± 6.11 (12)	41.7^{A} ± 4.45 (12)	35.4^{A} ± 7.99 (11)
	Mean	45.6^{A} ± 3.80	48.2^{A} ± 5.73	44.9^{A} ± 4.37
b. *Schoenoplectus*				
	18-Oct-04	63.4^{A} ± 6.30 (15)	60.4^{A} ± 3.70 (15)	59.7^{A} ± 6.32 (15)
	16-Mar-05	29.9^{A} ± 3.50 (15)	28.2^{A} ± 3.88 (15)	35.0^{A} ± 3.75 (15)
	23-Jun-05	58.8^{A} ± 6.40 (15)	57.8^{A} ± 7.28 (15)	74.6^{A} ± 5.10 (15)
	7-Oct-05	51.4^{A} ± 8.11 (12)	61.1^{A} ± 10.1 (12)	39.8^{A} ± 8.73 (11)
	Mean	50.8^{A} ± 7.42	51.9^{A} ± 7.93	52.3^{A} ± 9.16

Appendix 10. The results of N-loading treatments on *Spartina patens* standing crop following treatment application. Data were ln(x+1) transformed prior to analysis to reduce heterogeneity of variance then de-transformed for presentation. Values represent mean ± standard error of *Spartina* (a) live, (b) dead and (c) total biomass (g 0.25 m^{-2}) in the ambient (O), low (N) and high (NN) nitrogen-loading treatments followed by sample size (n) in parentheses. Within each productivity type's sample period, means having different superscripted letters are significantly different.

		Nitrogen Loading Treatment		
Type	Date	O	N	NN
a. Live Biomass				
	18-Oct-04	17.2^{A} ± 2.2 (15)	28.0^{A} ± 4.5 (15)	26.1^{A} ± 8.5 (15)
	16-Mar-05	21.6^{A} ± 3.4 (15)	28.2^{A} ± 6.8 (15)	22.6^{A} ± 5.5 (15)
	23-Jun-05	20.0^{A} ± 4.3 (15)	19.2^{A} ± 3.8 (15)	19.6^{A} ± 5.3 (15)
	7-Oct-05	4.4^{A} ± 1.6 (12)	9.3^{A} ± 2.5 (12)	8.3^{A} ± 3.1 (11)
	Mean	15.8^{A} ± 3.9	21.2^{A} ± 4.5	19.2^{A} ± 3.8
b. Dead Biomass				
	18-Oct-04	56.5^{A} ± 7.1 (15)	60.2^{A} ± 12.2 (15)	43.0^{A} ± 9.7 (15)
	16-Mar-05	69.7^{A} ± 8.7 (15)	52.3^{A} ± 8.7 (15)	39.9^{A} ± 9.3 (15)
	23-Jun-05	42.7^{A} ± 6.9 (15)	32.6^{A} ± 5.3 (15)	30.1^{A} ± 6.8 (15)
	7-Oct-05	14.9^{A} ± 6.8 (12)	22.5^{A} ± 5.1 (12)	27.0^{A} ± 13.7 (11)
	Mean	46.0^{A} ± 11.7	41.9^{A} ± 8.7	35.0^{A} ± 3.8
c. Total Biomass				
	18-Oct-04	73.7^{A} ± 7.9 (15)	88.2^{A} ± 15.0 (15)	69.1^{A} ± 15.1 (15)
	16-Mar-05	91.3^{A} ± 11.6 (15)	80.6^{A} ± 12.8 (15)	62.6^{A} ± 13.2 (15)
	23-Jun-05	62.7^{A} ± 9.5 (15)	51.8^{A} ± 8.5 (15)	49.7^{A} ± 11.8 (15)
	7-Oct-05	19.4^{A} ± 7.9 (12)	31.8^{A} ± 5.9 (12)	35.3^{A} ± 16.5 (11)
	Mean	61.8^{A} ± 15.3	63.1^{A} ± 13.1	54.2^{A} ± 7.5

Appendix 11. The results of N-loading treatments on *Schoenoplectus americanus* standing crop following treatment application. Data were ln(x+1) transformed prior to analysis to reduce heterogeneity of variance then de-transformed for presentation. Values represent mean ± standard error of *Schoenoplectus* (a) live, (b) dead and (c) total biomass (g 0.25 m^{-2}) in the ambient (O), low (N) and high (NN) nitrogen-loading treatments followed by sample size (n) in parentheses. Within each productivity type's sample period, means having different superscripted letters are significantly different.

