2006

# Belowground biomass of Spartina alterniflora: seasonal variability and response to nutrients

Faith Armand Darby
*Louisiana State University and Agricultural and Mechanical College*

# BELOWGROUND BIOMASS OF *SPARTINA ALTERNIFLORA*: SEASONAL VARIABILITY AND RESPONSE TO NUTRIENTS

A Dissertation

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

in

The Department of Oceanography and Coastal Sciences

by

Faith Armand Darby
B. S., Our Lady of Holy Cross College, 2000

December 2006

## ACKNOWLEDGMENTS

I thank God for the opportunity to pursue my Ph.D. and for His continued presence in my life during this journey. I thank my parents, Royal Joseph "man" Armand and Gloria "Momma Glo" Weber Armand for instilling me with a love of knowledge, and especially my sister Mary-Ann, who encouraged me during the hard times and reminded me of my goals. I thank my children for cheering for me from the sidelines. I thank my daughter Autumn, who worked in the lab and understood my enthusiasm for roots. Thanks to my friends Prevalent and Kyron, who thought I was a little strange, but still loved me.

I am grateful for the opportunity to study under the guidance and encouragement of Dr. R. Eugene Turner. Thanks for your personal, financial and academic support. The exposure to wetlands has been rewarding and will never be forgotten. Thank you Dr. Nancy Rabalais and Emily Turner for making me feel welcomed in your home. I also thank my committee members: Dr. R. Gambrell, for his hands-on interest in my research; Dr. Jaye Cable whose compassion after hurricane Katrina made my granddaughter's life a little happier; Vincent Wilson, for his insight and encouragement, and Dr. Billy James William for accepting the position of Dean's Representative.

I thank Gaynell Gibbs and Terry Wimberly for helping me navigate through all graduate school deadlines and paper work. Also, thanks to Eric Swenson for creating the tools to use in my research.

A very special thanks to my fellow students and the Coastal Ecology Institute research associates: Whitney Broussard, Joe Baustian, Jennifer Spicer, Charles Milan, James Lee and John Plunket who helped me with field and lab work. Soraya- thank you for being there to encourage and help me with statistics, my life is richer for having known you. Thank you everyone who has made my dream possible.

**TABLE OF CONTENTS**

## ABSTRACT

*Spartina alterniflora* is a salt marsh macrophyte found from Canada to the Gulf of Mexico which often provides the dominant plant cover. Although *S. alterniflora* is well known for its high aboveground productivity, fifty to ninety percent of the total plant production occurs belowground. No previous studies address the seasonal variation of belowground biomass or the response of above-and belowground biomass to nutrients at the southern limits of its U. S. range. The objectives of this study were to: 1) document the seasonal variability of its above- and belowground biomass and test for responses to various combinations of N, P, and Fe supplements, 2) test the usefulness and variability of three functional indicators of nutrient use efficiency, resorption efficiency, resorption proficiency, and, 3) compare nutrient limitation controls in East coast and Gulf of Mexico salt marshes.

Various combinations of N additions resulted in more aboveground biomass, higher stem densities and longer stem lengths, but had no effect on the amount of belowground biomass. No change in the aboveground biomass observed when P was added, but there was a decrease in the live belowground biomass. The average N : P molar ratios in the above- and belowground tissues, and three resorption indices supported the hypothesis that the accumulation of biomass aboveground was limited by N, and by P belowground. Higher soil respiration and a lower Eh are anticipated additional soil property changes with nutrient enrichment.

The observations from these field trials formed a unified conclusion, which is that the widespread effects of coastal eutrophication leads to lower root and rhizome biomass, belowground production, and organic matter accumulation. The cumulative effects of increased nutrient loadings to salt marshes may be to decrease soil elevation and accelerate the conversion of emergent plant habitat to open water, particularly at the lower elevation range of the plant. These results support management actions supporting coastal marsh conservation through: 1)

reducing nutrient loading to coastal zones and not diverting more nutrients to coastal marshes, 2) solving water quality problems with a multiple nutrient approach, and, 3) choosing monitoring metrics based on both belowground and aboveground plant production.

# CHAPTER 1

# GENERAL INTRODUCTION

Salt marshes are productive marine ecosystems, are habitats for many species, and nursery grounds for several commercially-important species. *Spartina alterniflora* is a salt marsh macrophyte found from Canada to the Gulf of Mexico and often provides the dominant plant cover. *S. alterniflora* is an herbaceous, native, warm-season perennial grass that forms dense vegetative colonies along shorelines and inter-tidal flats. It is a robust and rapidly spreading plant tolerant of fluctuating water depths and salinities ranging from 0 to 35 psu. It spreads primarily by vegetative propagation, producing new stems from an extensive system of underground rhizomes. There are at least two growth forms of *S. alterniflora.* The tall form (1.5 m) is found along estuarine creeks and the short form (0.5 m) may be found in the high marsh (Ornes 1989). Although *S. alterniflora* is well known for its high aboveground primary productivity (Mendelssohn and Morris 2000), fifty to ninety percent of the annual production of *S. alterniflora* in eastern US salt marshes occurs belowground as roots and rhizomes (Valiela et al. 1976; Smith et al. 1979; Pomeroy and Wiegart 1981; Giblin and Howarth 1984). The root and rhizome biomass contributes to the accumulation of organic matter, thus maintaining the marsh's vertical position as sea level rises and the marsh soil compacts. There are no previous studies of the seasonal variations in the above- and belowground biomass of *S. alterniflora* at the southern limits of its U.S. range.

Plant production is usually limited by one or more nutrients, and plants play an important role in nutrient cycling. Plants with high annual productivity, i.e., *S. alterniflora* can extract large amounts of nutrients from their environment and store these nutrients in biomass and litter (Meuleman et al. 2002). It is well-established that nitrogen limits the aboveground production of *S. alterniflora* (Valiela and Teal 1974; Morris 1988; Visser 2006). The production of the roots and rhizomes of *S. alterniflora*, however, may not be higher as nitrogen availability increases.

Salt marsh soil microbes appear to be limited by phosphorus (Sundareshwar et al. 2003), for example, and Valiela et al. (1976) documented a decrease in the belowground biomass with increased nutrient availability. Also, most of the salt marsh fertilization experiments have focused on only nitrogen, and were conducted in Atlantic coast saltmarshes. The individual and synergistic effects of nitrogen, phosphorus, or iron have not been addressed. Learning more about the relationships between plant growth and nutrient limitations is important when viewed within the context of how human activities have increased the availability of nitrogen and phosphorus to coastal systems.

My dissertation research involved documenting the seasonal changes in the above- and belowground biomass of *S. alterniflora* in a Louisiana salt marsh from 2004 to 2005, and identifying when translocation and storage of resources occurred, i.e., when carbon and nutrients moved between the aboveground and belowground compartments. I included tissue analyses and other complementary measurements. I then compared various metrics of the belowground biomass productivity and the root : shoot ratios to those from other locations (Chapter 2).

Two fertilization experiments were conducted to examine the responses of: 1) the below- and aboveground biomass of *S. alterniflora* to additions of various amounts of nitrogen, 2) the below-and aboveground biomass to additions of nitrogen in combination with phosphorus and iron (Chapter 3).

Three functional indicators of nutrient availability were examined to test the usefulness and variability of these three indices in a salt marsh ecosystem: nutrient resorption efficiency, nutrient resorption proficiency, and nutrient use efficiency (Chapter 4). This examination was accomplished by using data on tissue nutrient concentration.

The geographic and regional differences in the above-and belowground responses to nutrient addition are examined in Chapter 5. Nutrient experiments were conducted in East Coast

and Gulf of Mexico marshes dominated by *S. alterniflora* using a single springtime addition of nitrogen, phosphorus or in combination.

Chapter 6 is a brief summary.

## LITERATURE CITED


GIBLIN, A. E. and R. W. HOWARTH. 1984. Porewater evidence for a dynamic sedimentary ion cycle in salt marshes. *Limnology and Oceanography* 29:47-63.

MENDELSSOHN, I. A. AND J. T. MORRIS. 2000. Eco-Physiological Controls on the Productivity of *Spartina alterniflora* Loisel. p. 59-80 *In* Concepts and Controversies in Tidal Marsh Ecology. M. Weinstein and K. Kreeger (eds.), Kluwer Academic Publishing, Dordrecht.

MORRIS, J. T. 1988. Pathways and controls of the carbon cycle in salt marshes. p. 497-510 In The Ecology and Management of Wetlands, D. D. Hooks (eds.), London, C room Helm.

ORNES, W. H. AND D. I. KAPLAN. 1989. Macronutrient status of tall and short forms of *Spartina alterniflora* in a South Carolina salt marsh. *Marine Ecology Progress Series* 55:63-72.

POMEROY, L. R. and R. G. WIEGART. (eds.). 1981. Ecosystem and Population Ecology of a Salt Marsh: A Synthesis. Springer.

SUNDARESHWAR, P. V., J. T. MORRIS, E. K. KOEPFLER, AND B. FORMWALT. 2003. Phosphorus limitation of coastal ecosystem processes. *Science* 299:563-565.

SMITH, K., R. R. GOOD, AND N. F. GOOD. 1979. Production dynamics for above-belowground components of a New Jersey *Spartina alterniflora* tidal marsh. *Estuarine Coastal Shelf Science* 9:189-201

TEAL, J. M. 1996. Interannual variability of a salt-marsh ecosystem. *Limnology and Oceanography* 4:802-809.

VALIELA, I. AND J. M. TEAL 1974. Nutrient limit in salt marsh vegetation, p 563-574 *In* R. J. Reimold and W. H. Queens (eds.), Ecology of Halophytes. Academic Press, New York.

VALIELA, I., J. M. TEAL AND N. Y. PERSSON. 1976. Production and dynamic experimentally enriched salt marsh vegetation: belowground biomass. *Limnology Oceanography* 21:245-252.

VISSER, Y. M. AND C. A. SASSER. 2006. The effect of multiple stressors on salt marsh end-of-season biomass. *Estuaries and Coasts* 29:331-342

# CHAPTER 2

# BELOW- AND ABOVEGROUND *SPARTINA ALTERNIFLORA* PRODUCTION IN A LOUISIANA SALT MARSH

## INTRODUCTION

Wetlands, and particularly tidal salt marshes, have long been recognized for their high rates of aboveground primary production (Whittaker 1975). The belowground biomass component, however, has received only limited attention, primarily because harvest techniques are labor-intensive and may be subjective because of the difficult process of visually separating live and dead roots and rhizomes (White and Howes 1994). It is important to improve our knowledge of roots and rhizomes (R&R) for several reasons. For example, roots and rhizomes are a considerable reservoir in the energy and material cycles in estuarine wetland communities (Schubauer and Hopkinson 1984) and inhibit erosion. The belowground biomass, which contributes to the volume and elevation of the marsh, appears to be much more important than inorganic matter for a marsh to maintain itself once established (Turner et al. 2001). If the belowground accumulation is not sufficient, then a marsh with abundant aboveground plant growth might quickly become open water when plants succumb in a "die-back" (Mendelssohn et al. 1981; Turner et al. 2004).

*S. alterniflora* is a dominant salt marsh macrophyte from Canada to the Gulf of Mexico. *S. alterniflora* is an herbaceous, native, warm-season perennial grass that forms dense vegetative colonies along shorelines and inter-tidal flats. It is a robust and rapidly spreading plant tolerant of fluctuating water depths and salinities ranging from 0 to 35 psu. It spreads primarily by vegetative propagation, producing new stems from an extensive system of underground rhizomes. Fifty to ninety percent of the annual production of *S. alterniflora* in eastern US salt marshes occurs belowground as root and rhizomes (Valiela et al. 1976; Smith et al. 1979; Giblin and Howarth 1984), with root : shoot ratios generally greater than 1 : 1 (Good et al. 1982; Boyer et al. 2000). The width and thickness of a colony are controlled by a number of site-specific conditions such as elevation, shoreline slope, the frequency, depth, and duration of flooding, and

a wide range of conditions along a latitudinal gradient, e.g., temperature and length of the growing season. Compared to plants in the southeastern U.S., for example, plants in the northeast have a short growing period and shoots developing during the summer are dead in the fall (Gallagher and Seliskar 1976; Gallagher 1983). The quantity and timing of the storage of the underground reserves and their translocation for aerial growth would be expected to change along this gradient.

The process of biomass translocation of nutrients from senescing leaves and shoots to belowground roots and rhizomes can be inferred from seasonal changes in the live biomass, while the changes in the dead biomass pool provide some indication of the decomposition rates and long-term accumulation of biomass (Conner and Chmura 2000; Gallagher 1983). The timing of the peak and minimum biomass must be known to understand the translocation and/or biomass storage dynamics, and knowledge of the temporal and spatial variability in translocation of the belowground biomass is essential to correctly interpret marsh accretion processes. The sampling frequency must be sufficient to precisely tell when the translocation of nutrients from above to belowground occurs (Gallagher 1983). Monthly sampling increases the possibility of obtaining more accurate information about the recoverable underground reserves, for example.

There are no previous studies of the seasonal variations in the above- and belowground biomass of *S. alterniflora* at the southern limits of its U.S. range. We attempted to fill this data gap by studying a Louisiana salt marsh in 2004 to 2005, and included tissue analyses and other complementary measurements, and compare the results to those from other locations.

## METHOD AND MATERIALS

### Field Sampling

The study was conducted in *Spartina alterniflora* dominated salt marsh located about 0.5 km west of the Louisiana Universities Marine Consortium (LUMC0N) laboratory, in Cocodrie,

LA (29° 15'N, 91° 21' W; Fig. 2.1). The tide range during sampling period was -0.23 to 0.59 m with a mean of 0.18 m. Tides occurred once or twice daily, and the mean tidal range changed seasonally in response to cold front passages in the winter and storm events in summer (Turner 2001). The salinity ranged from 7 to 20 psu.

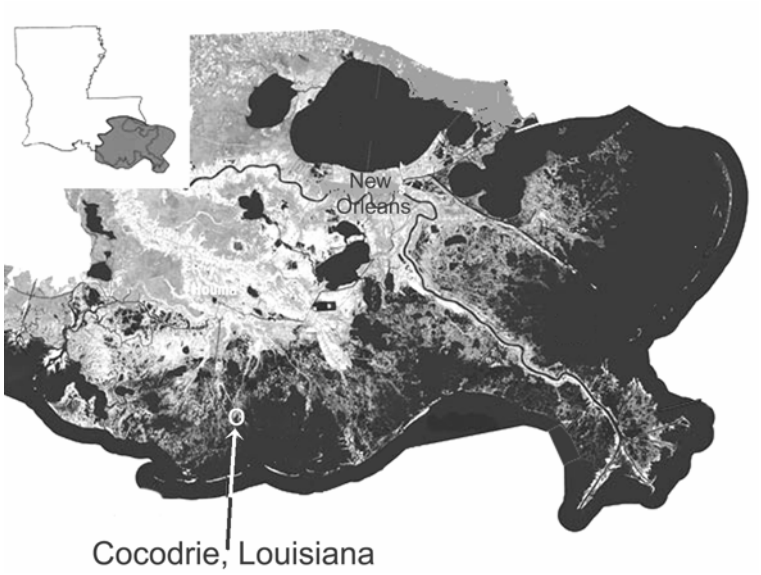


Fig. 2.1. The sampling location in Cocodrie, LA.

The monthly variation of above- and belowground biomass of *S. alterniflora* was documented from March 2004 to March 2005, and again in March 2006. A monospecific stand of *S. alterniflora* was sampled from a series of boardwalks constructed to facilitate sampling and to minimize damage to the marsh. The aboveground *S. alterniflora* was harvested by clipping vegetation at the sediment surface in 3 adjacent replicate 0.25 $m^2$ plots designated left, center, and right. All standing live and dead culms and litter were removed and placed into pre-labeled plastic bags and transported to the Louisiana State University (LSU) processing lab. Dead shoots and leaves were identified by their yellowish or brownish coloration and separated from living material. The live or dead plant material was put into pre-labeled paper bags, dried at 60° C for approximately 72 hours and weighed to the nearest 0.01 g. The annual net primary production was estimated using two harvest methods: the Smalley method corrects for mortality

between samples by summing monthly changes in live biomass and in dead biomass (Smalley 1959), and the Max-Min method uses differences in live biomass throughout the growing seasoning.

The belowground biomass was determined by collecting soil using a 40 cm long stainless steel tube with sharpened edges. An 11 cm diameter x 30 cm long sediment core was taken in the middle of each plot after the aboveground biomass sample was collected. The cores were extruded in the field and sliced into 0-10 cm, 10-20 cm and 20-30 cm segments. Each segment was put in labeled plastic bags and placed in a cooler for transport to the LSU lab where they were refrigerated until processed. Each segment was washed in a 1 mm sieve over a 0.5 mm sieve to prevent the loss of dead and fine root material. Live roots and rhizomes were separated from dead material with a suture set under running water for better separation (live roots and rhizomes are white and turgid, dead materials are dark and flaccid). Root color can be variously tinged pink or orange, possibly because pigmentation zones contain feeding deterrents, i.e., roots colonized by arbuscular mycorrhizal fungi are often yellow. The physiological significance of these pigments is unclear (Alastair et al. 2002). Discolored turgid roots were defined as live roots. Dead material included partially decayed root material. Live roots and dead belowground material were placed in paper bags, labeled, and dried to a constant weight at $60^{o}$ C, and weighed to the nearest 0.01 g. All belowground materials (roots and rhizomes) were sorted by a single individual (FAD) to assure continuity of sample processing, and to reduce potential sources of error. Monthly root + rhizome : shoot ratios (R&R : S) were determined by averaging the dry weight of the live above- and belowground biomass from the 3 plots. Dried plant and root material were ground in a General Electric grinder and sent to the LSU Soil Testing and Plant Analysis Lab where they were analyzed for metal and nutrient content.

N : P molar ratios were calculated to determine whether the site was N limited or P limited (Koerselman and Meulemen 1996) and to serve as a baseline measurement in a separate nutrient enrichment experiment (Chapter 3). A N : P molar ratio < 33 indicates N limitation whereas a N : P ratio > 33 suggests P limitation (Verhoeven et al.1996; USEPA 2002).

The results of a statistical analysis of monthly above- and of belowground biomass were compared to determine if the means were significantly different (at $p < 0.05$) based on Tukey's adjustment. The analysis was carried out using the general linear model procedure (ANOVA; SAS 2002-2003. A logarithmic transformation was used to test for normality of distribution.

## RESULTS

Aboveground Biomass

The live aboveground biomass was lowest in March 2004 (114.1 g $m^{-2}$), and increased steadily until the peak in September (876.8 g $m^{-2}$; Fig. 2.2). The biomass in March 2005 (589.9 g $m^{-2}$) was five times that of March 2004. March 2004 (114.1 g $m^{-2}$) and in March 2005 (589.9 g $m^{-2}$) were statistically different from each other. Thirteen monthly samples of the live aboveground biomass ranged from a minimum of 114.13 ± 30 g dry wt $m^{-2}$ (μ ± 1 Std. error; March 2004) to a maximum of 876.8 ± 23 g dry wt $m^{-2}$ (μ ± 1 Std. error; September 2004). The peak biomass of September (876.8 g $m^{-2}$) was significantly different ($p < 0.0001$) from values for the summer and winter months.