		Nitrogen Loading Treatment		
Type	Date	O	N	NN
a. Live Biomass				
	18-Oct-04	15.5 ^{A} ± 3.0 (15)	20.5 ^{A} ± 3.6 (15)	15.5 ^{A} ± 2.8 (15)
	16-Mar-05	1.5 ^{A} ± 0.3 (15)	2.7 ^{A} ± 0.7 (15)	3.4 ^{A} ± 0.7 (15)
	23-Jun-05	11.6 ^{B} ± 2.4 (15)	15.8 ^{AB} ± 2.8 (15)	28.5 ^{A} ± 5.0 (15)
	7-Oct-05	11.0 ^{A} ± 3.4 (12)	11.0 ^{A} ± 3.4 (12)	9.3 ^{A} ± 3.3 (11)
	Mean	9.9 ^{A} ± 3.0	12.5 ^{A} ± 3.8	14.2 ^{A} ± 5.4
b. Dead Biomass				
	18-Oct-04	36.0 ^{A} ± 8.6 (15)	25.2 ^{A} ± 2.3 (15)	21.6 ^{A} ± 3.3 (15)
	16-Mar-05	30.8 ^{A} ± 4.9 (15)	18.4 ^{A} ± 3.5 (15)	21.1 ^{A} ± 4.3 (15)
	23-Jun-05	22.8 ^{A} ± 4.7 (15)	21.6 ^{A} ± 3.2 (15)	15.1 ^{A} ± 1.4 (15)
	7-Oct-05	16.1 ^{A} ± 3.1 (12)	26.0 ^{A} ± 4.9 (12)	22.6 ^{A} ± 5.5 (11)
	Mean	26.4 ^{A} ± 4.4	22.8 ^{A} ± 1.8	20.1 ^{A} ± 1.7
C. Total Biomass				
	18-Oct-04	51.5 ^{A} ± 8.5 (15)	45.8 ^{A} ± 4.2 (15)	37.1 ^{A} ± 4.2 (15)
	16-Mar-05	32.2 ^{A} ± 5.0 (15)	21.2 ^{A} ± 3.7 (15)	24.5 ^{A} ± 4.4 (15)
	23-Jun-05	34.4 ^{A} ± 5.6 (15)	37.3 ^{A} ± 3.5 (15)	43.6 ^{A} ± 5.2 (15)
	7-Oct-05	27.1 ^{A} ± 5.2 (12)	37.0 ^{A} ± 6.8 (12)	31.9 ^{A} ± 8.1 (11)
	Mean	36.3 ^{A} ± 5.3	35.3 ^{A} ± 5.1	34.3 ^{A} ± 4.0

Appendix 12. The results of N-loading treatments on the *Spartina patens* aboveground cover following treatment application. Values represent mean ± standard error of percent (%) cover data for (a) live, (b) dead and (c) total cover (% m^{-2}) in the ambient (O), low (N) and high (NN) nitrogen-loading treatments followed by sample size (n) in parentheses. Within sample period, means having different superscripted letters are significantly different.

Type	Date	O	N	NN
		Nitrogen Loading Treatment		
a. Live Cover				
	18-Oct-04	16.0 ^{B} ± 3.3 (15)	27.7 ^{A} ± 4.0 (15)	20.7 ^{AB} ± 2.7 (15)
	16-Mar-05	10.3 ^{B} ± 1.5 (15)	17.7 ^{A} ± 1.6 (15)	15.7 ^{AB} ± 1.8 (15)
	23-Jun-05	11.1 ^{B} ± 1.6 (15)	18.0 ^{A} ± 1.9 (15)	15.4 ^{AB} ± 2.3 (15)
	7-Oct-05	3.0 ^{B} ± 0.5 (12)	7.3 ^{A} ± 1.6 (12)	4.7 ^{AB} ± 1.3 (11)
	28-Mar-06	6.0 ^{B} ± 1.3 (12)	15.4 ^{A} ± 2.6 (12)	10.3 ^{AB} ± 2.7 (11)
	22-Jun-06	12.9 ^{A} ± 3.1 (12)	27.9 ^{A} ± 4.9 (12)	20.5 ^{A} ± 4.7 (11)
	22-Sep-06	16.8 ^{A} ± 4.5 (12)	32.5 ^{A} ± 5.6 (12)	20.9 ^{A} ± 3.9 (11)
	Mean	10.9 ^{C} ± 1.9	20.1 ^{A} ± 3.3	15.5 ^{B} ± 2.3
b. Dead Cover				
	18-Oct-04	13.7 ^{A} ± 2.0 (15)	10.3 ^{A} ± 1.5 (15)	10.7 ^{A} ± 1.6 (15)
	16-Mar-05	13.7 ^{A} ± 1.7 (15)	12.0 ^{A} ± 1.2 (15)	13.3 ^{A} ± 1.5 (15)
	23-Jun-05	9.3 ^{A} ± 1.0 (15)	7.5 ^{A} ± 1.0 (15)	7.5 ^{A} ± 0.9 (15)
	7-Oct-05	7.8 ^{A} ± 2.2 (12)	12.1 ^{A} ± 2.3 (12)	11.5 ^{A} ± 2.7 (11)
	28-Mar-06	6.4 ^{A} ± 1.2 (12)	9.6 ^{A} ± 1.4 (12)	6.5 ^{A} ± 0.8 (11)
	22-Jun-06	0.0 ^{A} ± 0.0 (12)	0.0 ^{A} ± 0.0 (12)	0.0 ^{A} ± 0.0 (11)
	22-Sep-06	2.1 ^{A} ± 1.0 (12)	2.9 ^{A} ± 1.0 (12)	1.8 ^{A} ± 0.8 (11)
	Mean	7.6 ^{A} ± 2.0	7.8 ^{A} ± 1.8	7.3 ^{A} ± 1.9
c. Total Cover				
	18-Oct-04	29.7 ^{A} ± 3.8 (15)	38.0 ^{A} ± 4.2 (15)	31.3 ^{A} ± 2.8 (15)
	16-Mar-05	24.0 ^{A} ± 2.6 (15)	29.7 ^{A} ± 2.4 (15)	29.0 ^{A} ± 3.0 (15)
	23-Jun-05	20.3 ^{A} ± 1.9 (15)	25.5 ^{A} ± 2.2 (15)	22.9 ^{A} ± 2.2 (15)
	7-Oct-05	10.8 ^{A} ± 2.6 (12)	19.4 ^{A} ± 2.3 (12)	16.2 ^{A} ± 3.6 (11)
	28-Mar-06	12.4 ^{B} ± 2.3 (12)	25.0 ^{A} ± 2.5 (12)	16.8 ^{AB} ± 3.2 (11)
	22-Jun-06	12.9 ^{A} ± 3.1 (12)	27.9 ^{A} ± 4.9 (12)	20.4 ^{A} ± 4.7 (11)
	22-Sep-06	18.9 ^{A} ± 4.9 (12)	35.4 ^{A} ± 5.8 (12)	22.7 ^{A} ± 4.5 (11)
	Mean	18.4 ^{C} ± 2.6	28.7 ^{A} ± 2.4	22.8 ^{B} ± 2.2

Appendix 13. The results of N-loading treatments on *Schoenoplectus americanus* aboveground cover following treatment application. Values represent mean ± standard error of percent (%) cover data for (a) live, (b) dead and (c) total cover (% m^{-2}) in the ambient (O), low (N) and high (NN) nitrogen-loading treatments followed by sample size (n) in parentheses. Within sample period, means having different superscripted letters are significantly different.