The estimates of annual aboveground production using Smalley and Max-min methods were 1280.7 g dry wt $m^{-2}$ $yr^{-1}$ and 762 g dry wt $m^{-2}$ $yr^{-1}$, respectively. A statistically significant difference in biomass (ANOVA; $p < 0.0001$) in the seasonal biomass was seen from month-to-month. No discernable patterns were seen among months in the average number of stems or stem diameter. An increase in maximum stem height peaked between December and February

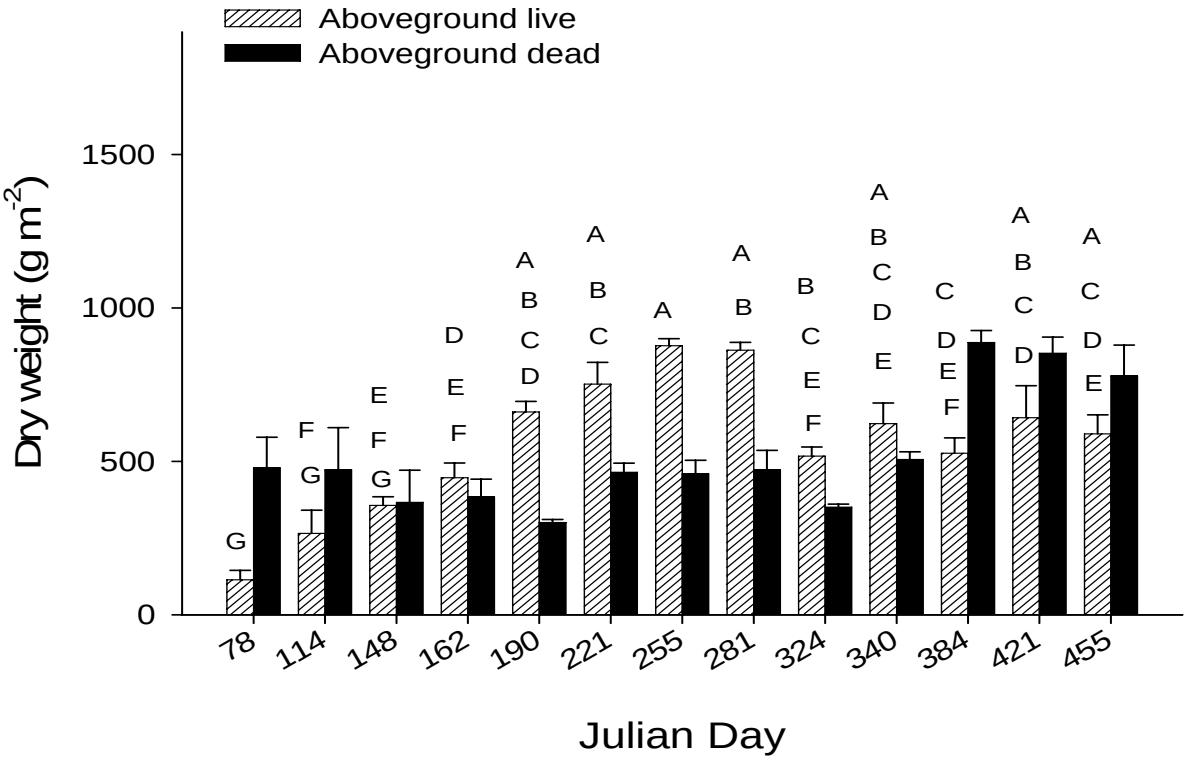


Fig. 2.2. The mean (± 1 Std. Err.) of three replicates of monthly aboveground live and dead biomass. The letters indicate the results of a Tukey's Studentized Range Test for differences in aboveground live biomass by month (g $m^{-2}$). Means with the same letter are not significantly different from each other (significance level < 0.05).

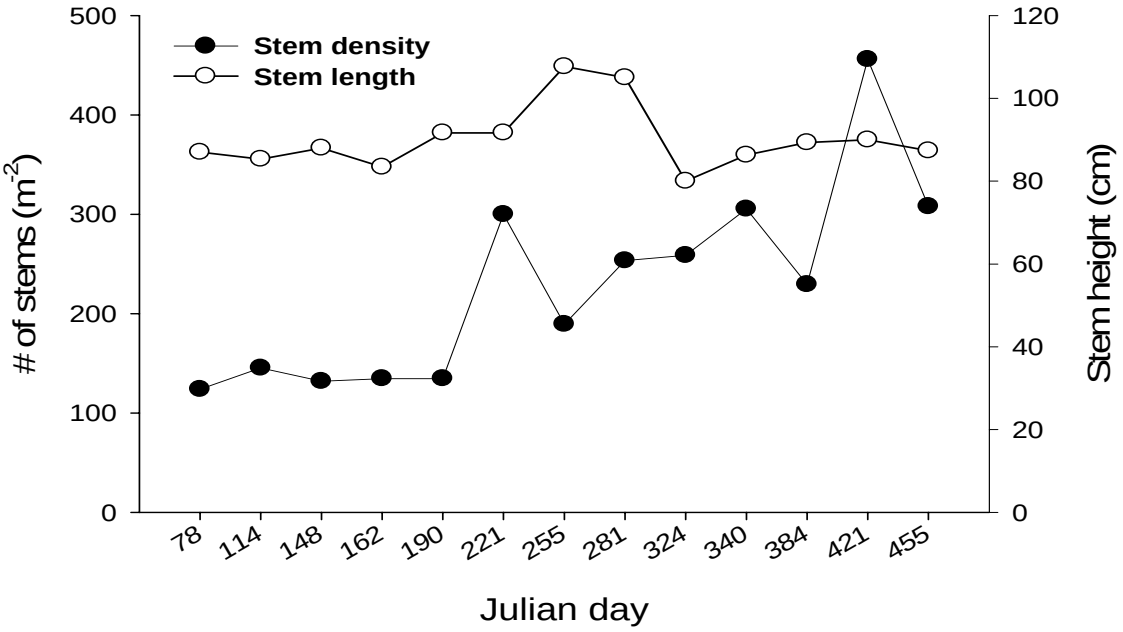


Fig. 2.3. The monthly values of the average stem density and length. One standard deviation was <10% of the mean in all samples.

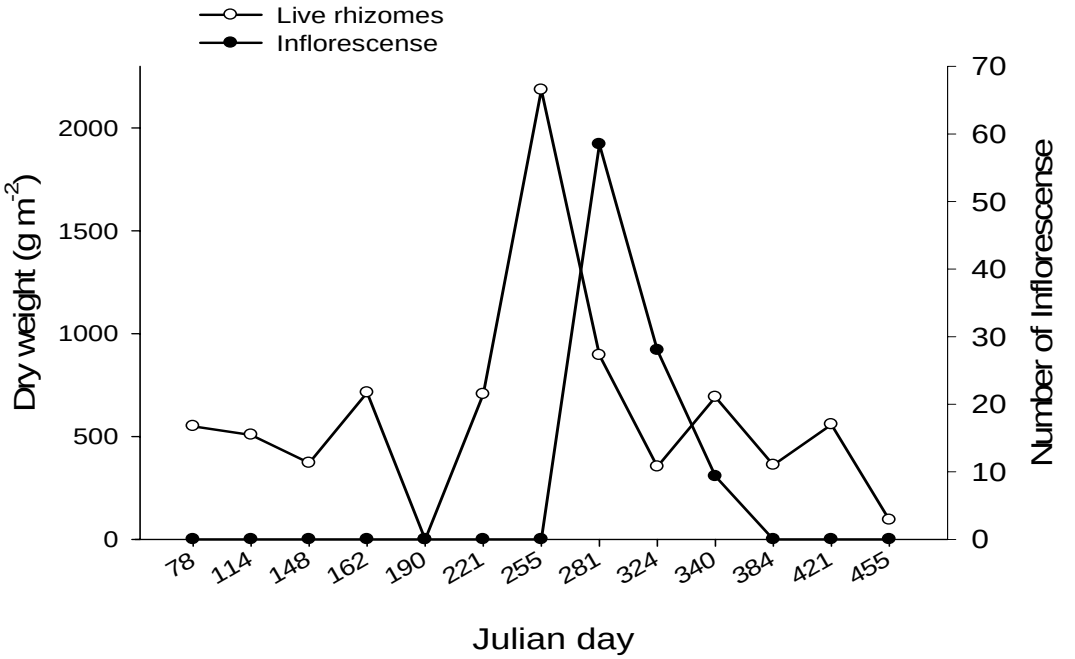


Fig. 2.4. Monthly values of rhizomes biomass (g $m^{-2}$; open circles) and number of stems with inflorescence (# $m^{-2}$; closed circles). Values are the mean of 3 replicates. The rhizome biomass increased after Julian day 190 (July) and peaked between 221 and 255 (August –September). A decline in rhizome biomass occurred as inflorescence production increased.

(Fig. 2.3). Inflorescence appeared in October (58 $m^2$) and lasted until December (9 $m^2$; Fig. 2.4).

The amount of dead aboveground biomass slightly declined from March (479 ± 100; (μ ± 1 Std. error) to July (301 ± 9; (μ ± 1 Std. error) as the aboveground live biomass increased (Fig. 2.2). The highest accumulation of aboveground dead biomass was in January (887.4 ± 3.8; (μ ± 1 Std. error) and remained relatively high through March 2005. The dead biomass decreased during the growing season as the amount of live biomass increased (Fig. 2.2). The highest accumulation of dead aboveground biomass was documented in January 2005 (887.4 ± 3.8; (μ ± 1 Std. error).

Belowground Biomass

A proliferation of live roots and rhizomes (1110 and 550 g $m^{-2}$, respectively) occurred in March 2004 prior to the spring burst in vegetative growth with a corresponding decrease in belowground biomass as the aboveground biomass increased (Fig. 2.5). The root biomass ranged from 76 ± 31 to 383 ± 69 g $m^{-2}$ (μ ± 1 Std. error) throughout the 13 month sampling period. Rhizomes virtually disappeared in July. A second peak of belowground biomass occurred in September (2337 g $m^{-2}$), when rhizomes comprised 2185 g $m^{-2}$ of the total biomass, and then declined in October with the production of inflorescence (58 ± 21 $m^{-2}$; μ ± 1 Std. error) indicating that there was some translocation from belowground to aerial production (Figs. 2.2 and 2.5). The rise and fall of rhizome biomass from September to October represented the majority of the total annual belowground production. The total belowground production for the year, obtained using the Smalley method, was 7887 g $m^{-2}$ $y^{-1}$. A logarithmic transformation for normality in distribution resulted in a statistically significant difference between the mean of total belowground biomass ($P<0.003$; R&R), and for the mean biomass of rhizomes ($P<0.001$).

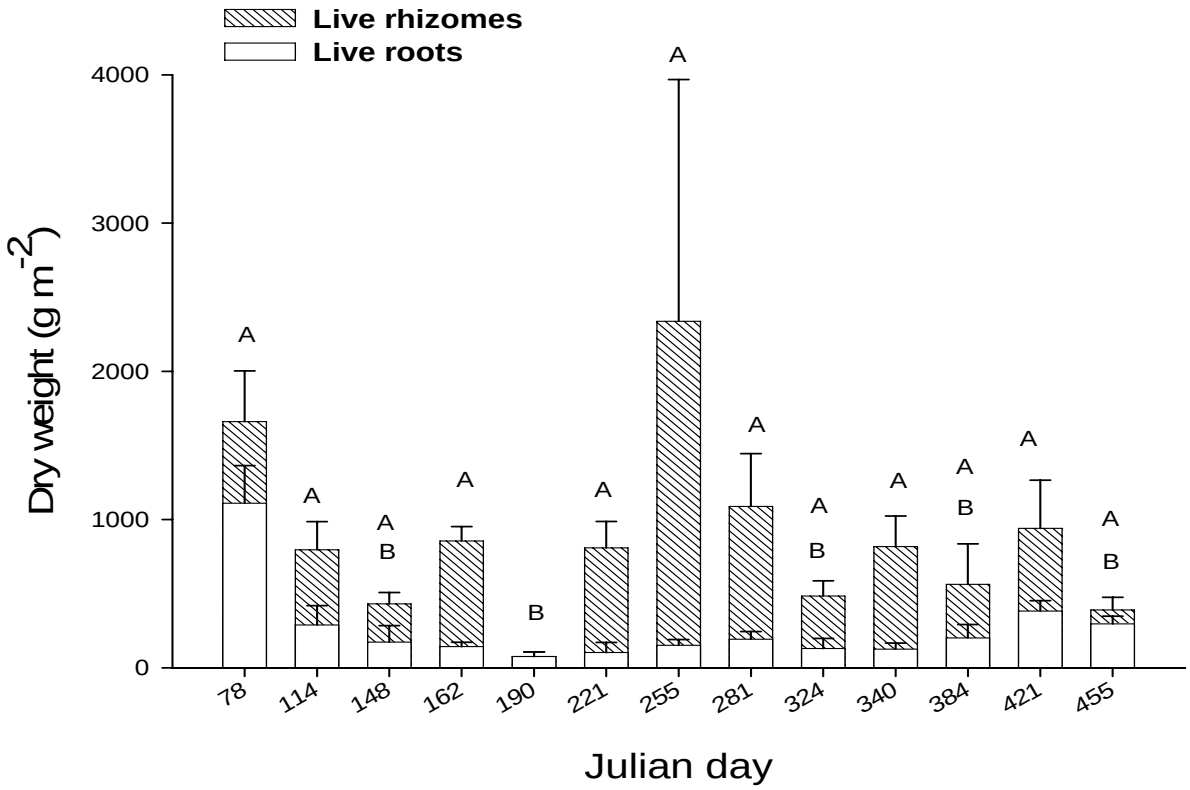


Fig. 2.5. The mean (± 1 Std. Err.) of three replicates of monthly root and rhizome biomass. Letters indicate the results of a Tukey's Studentized Range Test for differences in rhizome biomass by month (g $m^{-2}$). Means with the same letter are not significantly different from each other (significance level < 0.05). No significant differences were seen in root biomass by month. The high error bar for day 225 is the result of one high value.

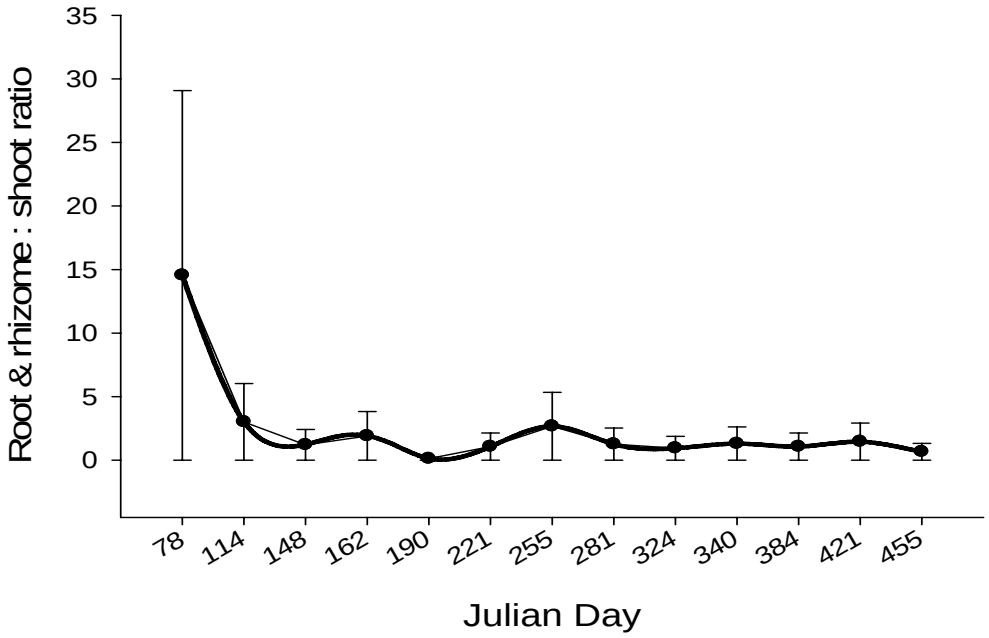


Fig. 2.6. The root and rhizome : shoot ratio (± 1 Std. Err.) between monthly mean values. The root and rhizome : shoot ratio in March 2004 (day 78) equaled 14, then declined and remained stable for the remainder of the sampling period..

Table 2.1. Mean biomass (g $m^{-2}$) of live roots and rhizomes in three sediment layers of *Spartina alterniflora*. The data represent the mean ± 1 standard deviation for 12 monthly samples. The rhizome biomass exceeds that of roots for all three segments.

| | 0-10 cm | 10-20 cm | 20-30 cm | 0-30 cm |
|---|---|---|---|---|
| Roots | 477.9 ± 86 | 165.7 ± 72 | 108.9 ± 95 | 752.5 ± 228 |
| Rhizomes | 734.0 ± 225 | 1080.1 ± 269 | 137.9 ± 92 | 1952.0 ± 427 |

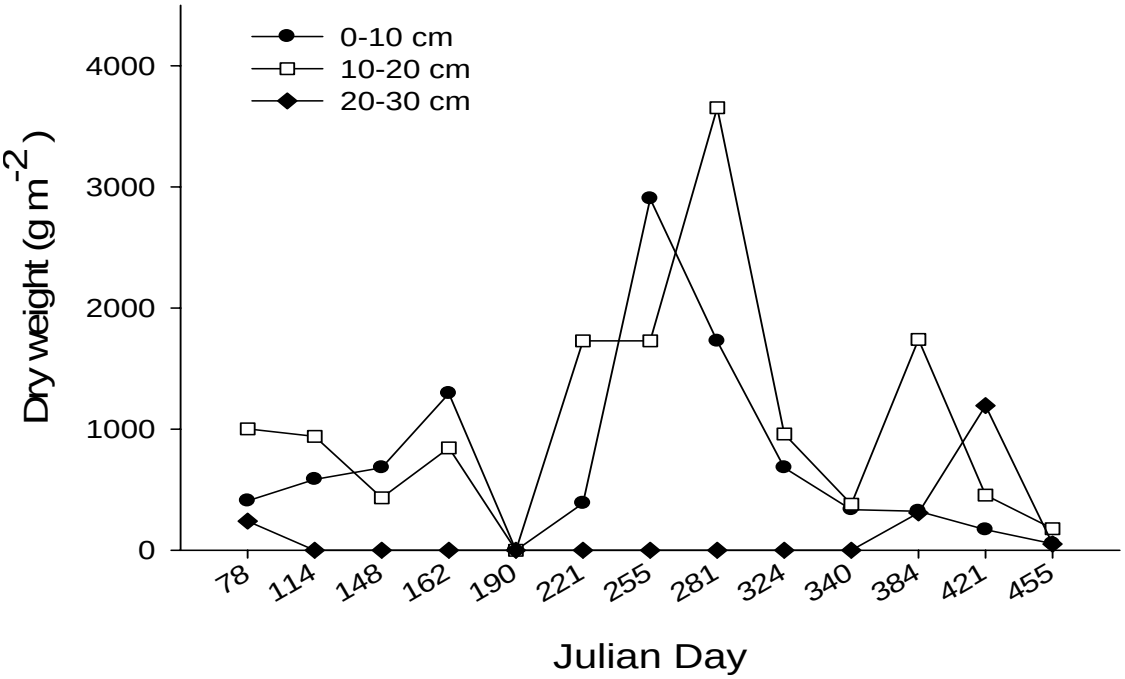


Fig. 2.7. The mean of three replicates of belowground rhizome biomass (g dry weight $m^{-2}$) in three different depths by month. Rhizomes were located in the 0-20 cm layer for most of the year. Rhizomes extended to a depth of 30 cm prior to the spring growth of aboveground biomass and peaked in fall and winter.

The mean R&R : shoot ratio was 2.6 ± 1, ranging from a minimum of 0.12 in mid-summer (July) to a maximum of 14.5 in early spring (March 2004; Fig. 2.6).

The largest amount of the root biomass was in the upper 1-10 cm throughout the one year sampling period (Table 2.1). In March, before the spring growth of aboveground biomass, the belowground biomass of roots was fairly uniform with depth, extending beyond 30 cm, and was sparse in the 20-30 cm core layer. This result for the roots was in contrast to the seasonal patterns observed in the vertical profile of live rhizome biomass (Fig. 2.7). Rhizomes were noticeably absent from the upper 0-10 cm layer with the exception in March (136 g $m^{-2}$), and slowly decreased from May to June from 144 to 282 g $m^{-2}$. The rhizome biomass nearly disappeared from all three layers by July, and were at highest levels in September (0-10 cm = 967 g $m^{-2}$; and 10-20 cm = 1218 g $m^{-2}$) before the production of inflorescence in October, but were absent in 20-30 cm layer. Rhizomes were present throughout the 0 to 30 cm profile from January through March 2005.

The depth profile of the dead belowground biomass exhibited a different pattern from the live fraction. Unlike the live R&R fraction, the dead fraction of the belowground biomass was greatest in the 20-30 cm section. The pool of dead biomass was consistently larger than the pool of live biomass (Fig. 2.8). The dead, for example, was 90% of the total biomass in May and 98% in July. The increases in the percent biomass in the dead fraction coincided with decreases in the live belowground biomass.

Tissue Nutrient Content

The monthly standing stock of N (NSS; g $m^{-2}$) was documented for the sampling period from March 2004 to February 2005. The NSS in the aboveground live biomass in March 2004 was 1.5 g N $m^{-2}$, and ranged between 1.5 to 8.8 g N $m^{-2}$ (Table 2.2). The NSS increased from 2.1

to 8.8 g N $m^{-2}$ from April to February. The NSS in senescing leaves and litterfall was lower than in the live biomass and ranged from 4.0 in March 2004 to 6.7 in February 2005 (g N $m^{-2}$). The standing stock of phosphorous (PSS) as live aboveground biomass ranged from 0.23 to 1.7 g P $m^{-2}$ for the entire sampling period (Table 2.2). The PSS was higher in the aboveground live biomass than in the aboveground dead biomass (maximum = 0.65 g P $m^{-2}$ in January 2005: minimum = 0.08 g P $m^{-2}$ in May). The levels of NSS in the belowground live biomass were comparable to that aboveground live biomass, with two exceptions in March 2004, when the NSS was 21.4 and 1.5g N $m^{-2}$, respectively, and again in September (21.4 belowground and 6.4 aboveground). However, the NSS in the belowground dead biomass was lowest in January 2005 (19.0 g N $m^{-2}$) and highest in May 2004 (66.7 g N $m^{-2}$). No apparent differences were observed in the PSS in the belowground live and dead biomass (range 1.4 - 0.07 g P $m^{-2}$ in the belowground live biomass and 0.6- 1.4 g P $m^{-2}$ in the belowground dead biomass; Table 2.2). The nitrogen : phosphorus molar ratios ranged from 14.2 to 20.2 in the aboveground live biomass and was 26.7 to 45 in belowground live biomass (Table 2.2). An analysis of the tissue nutrient concentrations indicated that the N: P molar ratios < 33 in the aboveground biomass and >33 in belowground biomass (Table 2.2; Fig.2.9).

The amount of aboveground biomass was substantially smaller in March 2004, compared to March 2005 (114 and 588 g $m^{-2}$, respectively), and 276 g $m^{-2}$ in 2006; Fig. 2.10). The belowground biomass in March 2004, 2005 and 2006 was 1660, 390, and 313 g $m^{-2}$, respectively. The corresponding R&R : S ratios were 14.5, 0.7, and 1.1 (Fig. 2.10).

The annual belowground productivity was estimated to be 7887 g $m^{-2}$ $yr^{-1}$ using the Smalley method. Southern marshes from South Carolina to Georgia have an estimated belowground productivity ranging from 777 to 4780 g $m^{-2}$ $yr^{-1}$, while northern marshes i.e., Massachusetts and New Jersey, ranged from 2300 to 3500 g $m^{-2}$ $yr^{-1}$ (Table 2.3). The R&R : S

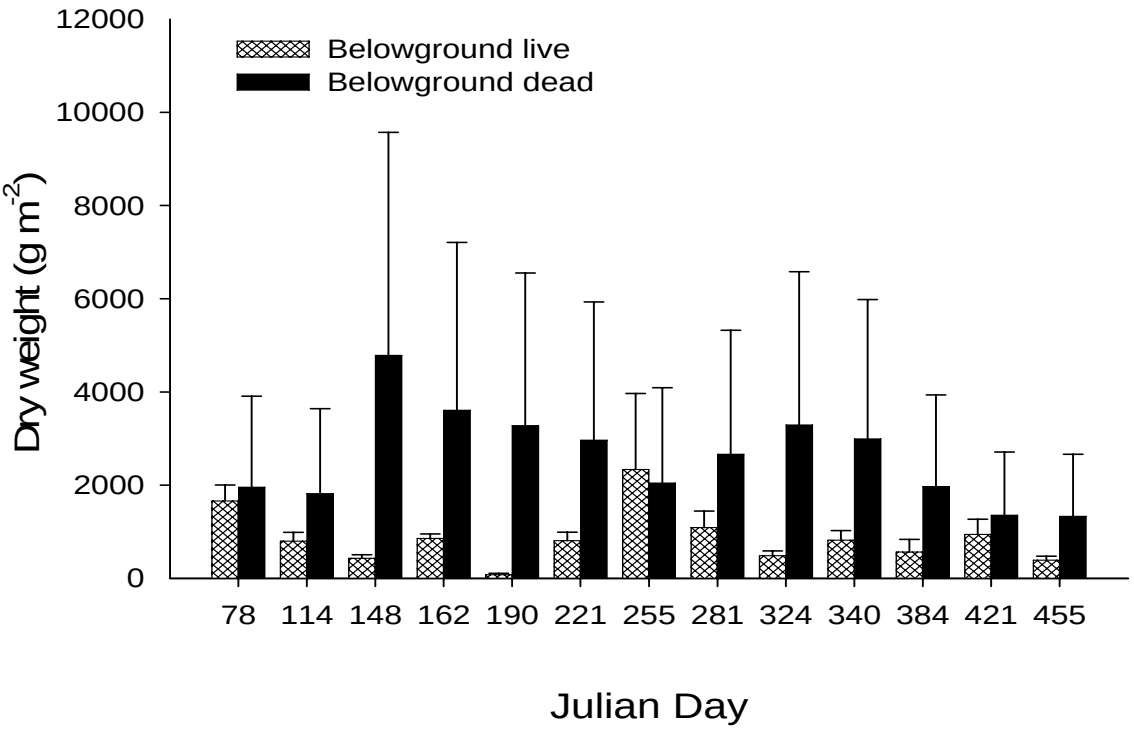


Fig. 2.8. The monthly belowground live and dead biomass of root and rhizomes. Values represent the mean of three replicates (± 1 Std. Err.). There were virtually no rhizomes in July (Julian day 190).

Table 2.2. Monthly nitrogen and phosphorous standing stock (g $m^{-2}$) of aboveground and belowground live and dead biomass and N : P ratios. The highest average monthly value and average N : P ratios for each column are listed in **bold**.

| | Aboveground | | | | | | Belowground | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Julian day | Nitrogen | | Phosphorous | | N : P | | Nitrogen | | Phosphorous | | N : P | |
| | live | dead | live | dead | live | dead | live | dead | live | dead | live | dead |
| 78 | 1.5 | 4.0 | 0.23 | 0.43 | 14.2 | 20.6 | **21.4** | 23.2 | 1.33 | 1.27 | 45 | 48.8 |
| 114 | 2.1 | 3.3 | 0.42 | 0.19 | 10.9 | 39.8 | 9.3 | 31.1 | 0.6 | 0.97 | 34.5 | **74.2** |
| 148 | 2.6 | 2.2 | 0.51 | 0.08 | 11.1 | **62.8** | 3.1 | **66.7** | 0.33 | 2.11 | **52.8** | 71 |
| 162 | 2.8 | 2.6 | 0.51 | 0.13 | 12.2 | 45.5 | 6.4 | 59.5 | 0.81 | 1.93 | 17.4 | 69.8 |
| 190 | 6.0 | 2.1 | 0.66 | 0.10 | **20.2** | 47.2 | 0.72 | 37.0 | 0.07 | 1.12 | 38.8 | 58.4 |
| 221 | 6.9 | 2.4 | 0.75 | 0.10 | 17.0 | 53.6 | 8.2 | 41.9 | 0.62 | 1.56 | 45.7 | 61.3 |
| 255 | 6.4 | 2.4 | 0.87 | 0.23 | 16.3 | 23.3 | **21.4** | 28.3 | **1.40** | **1.76** | 37.6 | 36 |
| 281 | 8.2 | 2.6 | 1.06 | 0.24 | 17.1 | 23.3 | 9.8 | 33.1 | 0.81 | 2.11 | 26.7 | 30.7 |
| 324 | 4.6 | 2.2 | 0.51 | 0.21 | 20.1 | 22.7 | 5.2 | 50.0 | 0.31 | **2.23** | 41.9 | 49.2 |
| 340 | 7.0 | 3.2 | 0.90 | 0.35 | 17.3 | 20.5 | 9.1 | 45.2 | 0.65 | 2.17 | 35.2 | 46.8 |
| 384 | 7.0 | 5.8 | 0.85 | **0.65** | 18.2 | 19.8 | 6.5 | 31.1 | 0.39 | 1.64 | 33.4 | 42 |
| 421 | **8.8** | **6.7** | **1.17** | 0.53 | 16.6 | 27.7 | 9.4 | 19.0 | 0.7 | 0.93 | 34.5 | 42.3 |
| Average | 5.3 | 3.3 | 0.70 | 0.27 | 15.9 | 33.9 | 9.2 | 38.8 | 0.7 | 5.33 | 37.0 | 52.5 |

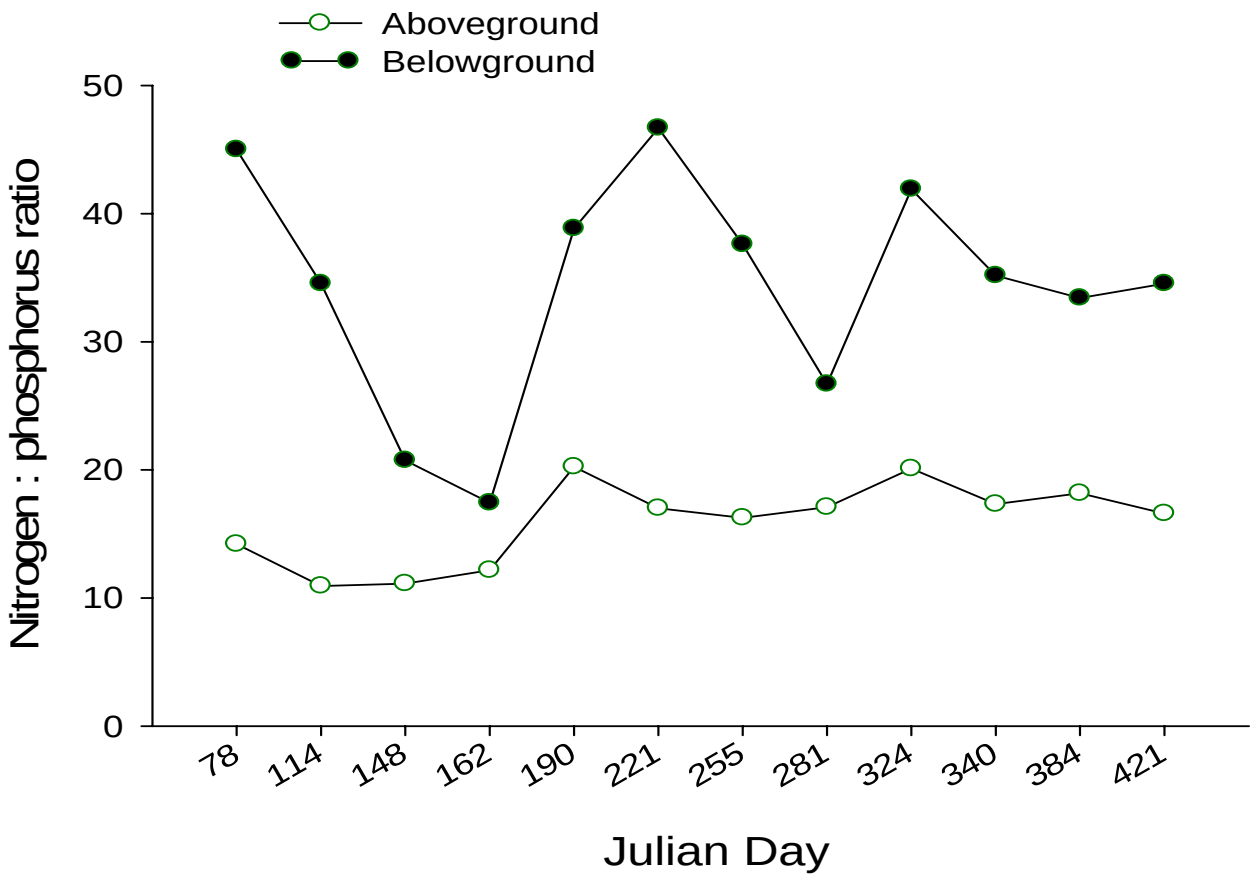


Fig. 2.9. The monthly N: P molar ratios of live above- and belowground biomass (<< 33 or >> 33) are considered to be N or P growth limited, respectively. The above graph indicates that the accumulation of aboveground biomass (open circles) was limited by N and the accumulation belowground biomass (closed circles) was limited by P.

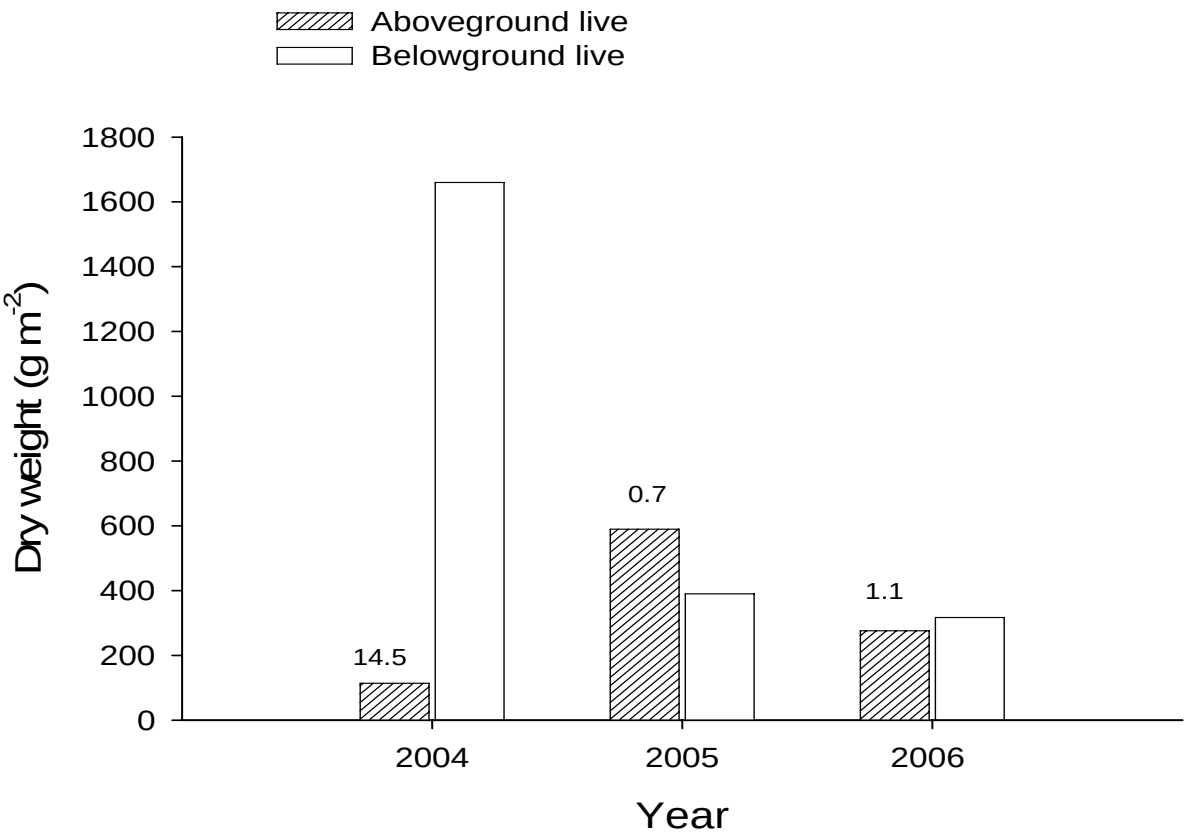


Fig. 2.10. Year-to-year variation in above- and belowground biomass in March from 2004 to 2006. The data represent the mean value of 3 replicates. The root : shoot ratio are indicated by the number above bars.

Table 2.3. Published values of belowground productivity (g dry wt $m^{-2}$ $yr^{-1}$) for *Spartina alterniflora* marshes. A variety of techniques were used to obtain these estimates (noted by letters). NR: height form is not reported.

| Sampling location | Height Form | Productivity (g dry wt $m^{-2}$ $yr^{-1}$) | Source |
|---|---|---|---|
| Nova Scotia, Canada | NR | 1051[a] | Livingstone & Patriquin (1981) |
| Massachusetts, USA | NR | 3500[b] | Valiela et al. (1976) |
| New Jersey, USA | Short | 2300[c] | Smith et al. (1979) |
| Virginia, USA | Medium | 676[d] | Blum (1993) |
| | Short | 2143[d] | Blum (1993) |
| North Carolina, USA | Short | 460[d] | Stroud & Cooper (1968) |
| | Tall | 500[d] | Stroud (1976) |
| South Carolina, USA | Short | 5445[e] | Dame & Kenny (1986) |
| | Medium | 775[e] | Dame & Kenny (1986) |
| | Tall | 2460[e] | Dame & Kenny (1986) |
| Georgia, USA | Short | 2020[c] | Gallagher & Plumley (1979) |
| | Tall | 2110[c] | Gallagher et al. (1980) |
| Georgia, USA | Medium | 4780[e] | Schubauer & Hopkinson (1984) |
| Louisiana, USA | Short | 7887[e] | This study |
| Brazil | NR | 569[f] | Lana et al. (1991) |

Key to productivity estimation methodology: [a] maximum live biomass; [b] maximum-minimum mass of dead materials; [c] maximum-minimum mass of total macro-organic material; [d] maximum-minimum mass of live biomass; [e] Smalley (1959); [f] Peak standing live and dead.

Table 2.4. Root + rhizome : shoot (R&R : S) ratios for *Spartina alterniflora* tall and short forms for several locations.

| Height form | R&R : S | Location | Source |
|---|---|---|---|
| Tall | 1.43 | Georgia | Gallagher (1974) |
| | 0.3-0.4 | North Carolina | Stroud (1976) |
| | 4.53 | New Jersey | Good & Frasco (1979) |
| | 8.25 | Massachusetts | Valiela et al. (1976) |
| Short | 3.72 | Alabama | Stout (1978) |
| | 48.9 | Georgia | Gallagher (1974) |
| | 1.2-1.3 | North Carolina | Stroud (1976) |
| | 4.7 | New Jersey | Smith et al. (1979) |
| | 5.4 | New Jersey | Good & Frasco (1979) |
| | 2.6 | Louisiana | This study |
| | 4.8 | Brazil | Lana et al. (1991) |

ratio in Louisiana was 2.6, which is within the range of values reported for other locations (Table 2.4).

## DISCUSSION

The seasonal aboveground biomass at the study site was lowest in March 2004 (114.1 g $m^{-2}$) and highest in September (876.8 g $m^{-2}$) and the annual aboveground production using the Smalley method was 1280.7 g dry wt $m^{-2}$ $yr^{-1}$. Theses values are within the range of previous estimates, which vary widely. Visser et al. (2006), for example, reported on a study conducted from 1978 to 1995 in two Louisiana marshes (at Airplane Lake and Lake Jessie). Plant biomass was harvested at these sites in September for most years, and they reported that the average peak biomass ranged from a high of 1,698 and 1,261 g $m^{-2}$ (1986) at Airplane Lake and Lake Jessie, respectively, and a low of 818 g $m^{-2}$ (1980) at Airplane Lake and 473 g $m^{-2}$ (1993) at Lake Jessie. Kaswadji et al. (1990) reported a similar estimate of the annual aboveground production for Airplane Lake using the same method (1113 g $m^{-2}$ $yr^{-1}$), and the peak standing crop in their study occurred in August (831 g $m^{-2}$). They also reported a relatively low standing biomass throughout the winter month. Perhaps, the lower values in aboveground biomass reported by Kadwadji et al. (1990) during the winter months, compared to the higher values of this study, are because the winter of 2004-05 was a relatively warm year.

The sampling frequency affects how well the peak standing crop is identified. Hopkinson et al. (1978), for example, sampled for 2 years at 8 week intervals which may have obscured the occurrence of the precise peak in the aboveground biomass.

The amount of aboveground dead biomass decreased in the spring as the amount of aboveground live biomass increased and with small fluctuations until winter. The seasonal variations in the aboveground dead biomass is attributable to variations in the turnover plant matter from live to dead, decomposition rates, and tidal flushing. On an annual basis the lowest

live : dead ratios have been reported in warmest climates of where this plant exists (Turner and Gosselink 1975; Lana et al. 1991).

The seasonal variations in belowground biomass were more pronounced than the changes in the live aboveground biomass (Figs. 2.2 and 2.8). Some have speculated that the extended growing season in southern marshes and the mild winter conditions there may minimize the amount of translocation between above- and belowground biomass pools (Good et al. 1982; McIntire and Dustan 1976). I found, however, that the amount of roots and rhizomes (R&R) declined with the onset of the spring growth of aboveground biomass, indicating a substantial translocation of resources from belowground to aboveground plant organs. Furthermore, there was a decline in rhizome biomass in September as the production of inflorescence increased (58 $m^{-2}$) indicating that there was some translocation of carbon and nutrients from belowground to aboveground plant organs. The rise and fall of rhizome biomass at this time represented the majority of the annual belowground production (Smalley method = 7887 g $m^{-2}$ $y^{-1}$). There was usually much more biomass as rhizome than roots, the exceptions being in March (roots 61% vs. rhizome 39%) and in July (100% roots). Schubauer and Hopkinson (1984) also found that rhizomes made up a greater portion of belowground biomass for a Georgia salt marsh. The belowground production in this Louisiana marsh is the highest reported value for a *S. alterniflora* marsh.

Seasonal patterns were observed in the depth profile of the live belowground biomass. The root biomass was substantial in the 30 cm soil profile early in the growing season, and then declined in all segments, which is consistent with the idea that there was a translocation of resources from belowground to aboveground production. Roots were concentrated in the top 0-10 cm for most of the 13 month sampling period, which may be related to higher rates of nitrogen fixation (Valiela et al. 1976). Gross et al. (1991) noticed the same pattern in the R&R

distribution in the soil profile for salt marshes ranging from Georgia to Nova Scotia. A noticeable seasonal change in how plant biomass was distributed with depth is the depth profile of rhizomes. Two major translocation events were identified, attributable to rhizome function, i.e. reproduction and storage. Just before the onset of the growing season and the fall, there were rhizomes present which declined with the onset of increased aboveground plant growth. I conclude that while the length and timing of the growing season varies along a latitudinal gradient, similar seasonal changes in root and rhizome biomass accumulations occur in Gulf of Mexico and Atlantic coast salt marshes.