Type	Date	O	N	NN
		Nitrogen Loading Treatment		
a. Live Cover				
	18-Oct-04	23.0^{A} ± 2.2 (15)	25.7^{A} ± 3.2 (15)	27.0^{A} ± 2.6 (15)
	16-Mar-05	12.0^{A} ± 1.1 (15)	10.3^{A} ± 1.2 (15)	10.7^{A} ± 1.3 (15)
	23-Jun-05	15.9^{B} ± 2.1 (15)	20.0^{AB} ± 2.6 (15)	23.0^{A} ± 2.9 (15)
	7-Oct-05	8.4^{A} ± 1.2 (12)	10.0^{A} ± 1.4 (12)	11.8^{A} ± 2.6 (11)
	28-Mar-06	16.2^{A} ± 2.3 (12)	13.3^{AB} ± 1.8 (12)	7.5^{B} ± 1.4 (11)
	22-Jun-06	28.3^{A} ± 6.1 (12)	20.0^{A} ± 3.3 (12)	26.4^{A} ± 7.0 (11)
	22-Sep-06	6.4^{A} ± 0.8 (12)	5.2^{A} ± 0.7 (12)	7.1^{A} ± 1.2 (11)
	Mean	15.7^{A} ± 3.0	14.9^{A} ± 2.7	16.2^{A} ± 3.4
b. Dead Cover				
	18-Oct-04	22.7^{A} ± 2.9 (15)	13.0^{B} ± 0.8 (15)	15.7^{B} ± 1.4 (15)
	16-Mar-05	16.3^{A} ± 1.2 (15)	15.0^{A} ± 1.2 (15)	16.3^{A} ± 1.5 (15)
	23-Jun-05	7.1^{A} ± 1.1 (15)	5.0^{A} ± 0.5 (15)	8.2^{A} ± 1.0 (15)
	7-Oct-05	14.8^{A} ± 2.4 (12)	10.0^{A} ± 3.2 (12)	15.4^{A} ± 3.9 (11)
	28-Mar-06	8.8^{A} ± 0.9 (12)	5.0^{B} ± 0.4 (12)	5.3^{B} ± 0.8 (11)
	22-Jun-06	0.0 ± 0.0 (12)	0.0 ± 0.0 (12)	0.0 ± 0.0 (11)
	22-Sep-06	11.2^{A} ± 2.0 (12)	10.0^{A} ± 1.2 (12)	9.1^{A} ± 1.9 (11)
	Mean	11.6^{A} ± 2.8	8.6^{B} ± 2.1	10.0^{AB} ± 2.3
c. Total Cover				
	18-Oct-04	45.7^{A} ± 3.2 (15)	38.7^{A} ± 3.2 (15)	42.7^{A} ± 2.5 (15)
	16-Mar-05	28.3^{A} ± 2.1 (15)	26.3^{A} ± 2.0 (15)	27.0^{A} ± 2.0 (15)
	23-Jun-05	22.9^{B} ± 2.3 (15)	25.5^{AB} ± 2.9 (15)	31.2^{A} ± 3.7 (15)
	7-Oct-05	23.2^{A} ± 3.2 (12)	23.8^{A} ± 3.9 (12)	27.2^{A} ± 5.9 (11)
	28-Mar-06	25.0^{A} ± 2.6 (12)	18.8^{AB} ± 1.8 (12)	12.8^{B} ± 1.8 (11)
	22-Jun-06	28.3^{A} ± 6.1 (12)	20.0^{A} ± 3.3 (12)	26.4^{A} ± 7.0 (11)
	22-Sep-06	17.7^{A} ± 2.3 (12)	13.6^{A} ± 1.3 (12)	16.2^{A} ± 1.8 (11)
	Mean	27.3^{A} ± 3.4	23.8^{A} ± 3.0	26.2^{A} ± 3.7

Appendix 14. The results of N-loading treatments on species richness. Values represent mean ± standard error of species present (# m^{-2}) in the plant community composition plots under the ambient (O), low (N) and high (NN) nitrogen-loading treatments followed by sample size (n) in parenthesis. Within each sample period, means having superscripted letters are significantly different.

Nitrogen Loading Treatment

Date	O	N	NN
18-Oct-04	2.6^{A} ± 0.2 (15)	2.7^{A} ± 0.2 (15)	2.4^{A} ± 0.1 (15)
16-Mar-05	2.2^{A} ± 0.1 (15)	2.6^{A} ± 0.2 (15)	2.4^{A} ± 0.2 (15)
23-Jun-05	2.9^{B} ± 0.2 (15)	4.0^{A} ± 0.3 (15)	3.1^{AB} ± 0.3 (15)
7-Oct-05	2.3^{AB} ± 0.1 (11)	2.8^{A} ± 0.2 (12)	2.1^{B} ± 0.2 (12)
28-Mar-06	3.4^{A} ± 0.3 (11)	4.0^{A} ± 0.4 (12)	3.8^{A} ± 0.4 (12)
22-Jun-06	4.2^{A} ± 0.6 (11)	3.6^{A} ± 0.4 (12)	4.5^{A} ± 0.9 (12)
22-Sep-06	4.3^{A} ± 0.4 (11)	4.1^{A} ± 0.3 (12)	3.6^{A} ± 0.5 (12)
Mean	3.1^{A} ± 0.3	3.4^{A} ± 0.3	3.1^{A} ± 0.3

Appendix 15. The results of disturbance treatment on mean stem height during following treatment application. Values represent the mean ± standard error of (a) *Spartina patens* and (b) *Schoenoplectus americanus* mean stem height (cm) under the control (C) and lethal (L) disturbance treatments followed by sample size (n) in parenthesis. Within each species sample period, means having different superscripted letters are significantly different.