The amount of dead belowground biomass increased in the spring, and accounted for 90% of the total biomass in May and 98% in July. The amount of live belowground biomass was lower than the amount of dead belowground biomass in 12 of 13 sampling trips. The amount of dead belowground biomass increased with depth, and consisted largely of highly decomposed roots and rhizomes in the 20-30 cm layer.

The seasonal patterns in NSS and PSS in the aboveground live biomass were similar. The NSS and PSS increased during the fall through winter and decreased during the active growing season. The dilution of tissue nitrogen as aerial biomass increases is one possible cause of the lower NSS levels as plant biomass increased (Ornes and Daniel, 1989). The NSS in belowground live biomass was comparable to that of the aboveground fraction, but the PSS in the belowground biomass was lower than that of the aboveground biomass. The PSS remained low the in fall and winter, and increased slightly during the growing season. The low PSS may have been caused by an increase in reducing conditions resulting from higher summer tides and increased duration of flooding which would make P more available.

The average N : P molar ratios in the aboveground plant tissue was < 33, indicating nitrogen limitation, but the N : P molar ratios in the belowground tissue was >33.

Consequently, the often-stated conclusion that aboveground biomass accumulation is limited by N appears true, but the belowground production appears limited by P. This conclusion, if substantiated, indicates a more complex nutritional status for water quality managers than a single-nutrient control perspective.

The amount of organic accumulation in these salt marsh sediments averages about 0.06 g $cm^{-2}$ $y^{-1}$ (Turner et al. 2001), which is about 10% of our estimate of the total annual belowground production. There are many ways to have a large effect on organic matter accumulation, because relatively large amounts of nutrients and carbohydrates are translocated between above- and belowground tissues throughout the year. A small change in the biomass production belowground, perhaps from a change in nutrient loading, could result in less (or more) biomass available to the aboveground plant tissues, or vice-versa, and have a dramatic affect on the long-term sustainability of the salt marsh. DeLaune et al. (1994) used an herbicide to kill the aboveground plant tissues, and there was a subsequent 15 cm fall in the plant's hummock surface within 2 years. This amount of vertical change would be difficult for *S. alterniflora* to adjust to, given its narrow tolerance to flooding (Mckee and Patrick 1988).

All of these monthly, seasonal and interannual changes in biomass above- and belowground demonstrate that the evaluation of the salt marsh ecosystem cannot be understood or evaluated in terms of only what is happening aboveground, or as though what happens aboveground is proportional or a satisfactory substitute indicator of what is driving changes belowground – and vice versa. Furthermore, it may be that, because of the dominance of the changes in biomass pools belowground compared to aboveground, what happens belowground may be more influential to the long-term maintenance of the salt marsh, than are changes in the aboveground components.

## LITERATURE CITED


ALASTAIR, F. 2002. Characteristics and function of root systems. p. 15-32 *In* Y. Waisel, A. Eshel and U. Kafkafi (eds.), Plant Roots: The Hidden Half. New York, Basel, Marcel Dekker, Inc.

ALEXANDER, C. E., M. A. BROUTMAN, AND D. W. FIELDS. 1986. An inventory of the coastal wetlands of the USA. National Oceanic and Atmospheric Administration. Rockville, MD.

BLUM, L. K. 1993. *Spartina alterniflora* root dynamics in a Virginia marsh. *Marine Ecology Progress Series* 102:169-178.

BOYER, K. E., J. C. CALLAWAY, AND J. B. ZEDLER. 2000. Evaluating the process of restored cordgrass (*Spartina foliosa*) marshes: Belowground biomass and tissue nitrogen. *Estuaries* 23:711-721.

CONNER, R. AND G. L. CHMURA. 2000. Dynamics of above-belowground organic matter in high latitude macrotidal saltmarsh. *Marine Ecology Progress Series* 204:101-110.

DAME, R. F. AND P. D. KENNY. 1986. Variability of *Spartina alterniflora* primary production in the euhaline North Inlet estuary. *Marine Ecology Progress Series* 32:71-80.

DELAUNE R. D., J. A. NYMAN, AND W. H. PATRICK, JR. 1994. Peat collapse, ponding and wetland loss in a rapidly submerging coastal marsh. *Journal of Coastal Research* 10:1021-1030.

ELLISON, A. A., M. D. BERTNESS, AND T. MILLER. 1986. Seasonal patterns in the belowground biomass of *Spartina alterniflora* (Gramineae) across a tidal gradient. *American Journal of Botany* 73:1548-1554.

GALLAGHER, J. L. 1974. Sampling macro-organic matter profiles in salt marsh plant root zones. *Soil Science Society of America Proceedings* 38:154-155.

GALLAGHER, J. L. 1983. Seasonal patterns in recoverable underground reserves in *Spartina alterniflora* Loisel. *American Journal of Botany* 70:212-215.

GALLAGHER, J. L. AND F. G. PLUMLEY. 1979. Underground biomass profiles and productivity in Atlantic coastal marshes. *American Journal of Botany* 66:156-161.

GALLAGHER, J. L., REIMOLD, R. A. LINTHHURST AND W. J. PFEIFFER. 1980. Aerial production, mortality and mineral accumulation-export dynamics in Spartina *alterniflora* and *Juncus roemerianus* plant stands in a Georgia salt marsh. *Ecology* 61:303-312.

GALLAGHER, J. L. AND D. M. SELISKER. 1976. The metabolism of senescing *Spartina alterniflora*. Annual Meeting Botany Society of America, New Orleans Abstract. p. 34

GIBLIN, A. E. AND R. W. HOWARTH. 1984. Porewater evidence for a dynamic sedimentary iron cycle in salt marshes. *Limnology and Oceanography* 29:47-63.

GOOD, R.E., N. F. GOOD, AND B. F. FRASCO. 1982. A review of primary production and decomposition dynamics of the belowground marsh component. p. 139-158 *In* V. S. Kennedy (ed.), Estuarine Comparisons. Academic Press, New York.

GOOD, R. E. AND B. R. FRASCO. 1979. Estuarine evaluation study; a four year report on production and decomposition dynamics of salt marsh communities: Manahawkin marshes, Ocean County, New Jersey. Report to New Jersey Department of Environmental Protection, Division of Fish, Game, and Shellfisheries, Trenton, New Jersey 105.

GROSS, M. F., M. A. HARDISKY, P. L. WOLF, AND V. KLEMAS. 1991. Relationship between aboveground and belowground biomass of *Spartina alterniflora* (Smooth Cordgrass). *Estuaries* 14:180-191.

HOPKINSON, C. S., J. G. GOSSELINK, AND R. T. PARRONDO. 1978. Aboveground production of seven marsh plant species in coastal Louisiana. *Ecology* 59:760-769.

HOWES, B. L., J. DACEY, AND J. M. TEAL. 1985. Annual C mineralization and belowground production of *Spartina alterniflora* in a New England salt marsh. *Ecology* 66:595-605.

HOWES, B. L., R. W. HOWARTH, AND J. M. TEAL. 1981. Oxidation-reduction potentials in a salt marsh: Spatial patterns and interactions with primary production. *Limnology Oceanography* 26:350-360.

KASWADJI, R. F., J. G. GOSSENLNK, AND R. E. TURNER. 1990. Estimation of primary production using five different methods in a *Spartina alterniflora* salt marsh. *Wetlands Ecology and Management* 1:57-64.

KOERSELMAN, W. AND A. F. M. MEULEMAN. 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33:1441-1450.

LANA, P. DA CUNHA, C. GUISS, AND S. T. DISARO. 1991. Seasonal variation of biomass and production dynamics for above- and belowground components of a *Spartina alterniflora* marsh in the euhaline sector of Paranaguá (SE Brazil). *Estuarine, Coastal and Shelf Science* 32:231-241.

LIVINGSTONE, D. C. AND D. G. PATRIQUIN. 1981. Belowground growth of *Spartina alterniflora* Loisel: Habitat, functional biomass and non-structural carbohydrates. *Estuarine Coastal Marine Science* 12:579-578.

LÓPEZ-BUCIO, J., A. CRUZ-RAMIREZ, AND L. HERRERA-ESTRELLA. 2003. The role of nutrient availability in regulating root architecture. *Opinion in Plant Biology* 6:280-287

.

MCINTIRE, G. L. AND W. M. DUNSTAN. 1976. Nonstructural carbohydrates in *Spartina alterniflora* Loisel. *Botanica marina* 19:93-96.

MCKEE, K. L. AND W. H. PATRICK, JR. 1988. The relationship of smooth cordgrass (*Spartina alterniflora*) to tidal datums: A review. *Estuaries* 11:143-151.

MENDELSSOHN, I. A., K. L. MCKEE, and W. H. PATRICK JR. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science* 214:439-441.

MENDELSSOHN, I. A. AND J. T. MORRIS. 2000. Eco-Physiological controls on the Productivity of *Spartina alterniflora* Loisel. p. 59-80 *In* Concepts and Controversies in Tidal Marsh Ecology. M. Weinstein and K. Kreeger (eds.), Kluwer Academic Publishing, Dordrecht.

ORNES, W. H. AND D. I. KAPLAN. 1989. Macronutrient status of tall and short forms of *Spartina alterniflora* in a South Carolina salt marsh. *Marine Ecology Progress Series* 55: 63-72.

POMEROY, L. R. AND R. G. WIEGART (eds.). 1981. Ecosystem and Population Ecology of a Salt Marsh: A Synthesis. Springer.

SCHUBAUER, J. P. AND C. S. HOPKINSON. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnology and Oceanography* 29:1052-1063.

SMALLEY, A. E. 1959. The role of two invertebrate populations, *Littorina irrorate* and *Orchelimum fidicinium*, in the energy flow of a salt marsh ecosystem. Ph.D. thesis, University of Georgia, Athens.

SMITH, K., R. R. GOOD, AND N. F. GOOD. 1979. Production dynamics for above-belowground components of a New Jersey *Spartina alterniflora* tidal marsh. *Estuarine Coastal Shelf Science* 9:189-201.

STOUT, J. P. 1978. An analysis of annual growth and productivity of *Juncus roemerianus* Sheele and *Spartina alterniflora* Loisel in coastal Alabama. Ph.D. dissertation, North Carolina State University, Raleigh.

STROUD, L. M. 1976. Net primary production of belowground material and carbohydrate patterns of two height forms of *Spartina alterniflora* in two North Carolina marshes. Ph. D. Dissertation, North Carolina State University, Raleigh.

STROUD, L. M. AND A. W. COOPER. 1968. Color infrared aerial photographic interpretation and net primary productivity of a regularly flooded North Carolina marsh. Report 14, North Carolina Water Resource Institute, Raleigh, p 1-86.

TURNER, R. E. 2001. Of manatees, mangroves, and the Mississippi River: Is there an estuarine signature for the Gulf of Mexico? *Estuaries* 24: 139-150.

TURNER, R. E. AND J. G. GOSSELINK. 1975. A note on standing crops of *Spartina alterniflora* in Florida and Texas. *Contributions in Marine Science* 19:113-118.

TURNER, R. E., E. M. SWENSON, AND C. S. MILAN. 2001. Contrasting organic and inorganic content in recently accumulated salt marsh sediments. p. 583-595 *In* M. Weinstein and D. D. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Dordrecht, The Netherlands.

TURNER, R. E., E. M. SWENSON, C. S. MILAN, J. M. LEE, AND T. A. OSWALD. 2004. Below-ground biomass in healthy and impaired marshes. *Ecological Research* 19:29-35.

UNITED STATES ENVIRONMENTAL PROTECTION AGENCY 2002. Methods for evaluating wetland conditions: Vegetation-based indicators of wetland nutrient enrichment, Office of Water, U. S. Environmental Protection Agency, Washington, DC. EPA-822-R-02-024.

VALIELA, I., J. M. TEAL, AND N. Y. PERSSON. 1976. Production and dynamic experimentally enriched salt marsh vegetation: belowground biomass. *Limnology Oceanography* 21:245-252.

VISSER, Y. M. AND C. A. SASSER. 2006. The effect of multiple stressors on salt marsh end-of-season biomass. *Estuaries and Coasts* 29:331-342.

WHITE D. S. AND B L. HOWES. Translocation, remineralization, and turnover of nitrogen in the roots and rhizomes of *Spartina alterniflora* (Graminae). *American Journal of Botany* 81:1225-1234.

WHITTAKER, R. H. 1975. Communities and Ecosystems. 2nd edition. Macmillan, New York.

# CHAPTER 3

## BELOW- AND ABOVEGROUND BIOMASS OF *SPARTINA ALTERNIFLORA*: RESPONSE TO NUTRIENT ADDITION IN A LOUISIANA SALT MARSH

## INTRODUCTION

More than a dozen experiments have established that nitrogen limits the aboveground production of the salt marsh macrophyte *Spartina alterniflora* (Valiela and Teal 1974; Morris 1988; Visser 2006) The majority of the annual total biomass production occurs belowground, however, and reaches a higher peak in warmer climates (Chapters 2 and 5). The root and rhizome biomass contributes to the accumulation of organic matter necessary to maintain the marsh vertical position as sea level rises and the marsh soils compact, reduces erosion, and is the basis for benthic substrate important to various feeding guilds, including those supporting commercially-valuable fisheries. *S. alterniflora* root and rhizome production, however, may not be limited by nitrogen availability because these structures are foraging for nutrients in a P limited soil community (Sundareshwar et al. 2003; Huang and Morris 2005). In other words, the aboveground plant tissue may be limited by nitrogen, but the belowground production may be limited by phosphorous.

The few studies on belowground production of *S. alterniflora* have neglected, with one exception, to study the effects of nutrient limitation on belowground plant production. Valiela et al. (1976) demonstrated that belowground biomass accumulation of *S. alterniflora* could be affected by different nutrient additions (various combinations of sewage sludge, urea and phosphate fertilizer additions). However, those fertilization experiments did not isolate the effects of P additions, because P was added only in combination with other nutrients. Besides N and P, iron may also affect *S. alterniflora* production (Valiela et al. 1975). Improving our understanding of the relative importance of various nutrients on coastal marsh production is of heightened importance because of the dramatic rise in non-point source pollution (Carpenter et al. 1998; Deegan 2002; Wigand et al. 2003) and the ubiquitous influence of N in over-enrichment (Vitousek et al. 1997; Rabalais 2002). It was the purpose of this study to document

the response of the above- and belowground biomass of *S. alterniflora* to various combinations of N, P, and Fe in a factorial arrangement experiment meant to isolate the relative influence of each element under field conditions.

## METHODS AND MATERIALS

The study was conducted in a *Spartina alterniflora* dominated salt marsh located west of the Louisiana Universities Marine Consortium (LUMC0N) laboratory, in Cocodrie, LA (29° 15'N, 91° 21' W). This is the same study area described in Chapter 1. The tide range during sampling period was -0.23 to 0.59 m with a mean of 0.18 m. The salinity ranged from 7 to 20 psu. A monospecific stand of *Spartina alterniflora* was sampled from a series of boardwalks constructed to facilitate sampling and to minimize damage to the marsh. Two experiments were established consisting of 0.25 $m^2$ plots with at least 0.5 m between plots. Eighteen plots of triplicate treatments were manipulated by monthly additions of 6 levels of nitrogen 0, 46, 93, 186, 372, 744 kg $ha^{-1}$ $mo^{-1}$ designated as the C, N46, N93, N186, N372, and N744 plots, respectively. Eighteen plots of triplicate treatments were part of a 3 X 6 factorial arrangement of eighteen plots in which various combinations of 744, 22, and 60 kg $ha^{-1}$ $mo^{-1}$ N (ammonium sulfate 33%), P (superphosphate; 18%), and Fe (ironite; 1%), respectively, were broadcasted monthly at low tide beginning April 2004 through September 2004. These plots are labeled the C, N744, P, NP, NFe, PFe, and NPFe treatments (Fig. 3.1). These loading rates are within the range of N and P loadings in New England (Wigand et al. 2003), and the Gulf of Mexico (Turner et al. 1999). Wigand et al. for example, measured N loading rates of 32, 472 kg N $yr^{-1}$, and are comparable to Valiela et al who applied N at a rate of 25 g $m^{-2}$ $wk^{-1}$.

The aboveground *S. alterniflora* was harvested by clipping vegetation at the sediment surface. All standing live and dead culms and litter were removed and placed into pre-labeled

plastic bags and transported to the Louisiana State University (LSU) processing lab. Dead shoots and leaves were identified by their yellowish or brownish coloration and separated from living material. The live or dead plant material was put into pre-labeled paper bags, dried at 60 $^{o}$C for approximately 72 hours and weighed to the nearest 0.01 g.

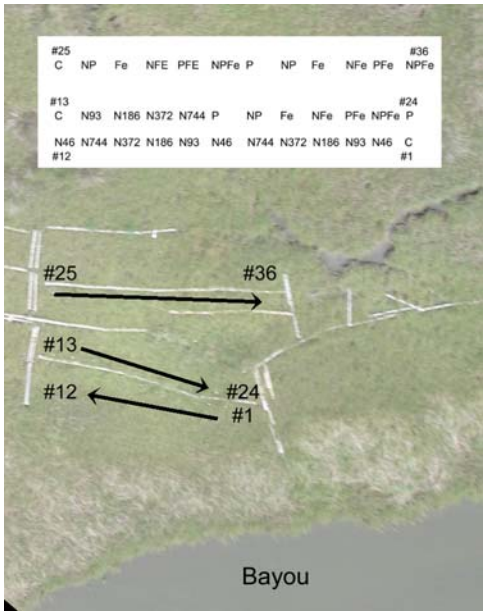


Fig. 3.1. The arrangement of nutrient addition along three boardwalks near the LUMCON facilities. The nutrient dose abbreviations are described in the text.

The belowground biomass was determined by collecting soil using a 40 cm long stainless steel tube with sharpened edges. An 11 cm diameter x 30 cm long sediment core was taken in the middle of each plot after the aboveground biomass sample was collected. The cores were extruded in the field and sliced into 0-10 cm, 10-20 cm and 20-30 cm segments. Each segment was put in labeled plastic bags and placed in a cooler for transport to the LSU lab where they were refrigerated until processed. Each segment was washed in a 1 mm sieve over a 0.5 mm sieve to prevent the loss of dead and fine root material. Live roots and rhizomes were separated from dead material with a suture set under running water for better separation (live roots and

rhizomes are white and turgid, dead materials are dark and flaccid). Root color can be variously tinged pink or orange, possibly because pigmentation zones contain feeding deterrents, i.e., roots colonized by arbuscular mycorrhizal fungi are often yellow. The physiological significance of these pigments is unclear (Alastair et al. 2002). Discolored turgid roots were defined as live roots. Dead material included partially decayed root material. Live roots and dead belowground material were placed in paper bags, labeled, and dried to a constant weight at 60$^{o}$ C, and weighed to the nearest 0.01 g. All belowground materials (roots and rhizomes) were sorted by a single individual (FAD) to assure continuity of sample processing, and to reduce potential sources of error. The root + rhizome : shoot ratio (R&R : S) for each treatment was determined by averaging the dry weight of the live above- and belowground biomass from the 3 replicates. Dried plant and root material were ground and sent to the LSU Soil Testing and Plant Analysis Lab where they were analyzed for metal and nutrient content. PVC pipes were inserted into the center of each plot at a depth of 10 cm for the purpose of collecting pore water. Pore water was collected by aspirating all of the standing water from the tube which was allowed to re-fill before drawing sample. Pore water samples were drawn before the monthly fertilization. Soil Eh was measured at 10 cm depth using three Eh probes (brightened platinum) cleaned and tested in the laboratory before and after field trip. Eh was measured using a digital voltmeter as the potential (mV) of a calomel electrode against the Eh probe.

N : P molar ratios were calculated to determine whether the site was N limited or P limited. An N : P molar ratio < 33 indicates N limitation whereas N : P > 33 suggests P limitation (Koerselman and Meulemen 1996; USEPA 2002).

The results of a statistical analysis of monthly above- and belowground biomass were compared to determine if the means were significantly different ($p < 0.05$) based on Tukey's

adjustment. The analysis was carried out using the general linear model procedure and 3 X 6 factorial arrangements (ANOVA; SAS 2002-2003).

## RESULTS

Aboveground Biomass

A statistically significant difference was seen in the amount of live aboveground biomass among treatments compared to that in the C plots ($p < 0.01$; Fig. 3.2). The aboveground biomass was 18% to 138% higher than in the C plots and ranged from 641 ± 224 g $m^{-2}$ (mean ± 1 Std. Dev.) in the C plot to 1527 ± 340 g $m^{-2}$ in plot N744. No statistically significant difference was seen among the N196, N372, and N744 plots, or among the C, N46, and N93 plots (Fig. 3.2). The aboveground dead biomass ranged from 397 ± 279 g $m^{-2}$ for the Control plot to 897 g $m^{-2}$ ± 524 in plot N744 (Fig. 3.2).