		Disturbance Treatment	
Species	Date	C	L
a. *Spartina*			
	18-Oct-04	50.2^{A} ± 5.02 (5)	27.9^{A} ± 11.88 (5)
	16-Mar-05	48.0^{A} ± 3.00 (5)	3.6^{B} ± 3.58 (5)
	23-Jun-05	43.0^{A} ± 4.06 (5)	0.0^{B} ± 0.00 (5)
	7-Oct-05	44.9^{A} ± 11.60 (4)	0.0^{B} ± 0.00 (4)
	Mean	46.5^{A} ± 1.60	7.9^{B} ± 6.70
b. *Schoenoplectus*			
	18-Oct-04	83.4^{A} ± 6.44 (5)	7.1^{B} ± 7.12 (5)
	16-Mar-05	32.5^{A} ± 4.43 (5)	10.5^{B} ± 6.59 (5)
	23-Jun-05	69.2^{A} ± 12.67 (5)	32.3^{A} ± 6.96 (5)
	7-Oct-05	53.8^{A} ± 18.54 (4)	39.4^{A} ± 18.2 (4)
	Mean	59.7^{A} ± 10.90	22.3^{A} ± 8.00

Appendix 16. The results of disturbance treatment on *Spartina patens* standing crop following treatment application. Data were ln(x+1) transformed prior to analysis to reduce heterogeneity of variance then de-transformed for presentation. Values represent mean ± standard error of *Spartina* (a) live, (b) dead and (c) total biomass (g 0.25 m^{-2}) under the control (C) and lethal (L) disturbance treatments followed by sample size (n) in parenthesis. Within each productivity type's sample period, means having different superscripted letters are significantly different.

		Disturbance Treatment			
Type	Date	C		L	
a. Live Biomass					
	18-Oct-04	$13.6^{A} \pm 3.6$	(5)	$1.9^{B} \pm 1.6$	(5)
	16-Mar-05	$20.3^{A} \pm 4.8$	(5)	$0.0^{B} \pm 0.0$	(5)
	23-Jun-05	$19.4^{A} \pm 5.9$	(5)	$0.0^{B} \pm 0.0$	(5)
	7-Oct-05	$1.9^{A} \pm 0.7$	(4)	$0.0^{B} \pm 0.0$	(4)
	Mean	$13.8^{A} \pm 4.2$		$0.5^{B} \pm 0.5$	
b. Dead Biomass					
	18-Oct-04	$53.0^{A} \pm 16.0$	(5)	$64.0^{A} \pm 17.8$	(5)
	16-Mar-05	$78.9^{A} \pm 13.9$	(5)	$58.5^{A} \pm 13.8$	(5)
	23-Jun-05	$55.7^{A} \pm 12.2$	(5)	$18.3^{B} \pm 7.7$	(5)
	7-Oct-05	$5.5^{A} \pm 0.7$	(4)	$0.6^{B} \pm 0.3$	(4)
	Mean	$48.3^{A} \pm 15.4$		$35.3^{A} \pm 15.4$	
c. Total Biomass					
	18-Oct-04	$66.6^{A} \pm 18.1$	(5)	$65.9^{A} \pm 19.2$	(5)
	16-Mar-05	$99.2^{A} \pm 18.0$	(5)	$58.5^{A} \pm 13.8$	(5)
	23-Jun-05	$75.1^{A} \pm 15.6$	(5)	$18.3^{B} \pm 7.7$	(5)
	7-Oct-05	$7.4^{A} \pm 0.8$	(4)	$0.6^{B} \pm 0.3$	(4)
	Mean	$62.1^{A} \pm 19.5$		$35.8^{A} \pm 15.7$	

Appendix 17. The results of disturbance treatment on *Schoenoplectus americanus* standing crop following treatment application. Data were ln(x+1) transformed prior to analysis to reduce heterogeneity of variance then de-transformed for presentation. Values represent mean ± standard error of *Schoenoplectus* (a) live, (b) dead and (c) total biomass (g 0.25 m^{-2}) under the control (C) and lethal (L) disturbance treatments followed by sample size (n) in parenthesis. Within each productivity type's sample period, means having different superscripted letters are significantly different.