No statistically significant difference was seen in the amount of live aboveground biomass in the N, NP or NFe plots (Fig. 3.3). There was, however, a statistically significant difference ($p < 0.01$) between the aboveground live biomass in the C, P, Fe, PFe, and NPFe plots when compared to the aboveground live biomass in the N, NP, and NFe plots (Fig. 3.3). The amount of dead aboveground biomass in the factorial arrangement experiment ranged from 318 to 897 g $m^{-2}$.

Similar patterns were seen in stem density and length with N fertilization. Stem density increased by 10 - 57% with increasing N addition and ranged from 308 (average) stems $m^{-2}$ in the Control plots to 463 stems $m^{-2}$ in the N744 plots. In addition, the average stem length increased by 11 to 23% above that in the C plots. No apparent changes in stem density or length were seen in the P, Fe or PFe plots. However, compared to the Control plot, there was a 63% increase in stem density and a 28% increase in stem length in the NP plot. Stem density also

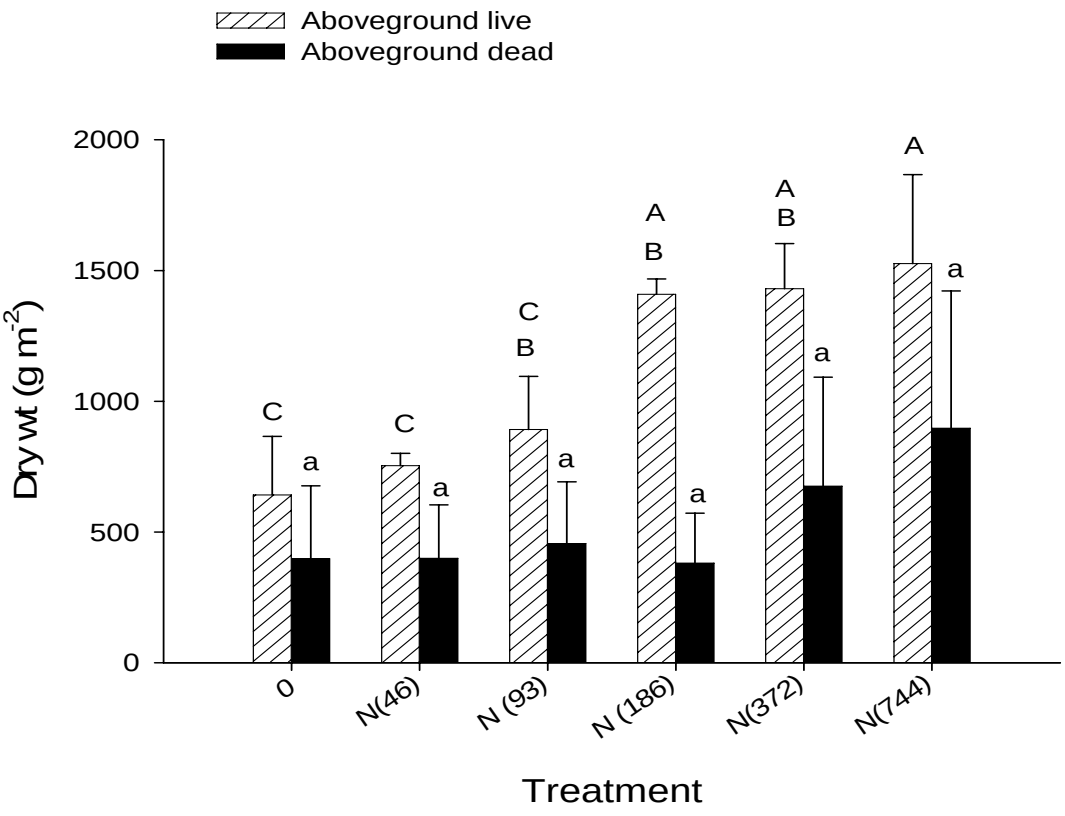


Fig. 3.2. The mean aboveground live and dead biomass (g $m^{-2}$; mean ± 1 Std. Dev.) of 3 replicates of N treatment plots. Letters indicate the result of a Tukey's Studentized Range Test for differences in aboveground live and dead biomass by N treatment. Means with the same letters are not statistically different from each other (level of significance 0.05).

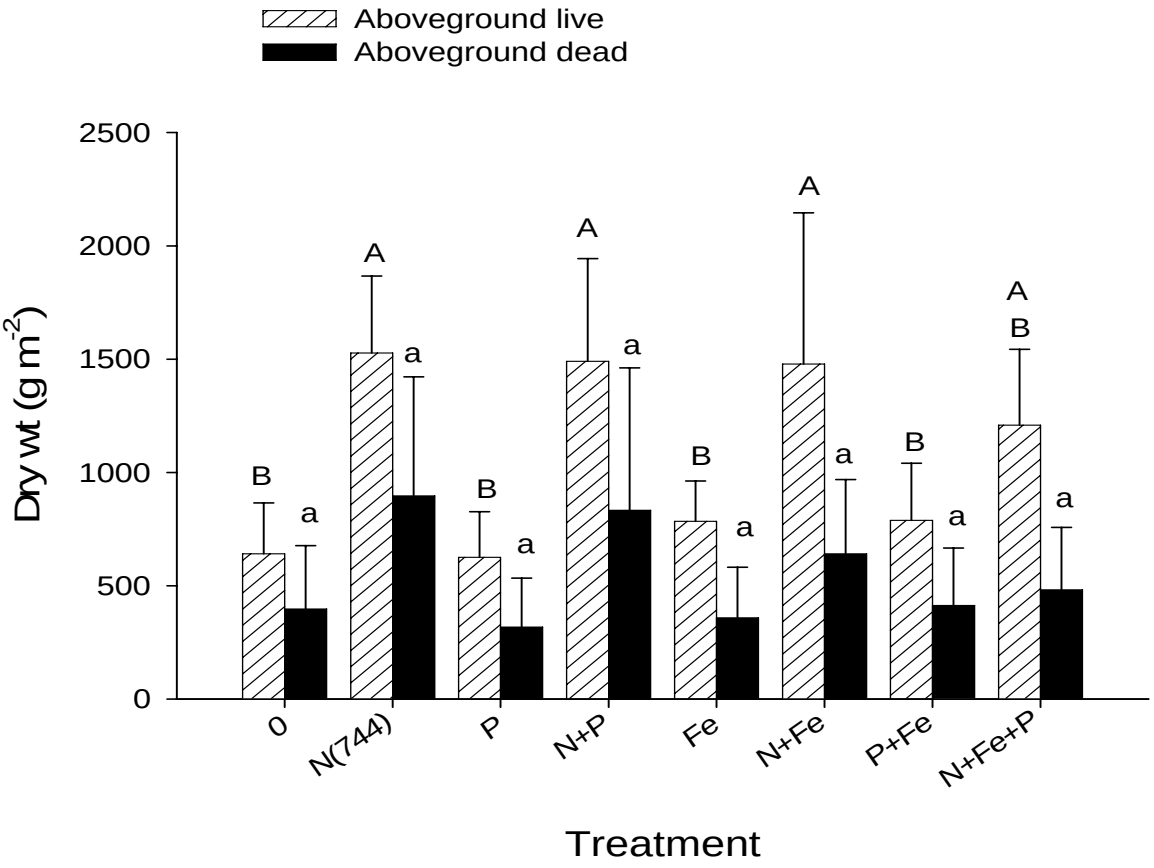


Fig. 3.3. The mean aboveground live and dead biomass (g $m^{-2}$; mean ± 1 Std. Dev.) of 3 replicates of nutrient treatment plots. Letters indicate the results of a Tukey's Studentized Range Test for differences in aboveground live and dead biomass by nutrient treatment. Means with the same letters are not statistically different from each other (level of significance 0.05). Treatment dosages are N =744, P =22, and Fe = 60 kg $ha^{-1}$ $mo^{-1}$.

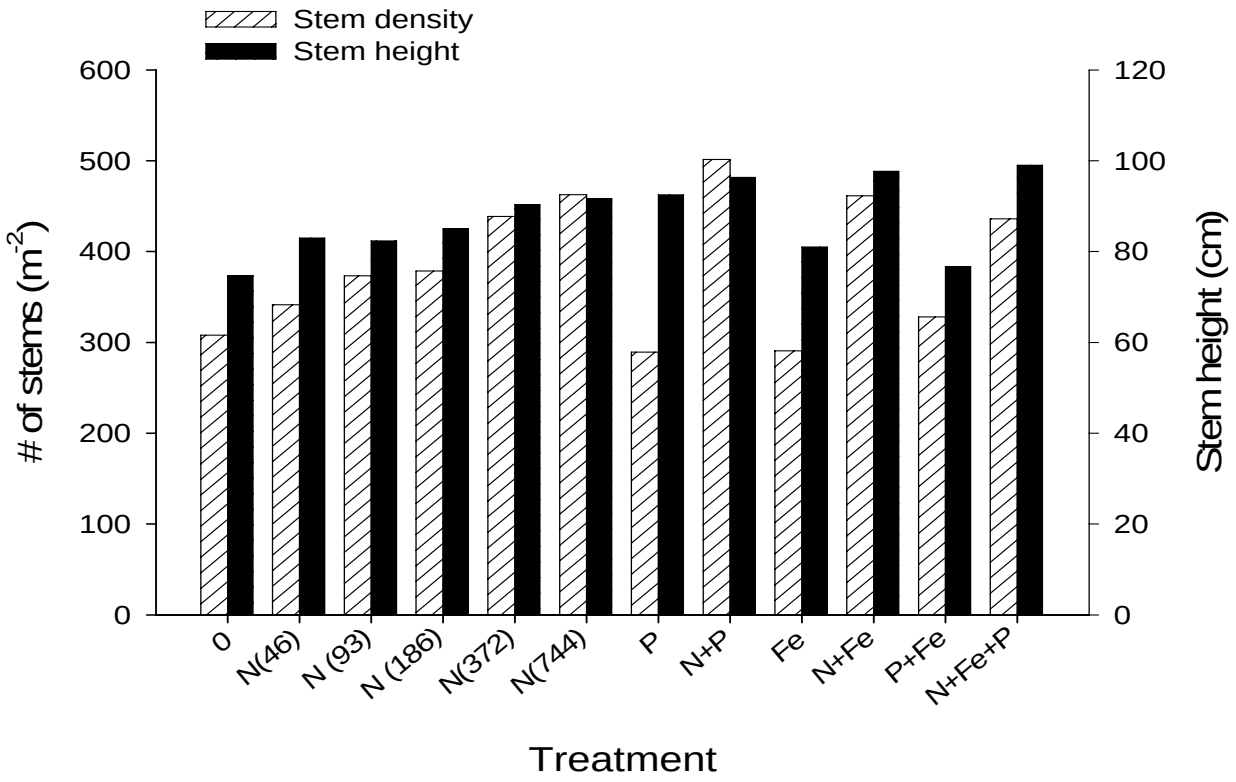


Fig. 3.4. The values of average stem density (g $m^{-2}$) and length for all treatments. A standard deviation is not shown, and was <10% of the mean in all samples.

increased in the NP and NFe plots, but the average stem length remained unchanged in all plots. (Fig. 3.4).

Belowground Biomass

No statistically significant differences in the live or dead belowground biomass were seen with only N additions (Fig. 3.5). A statistically significant difference in the live belowground biomass ($p < 0.01$) was noted in the factorial arrangement experiment (Fig. 3.6). The live belowground biomass decreased by 40-60% with P and Fe additions, and also when P and Fe were added in combination with N (Fig. 3.6). The lowest live belowground biomass was in the PFe plot ($483 \pm 3$ g $m^{-2}$). No difference, however, was seen in the amount of dead belowground biomass accumulation among the treatments.

The average root : rhizome ratio for all treatment plots (<1 : 1) was below that of the C treatment (2 : 1) with the exception of the N46 plot which did not differ from that in the C plot (Fig. 3.7).

The majority of the live root biomass for all treatment dosages was located in the 0 - 10 cm depth layer. The vertical distribution of the live rhizome biomass was distributed throughout the 0 - 30 cm profile, with the majority of the live rhizome biomass located in the 0-10 cm depth layer. The largest amount of live rhizome biomass was in the 0 - 10 cm segment of the C plot and in the N46 plot (565.7 and 602.7 g $m^{-2}$, respectively; Table 3.1). The largest amount of live rhizome in the 10 - 20 segments was 503.6 g $m^{-2}$ for the N186 plot. The 20 - 30 segment with the lowest rhizome biomass was in the NP treatment (7.7 g $m^{-2}$) and highest in the N46 plot (135.3 g $m^{-2}$).

The nitrogen standing stock (NSS) in the aboveground live biomass was highest in the treatment plot with the highest N addition (N744; 18.7 g N $m^{-2}$) and lowest in the C plots (6.4 g N $m^{-2}$). The phosphorous standing stock in the aboveground live biomass was highest in the C

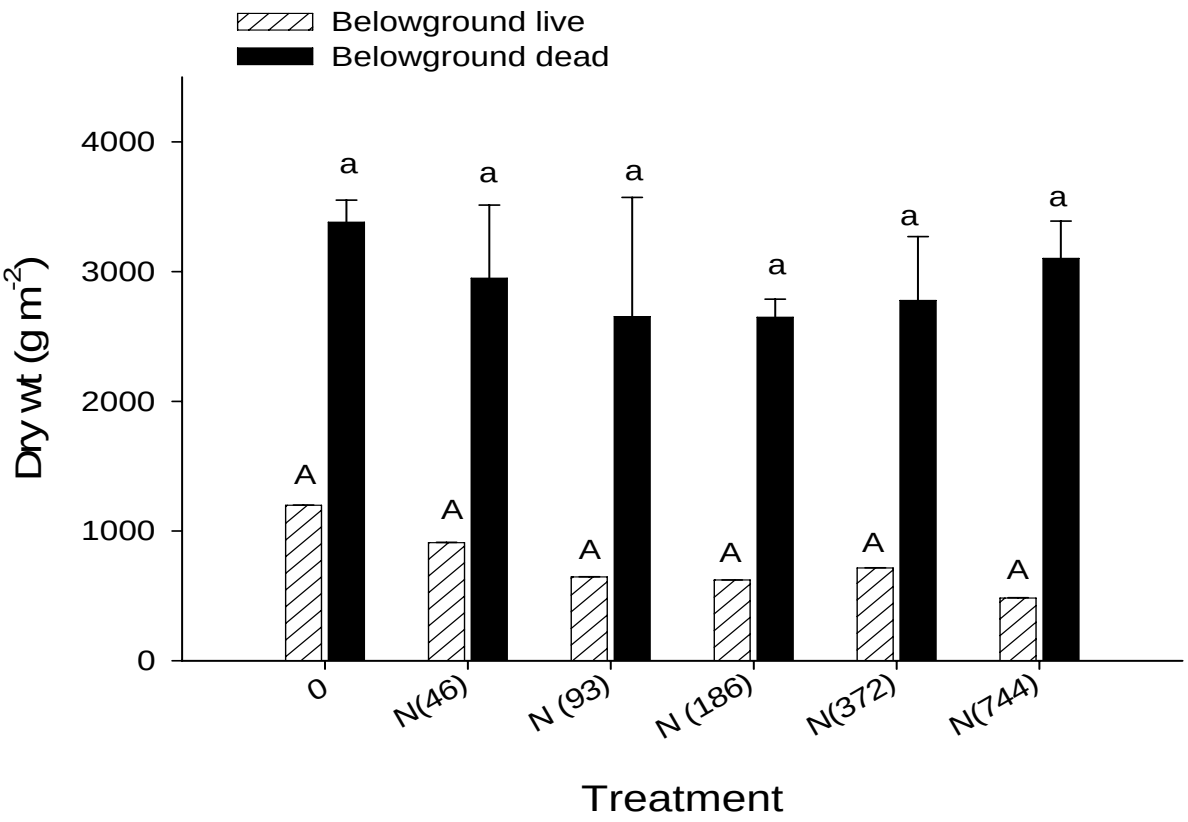


Fig. 3.5. The mean belowground live and dead biomass (g $m^{-2}$; mean ± 1 Std. Dev.) of 3 replicates of N treatment plots. Letters indicate the results of a Tukey's Studentized Range Test for differences in the aboveground live and dead biomass by N treatment (level of significance 0.05). Means with the same letters are not statistically different from each other.

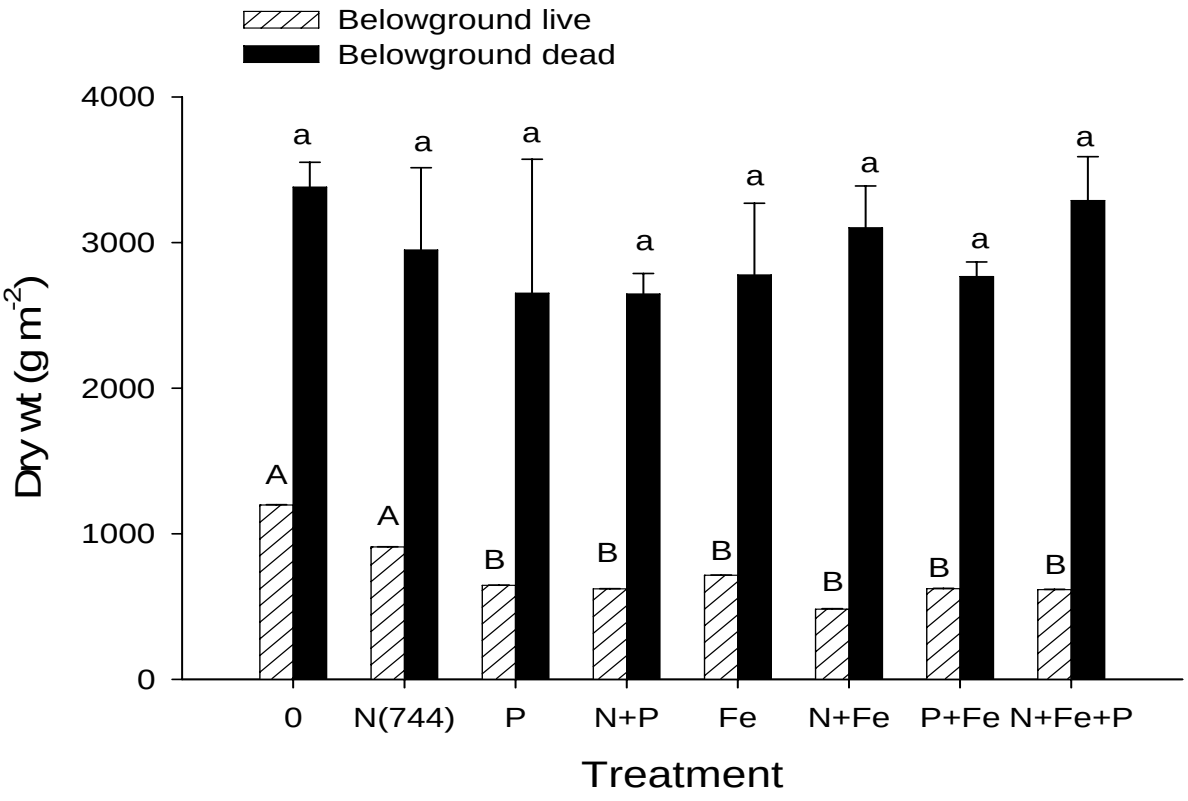


Fig. 3.6. The mean belowground live and dead biomass (g $m^{-2}$; mean ± 1 Std. Dev.) of 3 replicates of nutrient treatment plots. Letters indicate the result of a Tukey's Studentized Range Test for differences in aboveground live and dead biomass by nutrient treatment (level of significance 0.05). Means with the same letters are not statistically different from each other. The treatment dosages were N =744, P =22 and Fe = 60 kg $ha^{-1}$ $mo^{-1}$.

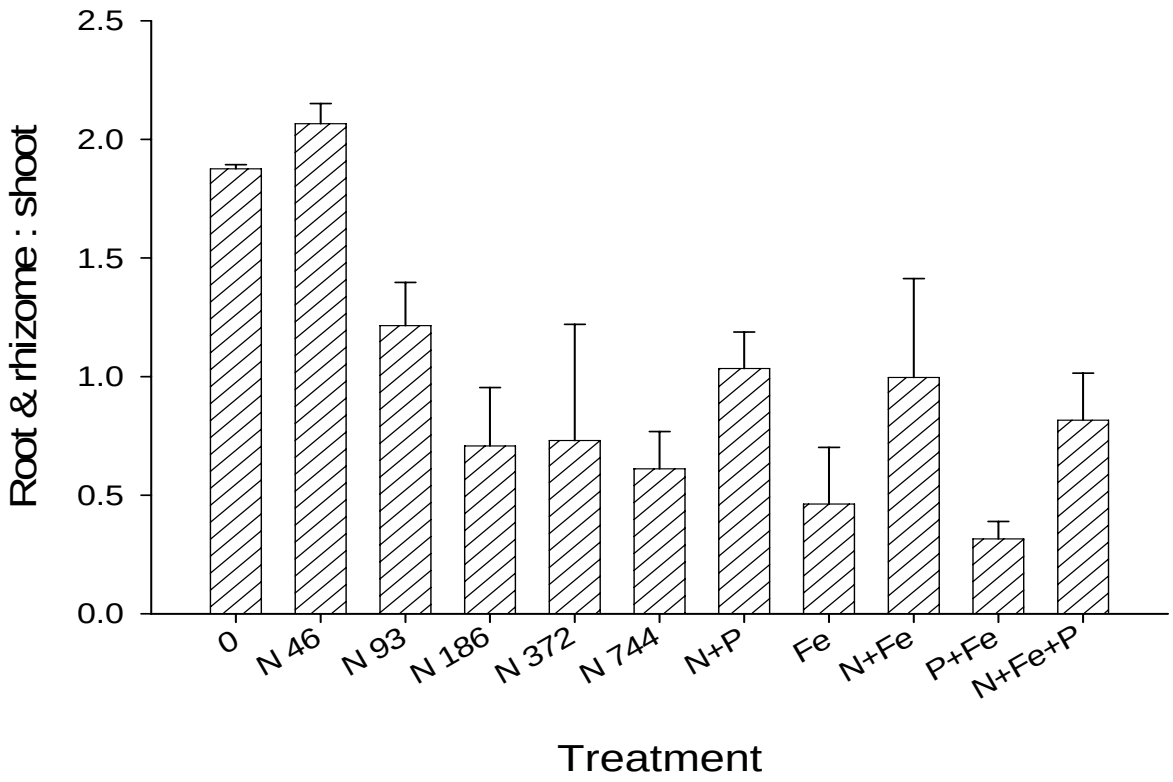


Fig. 3.7. The root and rhizome : shoot ratio (mean ± 1 Std. error) in the various treatments.

Table 3.1. The depth distribution of for live roots and rhizomes and the cumulative total in (g $m^2$).

| Treatment g $ha^{-1}$ $mo^{-1}$ | Live roots g $m^{-2}$ | | | Live rhizomes g $m^{-2}$ | | | Roots cumulative total | Rhizomes cumulative total |
|---|---|---|---|---|---|---|---|---|
| | 0-10 cm | 10-20 cm | 20-30 cm | 0-10 cm | 10-20 cm | 20-30 cm | 0-30 cm | 0-30 cm |
| 0.0 | 361.4 | 14.3 | 0.0 | 565.7 | 225.1 | 41.2 | 375.7 | 832.0 |
| N(46) | 367.7 | 5.2 | 0.0 | 602.7 | 279.7 | 135.3 | 372.9 | 1017.7 |
| N (93) | 232.4 | 2.1 | 0.0 | 534.0 | 171.2 | 53.6 | 234.5 | 758.7 |
| N (186) | 355.5 | 4.2 | 3.5 | 293.3 | 170.5 | 44.2 | 363.2 | 507.9 |
| N(372) | 474.2 | 4.5 | 2.1 | 271.3 | 503.6 | 78.3 | 480.8 | 853.2 |
| N(744) | 419.9 | 1.0 | 0.0 | 174.3 | 248.0 | 66.8 | 420.9 | 489.1 |
| P | 347.5 | 1.7 | 0.0 | 139.5 | 117.6 | 89.4 | 349.3 | 346.5 |
| NP | 282.5 | 6.6 | 0.0 | 157.9 | 168.0 | 7.7 | 289.1 | 333.6 |
| Fe | 315.9 | 8.0 | 0.0 | 173.2 | 181.6 | 36.2 | 323.9 | 391.0 |
| NFe | 244.9 | 0.0 | 0.0 | 161.8 | 72.5 | 23.7 | 244.9 | 258.0 |
| PFe | 297.8 | 17.0 | 0.0 | 30.6 | 142.6 | 135.3 | 314.8 | 308.6 |
| NFeP | 295.7 | 0.3 | 0.0 | 150.6 | 155.2 | 14.3 | 296.0 | 320.0 |

Table 3.2. The nitrogen and phosphorous standing stock (g $m^{-2}$) of aboveground and belowground live and dead and N : P molar ratios for each nitrogen addition treatment. The highest values are listed in **bold**.

| Treatment (g $m^{-2}$ $mo^{-1}$) | Aboveground | | | | | | Belowground | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Nitrogen | | Phosphorous | | N : P | | Nitrogen | | Phosphorous | | N : P | |
| | live | dead | live | dead | live | dead | live | dead | live | dead | live | dead |
| 0.0 | 6.4 | 2.6 | 0.86 | 0.19 | 16.4 | 30.8 | 22.6 | 45.3 | 4.07 | 2.70 | 37.5 | 37.2 |
| N 46 | 8.4 | 2.5 | 0.93 | 0.21 | 19.9 | 26.8 | 24.7 | 47.9 | 1.51 | 2.39 | **73.0** | 44.3 |
| N 93 | 8.9 | 3.2 | 0.95 | 0.24 | 20.8 | 29.2 | 20.1 | **48.8** | 2.29 | **2.77** | 52.6 | 39.0 |
| N 186 | 12.4 | 3.6 | 1.28 | 0.22 | 21.3 | **35.8** | 15.9 | 47.5 | 4.68 | 2.25 | 15.1 | **46.6** |
| N 372 | 15.2 | 6.2 | 1.35 | **0.46** | 24.8 | 29.9 | **26.5** | 43.7 | **7.83** | 2.67 | 15.5 | 36.1 |
| N 744 | **18.7** | **8.4** | **1.56** | 0.55 | **26.5** | 33.5 | 18.4 | 41.0 | 1.87 | 2.19 | 60.1 | 41.3 |
| Average | 9.1 | 4.4 | 1.16 | 0.31 | 21.6 | 31.0 | 21.4 | 45.7 | 3.70 | 2.50 | 42.3 | 40.8 |

Table 3.3. The nitrogen and phosphorous standing stock (g $m^{-2}$) of aboveground and belowground live and dead biomass and the N : P ratios for each factorial experiment treatment. The highest values are listed in **bold**.

| Treatment | Aboveground | | | | | | Belowground | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (g $m^{-2}$ $mo^{-1}$) | Nitrogen | | Phosphorous | | N : P | | Nitrogen | | Phosphorous | | N : P | |
| | live | dead | live | dead | | | live | dead | live | dead | live | dead |
| 0.0 | 6.4 | 2.6 | 0.86 | 0.19 | 16.4 | 30.8 | **22.6** | **45.3** | 4.07 | **2.70** | 37.5 | 37.2 |
| N 744 | **18.7** | 8.4 | 1.56 | **0.55** | **26.5** | 33.5 | 18.4 | 41.0 | 1.87 | 2.19 | 60.1 | 41.3 |
| P | 6.3 | 1.9 | 0.88 | 0.15 | 15.8 | 28.2 | 11.3 | 36.7 | 2.55 | 2.01 | 44.5 | 40.4 |
| NP | 18.5 | **7.7** | **1.94** | 0.51 | 21.0 | 33.8 | 11.3 | 36.4 | **5.28** | 1.99 | 9.4 | 40.4 |
| Fe | 8.0 | 2.6 | 0.99 | 0.18 | 17.9 | 31.7 | 12.3 | 36.8 | 3.10 | 2.37 | 42.6 | 34.4 |
| NFe | 16.7 | 6.0 | 1.77 | 0.35 | 20.8 | **37.6** | 8.9 | 42.8 | 2.54 | 1.97 | 16.2 | **48.0** |
| PFe | 5.5 | 2.9 | 0.40 | 0.21 | 16.4 | 30.6 | 12.3 | 38.8 | 4.94 | 2.06 | 11.1 | 41.7 |
| NFeP | 11.9 | 4.8 | 0.76 | 0.30 | 21.0 | 34.9 | 11.2 | **45.3** | 0.64 | 2.39 | **78.1** | 42.0 |
| Average | 11.5 | 4.6 | 1.33 | 0.31 | 19.5 | 32.6 | 13.5 | 40.1 | 2.78 | 2.21 | 37.5 | 40.7 |

plots and decreased as more N was added to the plots. The NSS and PSS in the belowground live biomass were highest in the N372 plots (26.5g N $m^{-2}$ and 7.8 g P $m^{-2}$y). The N : P molar ratio in the aboveground live biomass was highest in the N744 plots (26.5) and lowest in the C plots (16.4). The N : P molar ratio in the belowground biomass was highest in the N46 plots (73.0) and lowest in N186 plots (15.1; Table 3.2).

The NSS in aboveground live biomass in the factorial experimental treatment was highest in N744 plots (18.7 g N $m^{-2}$), and NP plots (18.5 g N $m^{-2}$; Table 3.3). The PSS in the aboveground live biomass was highest (1.9 g $m^{-2}$) in the NP plots. The highest NSS for belowground live biomass was 26.5 g $m^{-2}$, in the N372 plots (Table 3.3). The belowground live biomass highest PSS was 4.9 g $m^{-2}$ in the PFe plots. The N : P molar ratio for the aboveground live biomass in the factorial treatment was highest at the N744 plots (26.5) and belowground live highest N : P molar ratio was NFeP plots 78.1 (Fig. 3.8).

The ammonium concentration in porewater fluctuated among all treatment dosages for both experiments. The concentration of ammonium was highest in the N744 plot and NFe plots (4867 and 4773 μmol $l^{-1}$, respectively (Fig. 3.9). The concentration of phosphate in porewater was highest in the C plot (42.0 μmol $l^{-1}$). Personal observations indicated that there was an accumulation of $H_2S$ in the porewater tubes.

## DISCUSSION

Two kinds of responses were observed in experimental plots with various additions of added nutrients. The first observation is that the accumulation of the aboveground biomass in the study site was clearly limited by N, and not by P, Fe or a combination of all three elements. The aboveground live biomass, and the stem number and length, responded positively to increases in N, and equaled that in plots with N applied in combination with P or Fe or P + Fe. Further, no stimulation in the growth of aboveground biomass occurred when P or Fe was

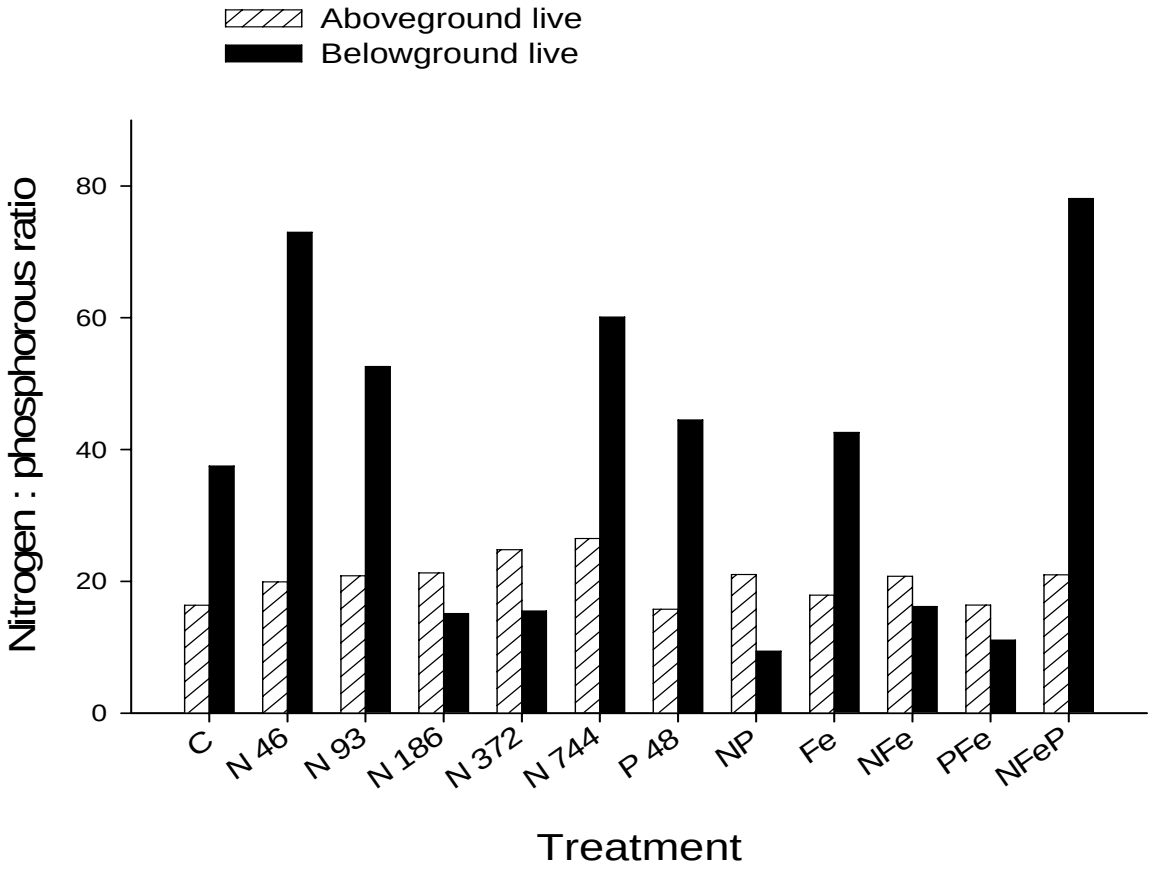


Fig. 3.8. The N : P molar ratios of live above-and belowground biomass by treatment. A ratio < 33 or > 33 was considered to be N or P growth limited, respectively.

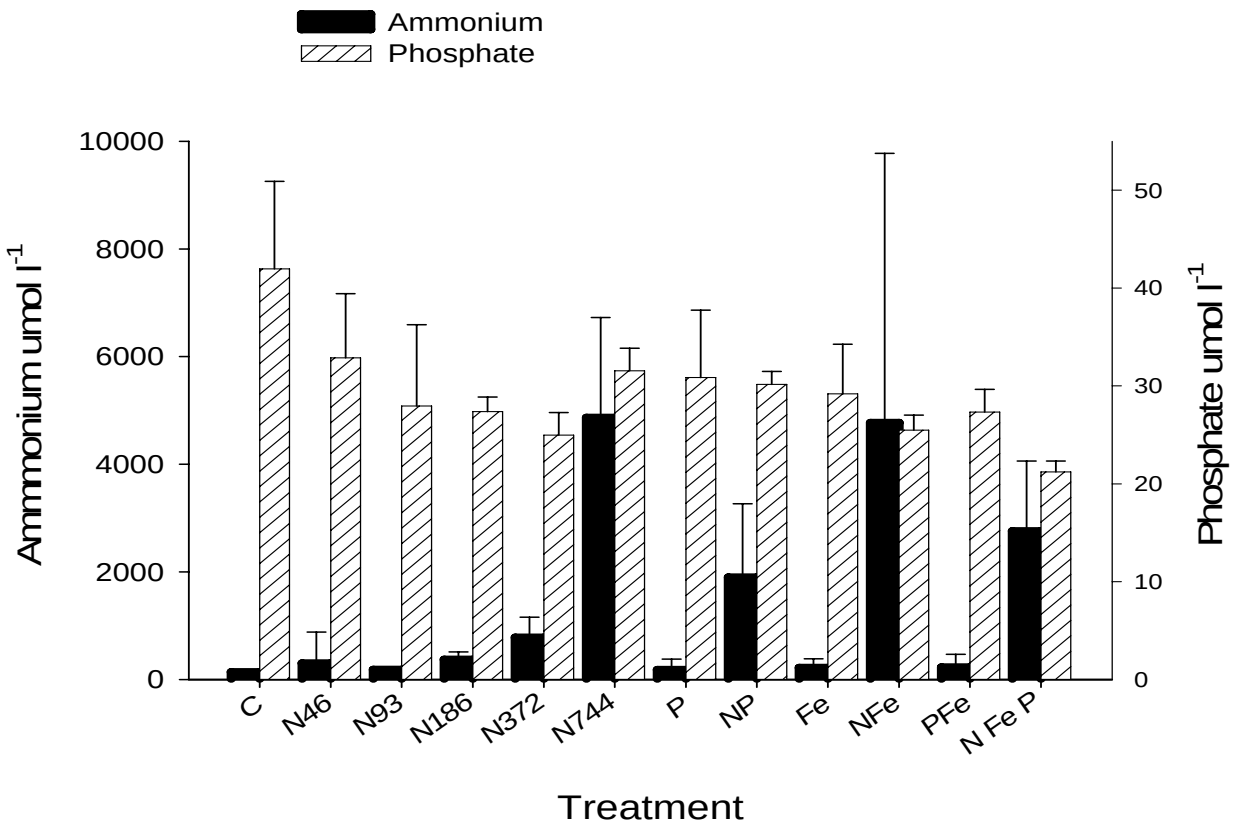


Fig. 3.9. Average porewater ammonium and phosphate at a depth of 10 cm (μmol $l^{-1}$; μ ± 1 Std dev.) in the treatment plots during the growing season.

applied separately or together. No difference in the NSS among treatment levels was seen and some native N may have been incorporated into the plant tissue. The molar N : P ratio in the control and experimental plots was also indicative of N limited aboveground growth. These changes in the aboveground biomass to nitrogen additions are consistent with the experimental results described for east coast salt marshes (Morris 1991) and the analysis of annual variations for salt marshes in Barataria Bay, LA (Visser and Sasser 2006).

A different response to nutrient additions was observed when changes in the belowground biomass were examined. The belowground biomass decreased in all plots that had P added, whether as P alone, or in combination with N, Fe, or N+P, but the belowground biomass did not change in response to N additions. The R & R : shoot ratio decreased with N additions because the live aboveground biomass increased, but the live belowground biomass did not. The N : P molar ratios of the live belowground biomass were > 33 indicating that the belowground biomass was P limited. These changes belowground lead to the conclusion that the P is a limiting nutrient of plant biomass belowground. The allocation of plant resources in the form of more roots and rhizomes in plots without P additions, compared to in plots with P additions, is because of the relatively sparse supply of readily-available P to the plant. The plant expends less energy foraging for a limiting nutrient when that nutrient becomes more available.

Most of the NSS belowground was in rhizomes, which were located, regardless of treatment, in the 20 – 30 cm soil layer. The majority of the live root biomass remained in the upper 0-10 cm layer close to the added nutrient source. Perhaps the rhizomes were storing some of the excess N not incorporated into the live aboveground biomass. The R&R contained a higher percentage of the NSS than found in the live aboveground biomass, suggesting a prominent role for R&R in the translocation of nutrients. Data described in Chapter 2 suggests

that there was a significant translocation of N reserves from below- to aboveground at the end of the growing season.

The PSS in the live belowground biomass was highest in plots with added P, even though the growth of live belowground biomass was lower in plots with added P. The amount of PSS may have been restricted by other factors than the availability of P. Bacterial numbers in rooting zones, for example, are usually higher in phosphorus treated plots (Sundareshwer et al. 2003). The porewater concentration of phosphate decreased with the application of N and other nutrients. Long periods of waterlogging causes phosphate to become less available (Valencia 1962: Patrick and Mahapatra 1968), perhaps as a result of precipitation in the oxidized rhizosphere (Ponnamperuma 1965). The fate of the applied N is unknown, although mineralization in waterlogged soils does not usually proceed beyond the ammonium stage in anaerobic conditions, but may be immobilized into organic N (Tusneem and Patrick 1971).

One of the striking results of this experiment is the different responses to N and P additions by the belowground and the aboveground biomass. The literature is replete with the conclusion that salt marshes are limited by N availability. This conclusion is certainly an accurate description of the plant's aboveground response to nutrient additions. Phosphorus, not nitrogen, appears to affect a response by plant belowground, and this response is to decrease the amount of plant biomass available for accumulation. This decrease in belowground plant biomass production in organic-rich soils could compromise the long-term survival of a salt marsh, especially a salt marsh located where organic accumulation is essential to maintain a physiologically-satisfactory position with regards to sea level rise. In this sense, which is a long-term view, a salt marsh ecosystem may be limited by phosphorus, not by nitrogen.

Some management implications of this conclusion are that the responses to low levels of eutrophication are immediate and produce a disproportionate change in belowground biomass.

Monitoring programs that include only the aboveground plant biomass will miss an important and sensitive indicator(s) of salt marsh health. A marsh may appear healthy based on a relatively high amount of aboveground biomass, but be unhealthy from an ecosystem point of view (Turner et al. 2004). Indicators of salt marsh health could be developed to become more sophisticated than a simple metric of tissue biomass and elemental composition, because these metrics surely vary in a way that is responsive to hydrologic conditions, for example.

## LITERATURE CITED


ALASTAIR, F. 2002. Characteristics and function of root systems. p. 15-32 *In* Y. Waisel, A. Eshel and U. Kafkafi (eds.), Plant Roots: The Hidden Half. New York, Basel, Marcel Dekker, Inc.

BURESH, R. J., DELAUNE, R. D., AND W. H. JR. PATRICK. 1980. Nitrogen and phosphorous distribution and utilization by *Spartina alterniflora* in a Louisiana Gulf Coast marsh. *Estuaries* 3:111-121.