Type	Date	Disturbance Treatment C		Disturbance Treatment L	
a. Live Biomass					
	18-Oct-04	19.9^{A} ± 6.4	(5)	0.0^{B} ± 0.0	(5)
	16-Mar-05	2.1^{A} ± 0.6	(5)	0.2^{B} ± 0.2	(5)
	23-Jun-05	12.7^{A} ± 4.7	(5)	6.8^{A} ± 5.1	(5)
	7-Oct-05	12.9^{A} ± 8.7	(4)	11.8^{A} ± 9.1	(4)
	Mean	11.9^{A} ± 3.7		4.7^{A} ± 2.8	
b. Dead Biomass					
	18-Oct-04	54.5^{A} ± 22.8	(5)	37.1^{A} ± 6.5	(5)
	16-Mar-05	32.6^{A} ± 7.2	(5)	19.9^{A} ± 6.0	(5)
	23-Jun-05	18.0^{A} ± 4.4	(5)	11.1^{A} ± 8.6	(5)
	7-Oct-05	13.4^{A} ± 3.7	(4)	12.0^{A} ± 6.9	(4)
	Mean	29.6^{A} ± 9.2		20.0^{A} ± 6.0	
c. Total Biomass					
	18-Oct-04	74.4^{A} ± 20.3	(5)	37.1^{A} ± 6.5	(5)
	16-Mar-05	34.7^{A} ± 7.7	(5)	20.1^{A} ± 6.0	(5)
	23-Jun-05	30.7^{A} ± 8.8	(5)	17.9^{A} ± 9.2	(5)
	7-Oct-05	26.3^{A} ± 11.5	(4)	23.7^{A} ± 15.2	(4)
	Mean	41.5^{A} ± 11.1		24.7^{B} + 4.3	

Appendix 18. The results of disturbance treatment on *Spartina patens* aboveground cover following treatment application. Values represent mean ± standard error of *Spartina* (a) live, (b) dead and (c) total cover (% m^{-2}) under the control (C) and lethal (L) disturbance treatments followed by sample size (n) in parenthesis. Within each cover type's sample period, means having different superscripted letters are significantly different.

		Disturbance Treatment	
Type	Date	C	L
a. Live Cover			
	18-Oct-04	24.0 ^{A} ± 8.4 (5)	0.2 ^{B} ± 0.2 (5)
	16-Mar-05	12.0 ^{A} ± 3.4 (5)	0.0 ^{B} ± 0.0 (5)
	23-Jun-05	10.0 ^{A} ± 1.6 (5)	0.2 ^{B} ± 0.2 (5)
	7-Oct-05	2.8 ^{A} ± 1.3 (4)	0.0 ^{A} ± 0.0 (4)
	28-Mar-06	7.5 ^{A} ± 3.2 (4)	0.0 ^{A} ± 0.0 (4)
	22-Jun-06	16.8 ^{A} ± 7.9 (4)	1.3 ^{A} ± 1.3 (4)
	22-Sep-06	17.5 ^{A} ± 9.2 (4)	0.8 ^{A} ± 0.5 (4)
	Mean	12.9 ^{A} ± 2.7	0.3 ^{B} ± 0.2
b. Dead Cover			
	18-Oct-04	17.0 ^{A} ± 3.0 (5)	29.0 ^{A} ± 8.0 (5)
	16-Mar-05	14.0 ^{A} ± 2.9 (5)	24.0 ^{A} ± 9.5 (5)
	23-Jun-05	9.0 ^{A} ± 1.9 (5)	11.6 ^{A} ± 9.6 (5)
	7-Oct-05	11.3 ^{A} ± 5.5 (4)	2.5 ^{A} ± 2.5 (4)
	28-Mar-06	7.5 ^{A} ± 2.5 (4)	0.0 ^{A} ± 0.0 (4)
	22-Jun-06	0.0 ^{A} ± 0.0 (4)	0.0 ^{A} ± 0.0 (4)
	22-Sep-06	2.5 ^{A} ± 2.5 (4)	0.0 ^{A} ± 0.0 (4)
	Mean	8.8 ^{A} ± 2.3	9.6 ^{A} ± 4.7
c. Total Cover			
	18-Oct-04	41.0 ^{A} ± 8.3 (5)	29.2 ^{A} ± 8.0 (5)
	16-Mar-05	26.0 ^{A} ± 4.3 (5)	24.0 ^{A} ± 9.5 (5)
	23-Jun-05	19.0 ^{A} ± 2.5 (5)	11.8 ^{A} ± 9.6 (5)
	7-Oct-05	14.0 ^{A} ± 6.7 (4)	2.5 ^{A} ± 2.5 (4)
	28-Mar-06	15.0 ^{A} ± 5.4 (4)	0.0 ^{A} ± 0.0 (4)
	22-Jun-06	16.8 ^{A} ± 7.9 (4)	1.3 ^{A} ± 1.3 (4)
	22-Sep-06	20.0 ^{A} ± 10.2 (4)	0.8 ^{A} ± 0.5 (4)
	Mean	21.7 ^{A} ± 3.6	9.9 ^{B} ± 4.6

Appendix 19. The result of disturbance treatment on *Schoenoplectus americanus* aboveground cover following treatment application. Values represent mean ± standard error of *Schoenoplectus* (a) live, (b) dead and (c) total cover (% m^{-2}) under the control (C) and lethal (L) disturbance treatments followed by sample size (n) in parenthesis. Within each cover type's sample period, means having different superscripted letters are significantly different.

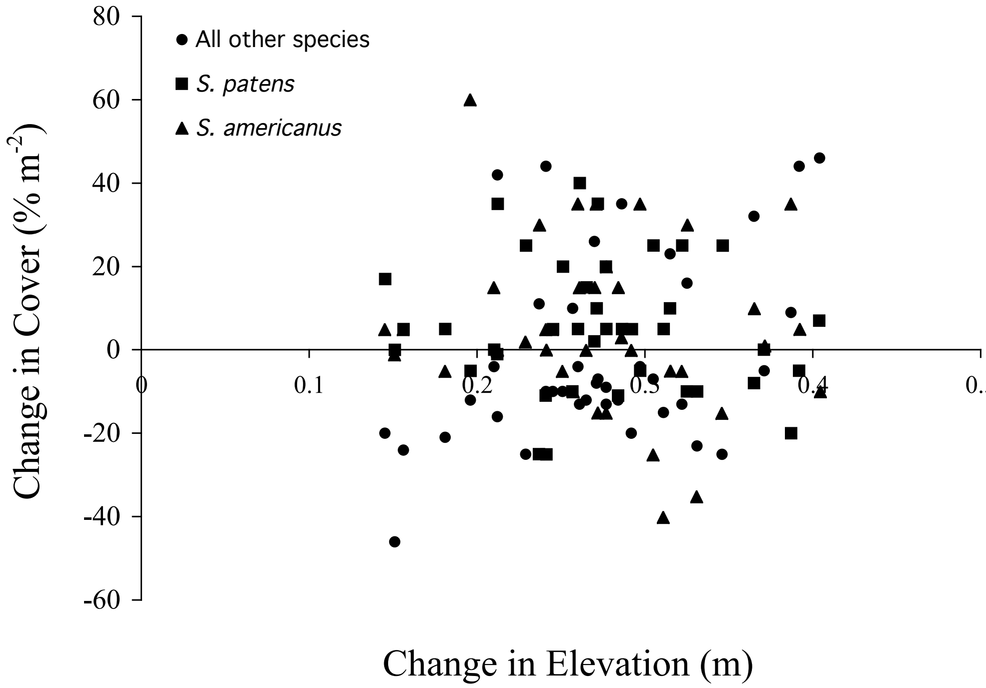
		Disturbance Treatment			
Type	Date	C		L	
a. Live Cover					
	18-Oct-04	17.0 ^{A} ± 4.9	(5)	0.2 ^{B} ± 0.2	(5)
	16-Mar-05	10.0 ^{A} ± 1.6	(5)	0.0 ^{B} ± 0.0	(5)
	23-Jun-05	14.6 ^{A} ± 3.8	(5)	1.8 ^{B} ± 0.9	(5)
	7-Oct-05	6.8 ^{A} ± 2.0	(4)	0.8 ^{B} ± 0.5	(4)
	28-Mar-06	11.3 ^{A} ± 1.3	(4)	2.3 ^{B} ± 0.6	(4)
	22-Jun-06	21.3 ^{A} ± 7.5	(4)	1.8 ^{A} ± 1.2	(4)
	22-Sep-06	5.0 ^{A} ± 0.0	(4)	0.8 ^{B} ± 0.5	(4)
	Mean	12.3 ^{A} ± 2.2		1.1 ^{B} ± 0.3	
b. Dead Cover					
	18-Oct-04	20.0 ^{A} ± 3.9	(5)	42.0 ^{A} ± 10.6	(5)
	16-Mar-05	14.0 ^{A} ± 2.4	(5)	21.0 ^{A} ± 6.8	(5)
	23-Jun-05	6.4 ^{A} ± 2.2	(5)	4.0 ^{A} ± 2.9	(5)
	7-Oct-05	12.0 ^{A} ± 3.6	(4)	2.0 ^{A} ± 1.2	(4)
	28-Mar-06	7.5 ^{A} ± 1.4	(4)	0.3 ^{B} ± 0.3	(4)
	22-Jun-06	0.0 ^{A} ± 0.0	(4)	0.0 ^{A} ± 0.0	(4)
	22-Sep-06	8.8 ^{A} ± 1.3	(4)	0.0 ^{B} ± 0.0	(4)
	Mean	9.8 ^{A} ± 2.4		9.9 ^{A} ± 6.1	
c. Total Cover					
	18-Oct-04	37.0 ^{A} ± 4.6	(5)	42.2 ^{A} ± 10.6	(5)
	16-Mar-05	24.0 ^{A} ± 3.7	(5)	21.0 ^{A} ± 6.8	(5)
	23-Jun-05	21.0 ^{A} ± 2.6	(5)	5.8 ^{B} ± 2.8	(5)
	7-Oct-05	18.8 ^{A} ± 4.5	(4)	2.8 ^{A} ± 1.6	(4)
	28-Mar-06	18.8 ^{A} ± 1.2	(4)	2.5 ^{B} ± 0.9	(4)
	22-Jun-06	21.2 ^{A} ± 7.5	(4)	1.8 ^{A} ± 1.2	(4)
	22-Sep-06	13.8 ^{A} ± 1.2	(4)	0.8 ^{B} ± 0.5	(4)
	Mean	22.1 ^{A} ± 2.8		11.0 ^{B} ± 5.8	