CARPENTER, S., N. F. CARACO, D. L. CORRELL, R. W. HOWARTH, S. N. SHARPLEY, AND V. H. SMITH. 1998. Nonpoint pollution of surface waters with phosphorous and nitrogen. *Issues in Ecology* 3:1-12.

CHAPIN, F. S. III. 1980. The mineral nutrition of wild plants. *Annual Review Ecological System* 11:233-260.

DEEGAN, L. A. 2002 Lessons learned: The effects of nutrient enrichment on the support nekton by seagrass and salt marsh ecosystem. *Estuaries* 25:727-742.

HUANG, X. AND J. T. MORRIS. 2005. Distribution of phosphatase activity in marsh sediments along an estuarine salinity gradient. *Marine Ecology Progress Series* 292:75-83.

KOERSELMAN, W. AND A. F. M. MEULEMAN. 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* 33:1441-1450

MITSUI, A. H. 1954. Inorganic nutrition, fertilization, and amelioration for lowland rice. Yokendo Ltd. Tokyo.

MORRIS, J. T. 1991. Effects of nitrogen loading on wetland ecosystems with particular reference to atmospheric deposition. *Annual Review of Ecology and Systematics* 22:257-279.

MORRIS, J. T. 1988. Pathways and controls of the carbon cycle in salt marshes. p. 497-510 *In* The Ecology and Management of Wetlands, (eds.) D. D. Hooks. London, Croom Helm.

PATRICK, W. H. AND R. D. DELAUNE. 1976. Nitrogen and phosphorous utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Estuaries and Coastal Marine Science*. 4:59-64.

PATRICK, W. H. JR. AND I. C. MAHAPATRA 1968. Transformation and availability to rice of nitrogen and phosphorus in waterlogged soils. *Advances in Agronomy*. 20:323-359

PEARSALL, W. H. 1950. The investigation of wet soils and its agricultural implications. *Emp. Journal of Experimental Agriculture* 18:289-298.

PONNAMPERUMA, F. N. 1965. The Mineral Nutrition of the Rice Plant. Johns Hopkins Press, Baltimore, Maryland.

RABALAIS, N. N. 2002. Nitrogen in aquatic ecosystems. *Ambio* 31:102-112.

SUNDARESHWAR, P. V., J. T. MORRIS, E. K. KOEPFLER, AND B. FORNWALT. 2003. phosphorus limitation of coastal ecosystem processes. Science 299:563-565.

TURNER, R. E., E. M. SWENSON, C. S. MILAN, J. M. LEE, AND T. A. OSWALD. 2004. Below-ground biomass in healthy and impaired marshes. *Ecological Research* 19:29-35.

TUSNEEM, M. E. AND W. H. PATRICK 1971. Nitrogen transformations in waterlogged soil. Louisiana State University, Department of Agronomy, Agricultural Experiment Station, Bulletin 657.

UNITED STATES ENVIRONMENTAL PROTECTION AGENCY 2002. Methods for evaluating wetland conditions: Vegetation-based indicators of wetland nutrient enrichment. Office of Water, U. S. Environmental Protection Agency, Washington, D C. EPA-822-R-02-024.

VALENCIA, I. G. 1962. Ph.D. dissertation, University of Wisconsin, Madison, Wisconsin.

VALIELA, I. AND J. M. TEAL. 1974. Nutrient limitation in salt marsh vegetation. p. 563-574 *In* R. J. Reimold and N. W. Queen (eds.), Ecology of Halophytes. Academic Press, New York.

VALIELA, I., J. M. TEAL, AND N. PERSSON. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnology and Oceanography* 21:245-252.

VALIELA, I., J. M. TEAL, AND W. J. SASS. 1975. Production and dynamics of salt marsh vegetation and the effects of experimental treatment with sewage sludge. *Journal of Applied Ecology* 12:973-982.

VISSER, Y. M. AND C. A. SASSER. 2006. The effect of multiple stressors on salt marsh end-of-season biomass. *Estuaries and Coasts* 29:331-342.

VITOUSEK, P. M., R. ABER, R. W. HOWARTH, G. E. LIKENS, P. A. MATSON, D. W. SCHINDLER, W. H. SCHILESINGER, AND G. D. TILMAN. 1997. Human alteration of the global nitrogen cycle: Causes and consequences. *Ecological Applications* 7:737-750.

WIGAND, C., R. A. MCKINNEY, M. A. CHARPENTER, M. M. CHINTALA, AND G. B. THURSBY. 2003. Relationships of nitrogen loading, residential development, and physical characteristics with plant structure in a New England salt marsh. *Estuaries* 26:1494-1504.

# CHAPTER 4

## BELOW- AND ABOVEGROUND *SPARTINA ALTERNIFLORA* NUTRIENT RESORPTION IN A LOUISIANA SALT MARSH

## INTRODUCTION

The dynamics of nutrient storage and resource use by plants is one of the main topics for discussion in plant ecology (Aerts and DeCaluwe 1994). Plants play an important role in nutrient cycling, and plants with high annual primary productivity can extract large amounts of nutrients from their environment and store these nutrients in biomass and litter (Meuleman et al. 2002). One major problem in the analysis of nutrient resorption in relation to soil fertility is that it is difficult to quantify soil fertility. Furthermore, soil extractable concentrations of nutrients do not adequately reflect nutrient availability by themselves (Willby et al. 2002). Maps of nutrient distribution in the soil, for example, show a wide range of nutrient concentrations (Robinson and Rorison 1988), and nutrient uptake by microbes and plants creates zones of nutrient depletion. The use of standing stocks of nutrients in plant biomass as an indicator of nutrient availability has some clear advantages over the analyses of soil chemistry. The nutrient content in plant biomass can be assumed to integrate fluxes of nutrient to plants over the entire growing season, whereas soil analyses measure only the instantaneous 'availability', which fluctuates strongly in space and time (Guisewell and Koerselman 2002).

Nutrient resorption is one of the most important of all strategies employed by plants to conserve nutrients and influence various processes, e.g., competition, nutrient uptake, and productivity (Killingbeck 1996). Nutrient resorption is the mobilization and removal of nutrients from senescing plant tissue, and the transport of these nutrients to storage sites in plant tissues (Chapin 1980; Killingbeck 1986). The primary value of leaf senescence to plant fitness is that certain breakdown products can be re-used (Aerts 1996) if nutrient supply from the soil is insufficient for growth (Chapin 1980). Nutrients which are not re-absorbed, however, will be circulated through litterfall. The litter must be decomposed and the nutrients contained in that

litter must be remineralized to become once again available for plant uptake (Aerts 1996), and these processes can take several years (Staaf and Berg 1982; Berg 1986).

Three measures of estimating nutrient resorption currently in use are: 1) nutrient use efficiency (NUE), 2) nutrient resorption efficiency (RE), and 3) nutrient resorption proficiency (RP) (Shaver and Melillo 1984; Killingbeck 1996; USEPA 2002). *Nutrient-use efficiency* is a measure of the effectiveness by which plants use nutrients to produce biomass, and is considered to be an important plant characteristic which combines a variety of nutrient uptake and release processes (Muelman et al. 2002). A high NUE value corresponds to relatively high rates of nutrient resorption when large amounts of biomass are produced with little loss of nutrients in litterfall (Vitousek 1982). *Nutrient resorption efficiency* is a measure of nutrient conservation and limitation. A plant growing in nutrient-poor soils, compared to a plant growing in nutrient-rich soils, will have a high RE value when it translocates a relatively large amount of nutrients to belowground tissues (Aerts et al. 1999; USEPA 2002). *Nutrient resorption proficiency* is the absolute levels to which nutrients are reduced to in senesced leaves. Nutrient resorption is highly proficient when N and P concentrations fall below 0.7% and 0.05%, respectively (Killingbeck 1996). According to Killingbeck (1996), a concentration of 0.3% for N or 0.01% for P in senesced leaves represents the lowest potential resorption in woody perennial tissues. Regardless of the differences in how they are calculated, these three indices of nutrient resorption are complimentary in nature and should be most effectively used when applied together.

Most studies on nutrient resorption from senescing leaves were performed in forested ecosystems and there are no data on nutrient resorption of salt marshes that I am aware of. Additionally, a large portion of these studies only consider the NUE of aboveground tissues, which may bias the results (Aerts 1990; Aerts and De Caluwe 1994), because root production

comprises a substantial part of the total plant production (Persson 1978; Sims and Singh 1978; Aerts et al. 1989; 1992a; Aerts and De Caluwe 1994). Further, the concentration of nutrients in root litter may differ from that in shoot litter (Aerts 1990).

The data used in the analyses described below are from a series of experimental nutrient treatments in a *Spartina alterniflora* salt marsh that demonstrated a clear limitation of aboveground biomass accumulation by nitrogen, and by phosphorus belowground. These field-based identifications of nutrient limitation provide a means to test the usefulness and variability of these three indices in a salt marsh ecosystem.

## METHODS AND MATERIALS

The study was conducted in a *Spartina alterniflora* dominated salt marsh located west of the Louisiana Universities Marine Consortium (LUMCON) in Cocodrie, LA (29° 15'N, 91° 21' W). The average soil nutrients in the region are 2.37% N, 0.8% P, and 68% organic matter (Chabreck 1972). The plant nutrient content data used in this study are the results of work described in Chapters 2 and 3. These chapters describe the results from a seasonal study of the above- and belowground biomass from March 2004 to February 2005, and from a factorial design experiment. The experiments consisted of triplicate treatments manipulated by monthly additions of 6 levels of nitrogen (0, 46, 93, 186, 372, 744 kg $ha^{-1}$ $mo^{-1}$) designated as the C, N46, N93, N186, N372, and N744 plots, respectively, and other plots in which various combinations of 744, 22, and 60 kg $ha^{-1}$ $mo^{-1}$ N (ammonium sulfate 33%), P (superphosphate; 18%), and Fe (ironite; 1%), respectively, were broadcasted monthly at low tide beginning April 2004 through September 2004. These second set of plots are labeled the C, N744, P, NP, NFe, PFe, and NPFe treatments.

Three measures of nutrient availability, resorption, and use efficiency were calculated for the above- and belowground biomass. Nutrient availability was determined by calculating the

nutrient resorption efficiency (RE), a measure of nutrient conservation and limitation. Nutrient resorption efficiency (RE) is defined as:

Aboveground:

$$RE = \frac{\text{N or P (g m}^{-2}\text{) in green biomass - N or P in standing dead biomass (g m}^{-2}\text{)}}{\text{N or P (g m}^{-2}\text{) in green biomass}}$$

Belowground:

$$RE = \frac{\text{N or P (g m}^{-2}\text{) in live roots and rhizomes - N or P in dead roots and rhizomes (g m}^{-2}\text{)}}{\text{N or P (g m}^{-2}\text{) in live roots and rhizomes}}$$

The nutrient use efficiency (NUE) was calculated by:

$$NUE = \frac{\text{Aboveground standing dead biomass (g m}^{-2}\text{)}}{\text{N or P in standing dead (g m}^{-2}\text{)}}$$

Nutrient resorption is the concentration of nitrogen and phosphorus in the plant tissue.

## RESULTS

Seasonal Variations Aboveground

The nutrient use efficiency of N (NUE-N) in the live *S. alterniflora* aboveground biomass did not vary much throughout the growing season and ranged from 121 March 2004, to 192 in September, with an annual average of 158 (Table 4.1). No statistically significant difference in the monthly NUE-N or NUE-P was identified for the sampling period. The highest nutrient use efficiency of P (NUE-P) in the aboveground biomass occurred in May (4882) and August 2004 (4652), with an annual mean of 2443 (Table 4.1).

The resorption efficiency for N (RE-N) in the aboveground biomass was highest in October 2004 (69%) and lowest (-170%) in March (Table 4.2). The RE-N in the aboveground

Table 4.1. The monthly nutrient utilization efficiency (NUE) of the above- and belowground biomass of *S. alterniflora.* The results from September's end-of-season nutrients are in **bold**. The values are the average of 3 replicate plots.

| | Nutrient use efficiency | | | |
|---|---|---|---|---|
| Julian day | Aboveground | | Belowground | |
| | N | P | N | P |
| 78 | 121 | 1125 | 84 | 1544 |
| 114 | 142 | 2545 | 67 | 2147 |
| 148 | 170 | 4822 | 72 | 2269 |
| 162 | 147 | 3029 | 71 | 2188 |
| 190 | 147 | 3133 | 72 | 2363 |
| 221 | 192 | 4652 | 71 | 1899 |
| 255 | **190** | **1999** | **72** | **1163** |
| 281 | 185 | 1948 | 81 | 1274 |
| 324 | 161 | 1653 | 66 | 1473 |
| 340 | 156 | 1447 | 66 | 1379 |
| 384 | 153 | 1366 | 63 | 1198 |
| 421 | 128 | 1602 | 71 | 1458 |
| Average | 158 | 2443 | 71 | 1696 |

Table 4.2. The monthly nutrient resorption efficiency (RE) of the above- and belowground biomass of S. *alterniflora.* The results from September's end-of-season nutrients are in **bold**.

| Nutrient resorption efficiency (%) | | | | |
|---|---|---|---|---|
| Julian day | Aboveground | | Belowground | |
| | N | P | N | P |
| 78 | -170 | -86 | -8 | 4 |
| 114 | -61 | 56 | -235 | -61 |
| 148 | 16 | 85 | -2038 | -534 |
| 162 | 8 | 75 | -834 | -139 |
| 190 | 66 | 85 | -5029 | -1509 |
| 221 | 65 | 87 | -414 | -152 |
| 255 | **62** | **74** | **-32** | **-26** |
| 281 | 69 | 77 | -238 | -160 |
| 324 | 53 | 58 | -858 | -622 |
| 340 | 54 | 61 | -395 | -232 |
| 384 | 17 | 23 | -376 | -319 |
| 421 | 24 | 54 | -103 | -32 |
| Average | 17 | 54 | -880 | -315 |

biomass was lowest early in the growing season, increased to 66%, and then remained relatively constant until January (2005) when the RE value decreased to 17%. The RE-P increased during the growing season from –85% in March to 77% in October. The mean annual resorption proficiency for N (RE-N) and P (RE-P) in the dead aboveground biomass was 17% and 54%, respectively (Table 4.2).

The nutrient resorption proficiency of N (RP-N) in the aboveground biomass was 0.59 in May (Table 4.3). The RP-N value remained below 0.7 until February. The RP-N value for March and April (2004) was 0.83 and 0.71, respectively. The RP-N in February 2005 was 0.78. The annual proficiency was for N was 0.65 (Table 4.3). The nutrient resorption of P (RP-P) in the aboveground biomass was 0.09 in March 2004, and from April to August it remained in the range of 0.04 to 0.02. The RP-P values were higher from September (2004) to February (2005) and ranged from 0.05 to 0.07. The annual RP-P value was 0.05 (Table 4.3).

Seasonal Variations Belowground

The belowground NUE-N values ranged from 63 to 84 and 1274 to 2,363 for NUE-P (Table 4.1). The highest NUE-P (2363) occurred in July (Table 4.4). The RE-N was statistically significantly different ($p< 0.01$) between above and belowground biomass, but not for NUE-P. The RE-N of the belowground biomass was -8.23% in March and continued to decline through out the sampling period (Table 4.2). The average annual RE-N belowground was -880%. The RE-P resorption value in the belowground biomass decreased from 4% in March and remained below zero for the year. The mean annual RE-P for the sampling period for period was -102%. A statistically significant difference ($p<.01$) was seen between the RE-P of the aboveground biomass and belowground biomass (Table 4.2).

The RP-N in the belowground biomass was 1.2% in March, 2004, the highest RP-N value occurred in January, 2005 (1.6%) and the annual RP-N value was 1.4% (Table 4.3). The RP-P

Table 4.3. The nutrient resorption proficiency (RP) of the above- and belowground biomass of *S. alterniflora*. The results from September's end-of-season nutrients are in **bold**.

| Nutrient resorption proficiency | | | | |
|---|---|---|---|---|
| Julian day | Aboveground | | Belowground | |
| | N | P | N | P |
| 78 | 0.83 | 0.089 | 1.19 | 0.065 |
| 114 | 0.71 | 0.039 | 1.49 | 0.047 |
| 148 | 0.59 | 0.021 | 1.39 | 0.044 |
| 162 | 0.68 | 0.033 | 1.41 | 0.046 |
| 190 | 0.68 | 0.032 | 1.39 | 0.042 |
| 221 | 0.52 | 0.021 | 1.41 | 0.053 |
| **255** | **0.53** | **0.050** | **1.38** | **0.086** |
| 281 | 0.54 | 0.051 | 1.23 | 0.078 |
| 324 | 0.62 | 0.061 | 1.51 | 0.068 |
| 340 | 0.64 | 0.069 | 1.510 | 0.073 |
| 384 | 0.66 | 0.073 | 1.58 | 0.083 |
| 421 | 0.78 | 0.062 | 1.40 | 0.069 |
| Average | 0.65 | 0.050 | 1.401 | 0.063 |

index was lowest (0.04%) in May and July (Table 4.3). The highest RP-P value occurred in September (0.09%), and the annual RP-P was 0.06% (Table 4.3).

Fertilization Effects Aboveground

No statistically significant differences were established in the NUE-N of the aboveground biomass for N among the various fertilizer treatments (Table 4.4). The NUE-N in the aboveground biomass increased from 609 (C plots) to 960 (N744) with increased N availability (Table 4.4). The average NUE-N among treatments was 640. The NUE-N was lowest in the Fe plots (489). The NUE-P in the aboveground biomass was in C plot was (8,477). The highest NUE-P was in the N744 plots (14,559). The average NUE-P value was 9241 (Table 4.4). A statistically significant difference was seen among the treatments NUE-P. The NUE values in plots N744 (14,559), NP (13,745), and NFe (11,744) were significantly different ($p<0.001$) from the other treatment plots.

The value for RE-N in the dead aboveground biomass was 59% for the control plot (Table 4.5). The highest RE-N was in the N186 plot (71%) and lowest in the PFe plots (48%). No statistically significant differences were observed, however, in the RE-N values among the various fertilizer treatments. The value of RE-P was highest in the P and N186 plots (both 83%). The average RE-P value of the aboveground biomass for all treatment plots was 73% (Table 4.5).

The value of RP-N in the aboveground biomass was 0.65, 0.62 and 0.61 for the Control, N46 and P plots, respectively (Table 4.6). The average RP-N in all treatment was .80 (Table 4.6). The value of RP-N for the aboveground biomass was 0.05 in the Control, N46 and N93 plots. The values of RE-N and RE-P in the control site indicate that there was some resorption of N, but not in plots receiving a moderate to high dose of N. The NUE-P in the aboveground biomass, however, exhibited higher recycling of P at the highest level of added N, while the RE-

Table 4.4. The nutrient utilization efficiency (NUE) of the above- and belowground biomass of *S. alterniflora* in the nutrient addition plots. The values are the average of 3 replicate plots for one growing season.

| | Nutrient use efficiency | | | |
|---|---|---|---|---|
| Treatment | Aboveground | | Belowground | |
| | N | P | N | P |
| Control | 609 | 8477 | 2522 | 42373 |
| N 46 | 640 | 7759 | 2701 | 54124 |
| N 93 | 646 | 8529 | 2656 | 46830 |
| N 186 | 407 | 6582 | 2253 | 47516 |
| N 372 | 733 | 9919 | 2199 | 35948 |
| N 744 | 960 | 14559 | 2122 | 39668 |
| P 48 | 520 | 6631 | 1917 | 35045 |
| N+P | 900 | 13745 | 1926 | 35216 |
| Fe | 489 | 7019 | 2095 | 32581 |
| NFe | 691 | 11744 | 2250 | 48856 |
| PFe | 596 | 8241 | 1975 | 37232 |
| NFeP | 491 | 7681 | 2386 | 45262 |
| Average | 640 | 9241 | 2250 | 41721 |

Table 4.5. The nutrient resorption efficiency (RE) of the above- and belowground biomass of *S. alterniflora* in the nutrient addition plots. The values are the average of 3 replicate plots for one growing season.

| | Nutrient resorption efficiency | | | |
|---|---|---|---|---|
| Treatment | Aboveground | | Belowground | |
| | % N | % P | % N | % P |
| Control | 59 | 78 | -101 | 34 |
| N 46 | 70 | 78 | -94 | -58 |
| N 93 | 64 | 74 | -142 | -21 |
| N 186 | 71 | 83 | -198 | 52 |
| N 372 | 59 | 66 | -65 | 66 |
| N 744 | 55 | 65 | -123 | -17 |
| P 48 | 69 | 83 | -224 | 21 |
| N+P | 58 | 74 | -223 | 62 |
| Fe | 67 | 81 | -200 | 24 |
| NFe | 64 | 80 | -379 | 22 |
| PFe | 48 | 48 | -217 | 58 |
| NFeP | 60 | 60 | -305 | -274 |
| Average | 62 | 73 | -189 | -3 |

P values remained unchanged. The RP-P values support the hypothesis that P in the aboveground tissues is recycled at the same rate independent of the amount of N added.