Appendix 20. The effect of disturbance treatments on species richness. Values represent mean ± standard error of species present (# m^{-2}) in the plant community composition plots under the control (C) and lethal (L) disturbance treatments followed by sample size (n) in parenthesis. Within each sample period, means having superscripted letters are significantly different.

	Disturbance Treatment	
Date	C	L
24-Apr-04	2.4^{A} ± 0.24 (5)	2.0^{A} ± 0.00 (5)
18-Oct-04	2.6^{A} ± 0.40 (5)	2.0^{A} ± 0.00 (5)
16-Mar-05	2.2^{A} ± 0.20 (5)	2.6^{A} ± 0.68 (5)
23-Jun-05	3.2^{A} ± 0.49 (5)	3.4^{A} ± 0.98 (5)
7-Oct-05	2.0^{A} ± 0.00 (4)	0.8^{A} ± 0.48 (4)
28-Mar-06	3.3^{A} ± 0.48 (4)	3.0^{A} ± 0.41 (4)
22-Jun-06	4.3^{A} ± 0.63 (4)	2.0^{A} ± 0.41 (4)
22-Sep-06	3.8^{A} ± 0.63 (4)	1.3^{B} ± 0.75 (4)
Mean	3.0^{A} ± 0.28	2.1^{A} ± 0.30

Appendix 21. Summary of tropical disturbances impacting the Northern Gulf of Mexico from 2004 to 2005. The impacts are those observed on the permanent research plots at Big Branch Marsh NWR during the first two years of research.

Disturbance	Date	Landfall	Impacts
Hurricane Bonnie	12-Aug-04	Apalachicola, FL	None recorded
Hurricane Ivan	16-Sep-04	AL-FL border	Wrack deposition and flooding
T.S. Matthew	10-Oct-04	Cocodrie, LA	Wrack deposition and flooding
Hurricane Cindy	5-Jul-05	Grand Isle, LA	Flooding
Hurricane Katrina	29-Aug-05	LA-MS border	Prolonged flooding, *Spartina patens* marsh ball formation, interior pond formation
Hurricane Rita	23-Sep-05	TX-LA border	Prolonged flooding



Appendix 22. Scatter plot of the effect of change in marsh surface relative elevation prior to (October 2004) and after Hurricane Katrina (October 2005) on the change in vegetative cover of *S. patens*, *S. americanus*, and all other species from October 2004 to October 2006. Linear effect of change in elevation change in vegetative cover as follows: *S. patens* (p=0.492; R^2 = 0.013), *S. americanus* (p=0.380; R^2 = 0.021), all other species (p=0.053; R^2 = 0.192).

VITA

Danielle Renee Meert was born in St. Louis, Missouri, on October 19, 1976, the daughter of Robert and Rosalie Meert. She received her Bachelor of Arts from St. Ambrose University in Davenport, Iowa. After graduation she worked as an English Teacher in South Korea for two years before joining the Peace Corps where she served as an Environmental Education Agent in Moanda, Gabon (Central Africa). Prior to entering graduate school at the University of New Orleans she worked as an Avian Technician for Virginia Tech. Danielle enjoys gardening and traveling and is the proud mother of Lilith Aelita.