Fertilization Effects Belowground

There were no statistically significant differences in NUE-N of the belowground biomass among the various fertilizer treatments (Table 4.4). The NUE-N in the belowground biomass was high for all treatment plots with an average NUE-N of 2,250 for all treatment plots (Table 4.4). The NUE-P in the belowground biomass was also exceptionally high compared to the Control (42,373) plot for all treatment levels, with an average value of 41,721. The RE-N in the dead belowground biomass was -101% for the control plot (Table 4.5). No positive values were identified for any treatment level (Table 4.5). The RP-N in belowground biomass ranged from 1.33 to 1.45 for all treatment plots. The average RP-N in all treatment was 1.38 (Table 4.6). The RP-P in the belowground biomass ranged from 0.06 to 0.09. The highest value of RP-P 0.09% was in the N372 plot, and the lowest of 0.06% was in the NFe plot (Table 4.6). The average RP-P was 0.07% for all treatment plots (Table 4.6). The NUE-P values in the belowground tissues showed that there was a lower P resorption with added P, and a higher P resorption with added N, or N + Fe. The RE-P values decreased when P and Fe were added together. The RP-P was reduced with added P, but not with a combination of P and Fe. This combination of results suggests that there is P, but not N, limitation of belowground plant tissues.

## DISCUSSION

Table 4.7 is a summary of results combined from the three indices. The N resorption indices indicate that N availability to the aboveground tissues was low, because the aboveground biomass resorbed a high percent of the N, and that P became less available during the growing season.

Table 4.6. The nutrient resorption proficiency (RP) of the above- and belowground biomass of *S. alterniflora* in the nutrient addition plots. The values are the average of 3 replicate plots for one growing season.

| | Nutrient resorption proficiency | | | |
|---|---|---|---|---|
| Treatment | Aboveground dead | | Belowground dead | |
| | N | P | N | P |
| Control | 0.65 | 0.047 | 1.34 | 0.080 |
| N 46 | 0.62 | 0.051 | 1.33 | 0.066 |
| N 93 | 0.71 | 0.053 | 1.36 | 0.077 |
| N 186 | 0.94 | 0.058 | 1.45 | 0.069 |
| N 372 | 0.92 | 0.068 | 1.41 | 0.086 |
| N 744 | 0.93 | 0.062 | 1.39 | 0.074 |
| P 48 | 0.61 | 0.048 | 1.38 | 0.076 |
| NP | 0.93 | 0.061 | 1.38 | 0.075 |
| Fe | 0.73 | 0.051 | 1.33 | 0.085 |
| NFe | 0.93 | 0.055 | 1.38 | 0.064 |
| PFe | 0.69 | 0.050 | 1.40 | 0.074 |
| NFeP | 0.98 | 0.063 | 1.38 | 0.073 |
| Average | 0.80 | 0.06 | 1.38 | 0.07 |

Table 4.7. A summary of the changes in the nutrient resorption indices from N and P additions.

| | How does added N increase the Resorption rates of N | How does added N increase the Resorption rates of P | How does added P increase the Resorption rates of N | How does added P increase the Resorption rates of P |
|---|---|---|---|---|
| Aboveground | | | | |
| NUE index | no change | higher? | mixed | lower |
| RE index | no change | no change | higher | lower |
| RP index | lower | no change | higher | lower |
| Belowground | | | | |
| NUE index | no change | no change | lower | lower |
| RE index | no change | no change | no change | lower |
| RP index | no change | no change | no change | no change |

The values of NUE-N in the belowground tissues demonstrated little variation during the growing season. There was also no change in the RE-N or RP-N values, which indicated that the growth of the belowground biomass was not limited by N. The NUE-P in the belowground biomass, however, increased from March to July, whereas the values for RE-P remained unchanged, and the, RP-P values in the belowground biomass increased. Thus, P was conserved belowground, but also a large amount was lost in the dead roots and rhizomes. One possible explanation for this difference between the N and P resorption values is that P is more subject to leaching from roots than N is.

No change in the NUE-N values was seen in the belowground biomass, reflecting a lower P resorption with P or P + Fe additions, and there was no apparent change in combination with other nutrients. The values for RE-N demonstrated erratic responses to the addition of N. No changes in the RP-N values were seen with any level of N, or N in combination with P and Fe. The values of NUE-P in the belowground biomass were inconsistent or did not change with the addition of N. The NUE-P values were lower when P or Fe was added individually. The values for RE-P demonstrated higher resorption with a combination of N + P, and lower resorption with P or Fe additions to the experimental plots. No obvious patterns were observed in the values of RE-P with added N. The RP-P index had no obvious changes with the N additions or any other added nutrients.

One of the main patterns observed in several studies is that the aboveground NUE-N, RE-N, and RP-N indices suggest decreasing nutrient resorption rates with increasing N availability (Vitousek 1982; Pastor et al. 1984). Perhaps N losses increase faster than productivity leading to a lower NUE-N. The lack of changes belowground in these three indices supports the conclusion that N does not limit growth belowground (no resorption of N took place). P

resorption did increase during the growing season at the time when there was a decrease in the belowground biomass. The resorption of P during the active growing season demonstrated that P is the limiting nutrient belowground.

The minimal change in the three resorption indices with N additions, and the resorption values of P, and the other changes or lack of changes all indicate that accumulation of belowground biomass was limited by P. It appears that adding P stimulates greater resorption rates aboveground and lowers resorption rates belowground. Nitrogen additions did not change the resorption rates of N or P.

These functional indicators are shown to be useful tools in establishing and understanding nutrient availability and the role of plants as nutrients move through and within salt marshes. These indices do not always provide the same response, however, and so it may be necessary to explore new methods and to develop additional data to accurately evaluate nutrient resorption in wetland environments.

## LITERATURE CITED


AERTS, R. 1990. Nutrient use efficiency in evergreen and deciduous species from heathlands. *Oceologia* 78:391-397.

AERTS, R. 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology* 84:597-608.

AERTS, R. AND H. DECALUWE. 1994. Nitrogen use efficiency of Carex species in relation to nitrogen supply. *Ecology* 75:2362-2372.

AERTS, R., J. T. A. VERHOVEN, AND D. F. WASHINGTON. 1999. Plant mediated controls on nutrient cycling in temperate fens and bogs. *Ecology* 80:2170-2181.

BERG, B. 1986. Nutrient release from litter and humus in coniferous forest soils- a mini review. *Scandinavian Journal of Forestry Research* 1:359-369.

CHABRECK, R. H. 1972. Vegetation, water and soil characteristics of the Louisiana coastal region. Louisiana State University Agricultural Experiment Station Bulletin 664.

CHAPIN, F. S. III, 1980. The mineral nutrition of wild plants. *Annual Review of Ecology Systematics* 11:233-260.

CHAPIN, F. S. AND L. MOILANEN. 1991. Nutritional controls over nitrogen and phosphorous resorption from Alaskan birch leaves. Ecology 72:709-715.

COLE, C.V., D. L. GRUNES, L. K. PORTER, AND S. R. OLSEN. 1963. The effects of nitrogen on short-term phosphorus absorption and translocation in corn (*Zea Mays*). *Soil Science Society of America Proceedings* 27:671-674.

CLARK, F. E. 1977. Internal cycling of "nitrogen" in shortgrass prairie. *Ecology* 58:1322-1333.

GUISEWELL, S. AND W. KOERSELMAN. 2002. Variation in nitrogen and phosphorous concentration of wetland plants. *Perspectives in Plant Ecology, Evolution and Systematics* 5:37-61.

HAYATI, A. A. AND M.C.F. PROCTOR. 1990. Plant-distribution in relation to mineral nutrient availability and uptake on a wet-heath site in south-west England. *Journal of Ecology* 78:134-151.

KILLINGBECK, K. T. 1986. The terminological revisited: making a case for use of the term resorption. *Oikos* 46:263-264

KILLINGBECK, K. T. 1996. Nutrients in senesced leaves: Key to the search for potential resorption and resorption proficiency. *Ecology* 77:1716-1727.

MARSCHNER, H. 1995. Mineral Nutrition in Higher Plants. London, United Kingdom, Academic Press.

MEULEMAN, A. F. M., J. P. BEEKMAN, AND J. T. A. VERHOEVEN 2002. Nutrient retention and nutrient use efficiency in *Phragmites australis* stands after wastewater application. *Wetlands* 22:712-721.

MIKKELSON, R. 2005. Nutrient use efficiency: Using nutrient budget. Western Nutrient Management Conference. Vol. 6, Salt Lake City, Utah.

MILLER, H. G., J. M. COOPER, AND J. D. MILLER. 1976. Effect of nitrogen supply on nutrients in litterfall and crown leaching in a stand of Corsican pine. *Journal of Applied Ecology* 13:233-248.

ROBINSON D. 1994. The responses of plants to non-uniformed supplies of nutrients. Transley *Review* no. 73, *New Phytology* 127:635-674.

ROBINSON D. AND I. H. RORISON 1988. Plasticity in grass species in relation to nitrogen supply. *Functional Ecology* 2:249-257.

SHAVER, G. R. AND J. M. MELILLO. 1984. Nutrient budgets of marsh plants: Efficiency concepts and relation to availability. *Ecology* 65:1491-1510.

STAAF, H. AND B. BERG. 1982. Accumulation and release of plant nutrients in decomposing Scots pine needle litter. II. Long-term decomposition in a Scots pine forest. *Canadian Journal of Botany* 60:1561-1568.

THIEN, S. J., AND W. W. MCFEE. 1972. Effect of nitrogen on phosphorus transport systems in *Zea Mays* L. *Soil Science Society of America Procedure* A36:617-620.

UNITED STATES ENVIRONMENTAL PROTECTION AGENCY. 2002. Methods for evaluating wetland conditions # 16. Vegetation-based indicators of wetland nutrient enrichment, Office of Water, Washington, D C.

WHEELER, B. D., S. C. SHAW, AND R. E. D. COOK. 1992. Phytometric assessment of the fertility of undrained rich-fen soils. *Journal of Applied Ecology* 29:466-475.

WHITE, R. E. 1973. Studies on mineral absorption by plants II. The interaction between metabolic activity and the rate of phosphorus absorption. *Plant Soil* 38:509-523.

WILLBY, N. J., I. D. PULFORD, AND T. H. FLOWERS. 2001. Tissue nutrient signatures predict herbaceous-wetland community response to nutrient availability. *New Phytologist* 152:463-481.

# CHAPTER 5

# NUTRIENT FORAGING IN SALT MARSHES: THE CONSEQUENCES OF EUTROPHICATION TO SALT MARSH ROOTS AND RHIZOMES

## INTRODUCTION

Nutrient supply is a broadly appreciated influence on plant composition, growth and productivity (Chapin 1980). Plants may adjust their nutrient foraging capacity by modifying root, rhizome and shoot morphology, and mass. Grassland plants, for example, exhibit lower root : shoot biomass ratios as soil fertility increases and aboveground production rises (Tilman and Wedin 1991). A decline in the root : shoot ratio may also occur in coastal marshes under the influences of cultural nutrient enrichment and affect the soil ecosystem. Valiela et al. (1976), for example, documented the stimulation of aboveground production and a reduced root + rhizome biomass under different experimental additions of nitrogen+phosphorus applied to tidally-flooded organic-rich salt marshes in Massachusetts, and they estimated that the consequences were equal to a 1 cm decrease in marsh elevation.

Coastal salt marshes maintain their vertical position within the upper portion of the local tidal range through the accumulation of inorganic and organic materials. The long-term health of an organic-rich salt marsh is dependent on the amount and fate of belowground organic production. In organic-rich salt marshes, soil density is primarily determined by the inorganic content and the accretion rate by the vertical accumulation of organics (Gosselink 1984; Turner et al. 2001). Differences between streamside and inland organic accumulation in a Virginia marsh, for example, are described by organic production belowground rather than decomposition or inorganic content (Blum 1993). A coastal marsh may convert to open water or upland vegetation if organic accretion is too low, or high, respectively. An aggressive new form of *Phragmites australis* apparently out-competes *S. alterniflora* on the upland side of the plant's distribution by producing greater root mass than *S. alterniflora* and raising the soil elevation (Bertness 2002; Rooth and Stevenson 2000). Soil elevation may be lowered, and to the detriment of the plant's existence, if either the root production is decreased or the decomposition

of accumulated organic matter is accelerated enough so that the net organic accumulation is less than relative sea level rise. The loss of root biomass is a diagnostic of plant health in Louisiana salt marshes, where root biomass was seven times higher in marshes categorized as 'healthy' compared to deteriorating 'unhealthy' marshes (Turner et al. 2004).

An implication of these observations is that the increases in nutrient loading to coastal systems, which are widespread (Cloern 2001; Rabalais 2002; National Research Council 2000; Howarth and Marino 2006), may alter marsh ecosystem functions and perhaps compromise the long-term stability of salt marshes by reducing root production and causing a consequential decline in soil organic accumulation. Morris and Bradley (1999), for example, found that, compared to unfertilized sites in a relatively mineral-rich South Carolina salt marsh, fertilization for 12 years increased soil respiration by 36% and decreased soil carbon accumulation by 40 C g $m^2$ $y^{-1}$, but did not cause a change in surface elevation. The effects of higher nutrient loading on soil organics would not be expressed equally along a latitudinal gradient or within the tidal range occupied, however, because of the varying effects of climate and flooding on sulfide accumulation, soil respiration, root production, and sediment quality. Temperature, for example, has a well-established effect on soil organic decomposition (Gill and Jackson 2000) and salt marsh plants have some abilities to adapt to some degree of flooding and salt stress (Mendelssohn et al. 1981; King et al. 1982). Further, soil porosity, wetness, and exchange capacity can also alter nutrient availability.

I report here on a combination of geographically diverse and regionally-specific sampling of belowground biomass under various nutrient addition experiments designed to determine the effects of nutrient loading on salt marsh ecosystems. I conducted these experiments in East Coast and Gulf of Mexico salt marshes dominated by *Spartina alterniflora* using a springtime

addition of N and or P, and monthly additions of N, P and Fe in a Louisiana salt marsh. The results from the end-of-summer sampling are discussed here.

## METHODS AND MATERIALS

Monospecific stands of *S. alterniflora* were sampled at Cocodrie and Empire, LA, Sapelo Island, GA, the Upper Phillips Creek Marsh within the Virginia Coast Reserve, VA, Narragansett Bay, RI, and at Sippewissett, MA. Descriptions of these marshes are in Darby and Turner (LA; manuscript), Schubenhauer and Hopkinson (1984; GA), Blum (1993; Va), Wigand et al. (1993; RI), and Valiela, Teal et al. (1976; MA).

Aboveground *Spartina alterniflora* was harvested by clipping vegetation at the sediment surface in adjacent replicated 0.25 $m^2$ plots designated as control or fertilized plots. The fertilized plots received 12-18-24 Osmocote$^{@}$ fertilizer additions in May 2005, and the biomass was sampled in September 2005. The single spring fertilizer dose was 2246 and 66 kg per ha per yr, N and P, respectively. These loading rates are also within the range of N and P loadings to Gulf of Mexico (GOM) estuaries (Turner et al. 1999) and are comparable to those of others (Mendelssohn 1979; Morris and Bradley 1999; Huang and Morris 2003). The aboveground biomass of *S. alterniflora* in one GOM estuary, Barataria Bay, changes with varying concentrations of nitrogen in tidal waters (Visser et al. 2006), supporting the idea that a minimum threshold for nutrient loading impacts on marsh productivity has already been exceeded there.

Additional standing stocks of live belowground and live aboveground biomass were manipulated by monthly additions of various combinations of N, P, and Fe in a triplicate experiment at Cocodrie, LA, concluded in September 2004 (Darby and Turner, ms.) when soil Eh was measured at 10 cm depth. The dosage consisted of a factorial design of various

combinations of 22 and 60 kg per ha per yr of P and Fe, respectively, and six different doses of N ranging between 0 and 8984 kg per ha per yr, in a total of 36 plots.

All standing live and dead culms and litter were removed from the control and fertilized plots and placed into pre-labeled plastic bags and transported to the Louisiana State University (LSU) processing lab. Dead shoots and leaves were identified by their yellowish or brownish coloration and separated from living material. The live or dead plant material was put into pre-labeled paper bags, and dried at 75$^{o}$ C for approximately 72 hours and weighed to the nearest 0.1 g.

Belowground biomass was collected using a 40 cm long stainless steel tube with sharpened edges. An 11 cm diameter x 30 cm long sediment core was taken in the middle of each plot after the aboveground biomass sample was collected. The cores were extruded in the field and sliced into 0-10 cm, 10-20 cm and 20-30 cm segments, each segment was placed in labeled plastic Ziplocs$^{@}$ bags, and then placed in a cooler for transport to the LSU lab where they were refrigerated until processed. Each segment was washed in a 1 mm sieve over a 0.5 mm sieve to prevent the loss of dead and fine root material. Live roots and rhizomes were separated from dead material with a suture set under running water for better separation (live roots and rhizomes are white and turgid, dead materials are dark and flaccid). Root color can be variously tinged pink or orange, possibly because of pigmentation zones, e.g., roots colonized by arbuscular mycorrhizal fungi are often yellow. Discolored turgid roots were defined as live roots. Dead material included partially decayed root material. Cores containing a large amount of rocks, shell, and miscellaneous debris, were placed in water and sorted with a small kitchen strainer. Live and dead roots floated while rocks etc. sank. Live roots and dead belowground material was bagged in paper bags, labeled, and dried at 60$^{o}$ C for to 72 hours, and weighed to

the nearest 0.01g. The belowground biomass data reported here are for the entire 30 cm sediment profile.

Soil Eh was measured at 10 cm depth using three Eh probes (brightened platinum) calibrated in the laboratory before and after the field trip. Eh was measured using a digital voltmeter as the potential (mV) of a calomel electrode against the Eh probe. The half-potential of the calomel electrode (+244 mV) was added to the measured potential to calculate Eh. There were three replicated plots of at least three Eh measurements in each plot, at 10 cm soil depth. The plant harvest and Eh measurements at Cocodrie, LA, were on 3 Sept. 2004 when the aboveground live biomass was at a seasonal maximum. Biomass collections at GA, VA, MA and Empire, LA, were later in September 2005. The results for August from three nutrient addition experiments in a Massachusetts salt marsh (Valiela et al. 1976) were included in the comparison, except for one result from a low fertilization experiment (urea), excluded because of the combination of small sample size (2) and large variance (two fold range).

## RESULTS AND DISCUSSION

### Belowground Biomass

A plant's response to a combination of nitrogen and phosphorus fertilizer added to the surface of ten salt marshes in Massachusetts, Virginia, and Louisiana and from three fertilized sites studied by Valiela et al. (1976) was to increase the aboveground live biomass by an average of 174% +/- 36% ($\mu$ = +/- 1 Std. dev.; n = 13) of the value at the unfertilized control sites (Fig. 5.1). This response was consistent with the results from more than a dozen field experiments (Morris 1991).

The belowground live biomass (total roots + rhizomes), however, was reduced at 12 of 13 fertilized sites. The average belowground biomass was 71% +/- 24% ($\mu$ +/- 1 Std. dev.; n = 13)

of the value at the unfertilized control sites. The changes in belowground live biomass in the fertilized plots were greatest when the biomass in the control plots was highest (Fig. 5.2). The change ranged from a +8% enhancement of belowground biomass at the sites with less than 200 g $m^{-2}$ belowground live biomass to a decline of 49% at sites with the highest belowground live biomass. There were no differences between the four sites fertilized with only P compared to the 13 sites fertilized with N+P. In other words, the environments with the highest amounts of roots and rhizomes had the greatest change in biomass when fertilizer was added.

The ratio of the live belowground biomass (roots and rhizomes , live aboveground plant biomass (R&R : S) ranged from 0.17 to 11 (n = 33) in east coast marshes and from 0.05 to 15 (n = 84) in Louisiana marshes (Fig. 5.3). The result of fertilization was to drive the R&R : S ratio lower along the continuum from low to high aboveground production. The kind of fertilizer applied (N, N+P, P) had an effect on this R&R : S ratio. There was a disproportionate change in aboveground and belowground live biomass that was dependent on whether or not P was added to the experimental plots. The ratio at sites fertilized with P, or with P in combination with N, was lower for the same amount of aboveground live biomass, compared to either unfertilized control sites or sites fertilized with only N. In other words, P additions alone had an equal or larger effect on the R&R : S ratio than did only N additions.

The effect of varying nutrient loading has a relatively constant effect on roots and rhizomes biomass. Rhizomes, a seasonal reserve of nutrients and carbon, make up an average seventy-four percent of the end-of-summer belowground live biomass in the sampled salt marshes (Fig. 5.4). There was no statistically-significant difference between the percent of belowground live biomass that was rhizome in the fertilized or unfertilized plots. This constancy between the biomass of the roots foraging for nutrients and the rhizomes acting as seasonal reserves at the end of the growing season suggests that fertilization did not introduce an

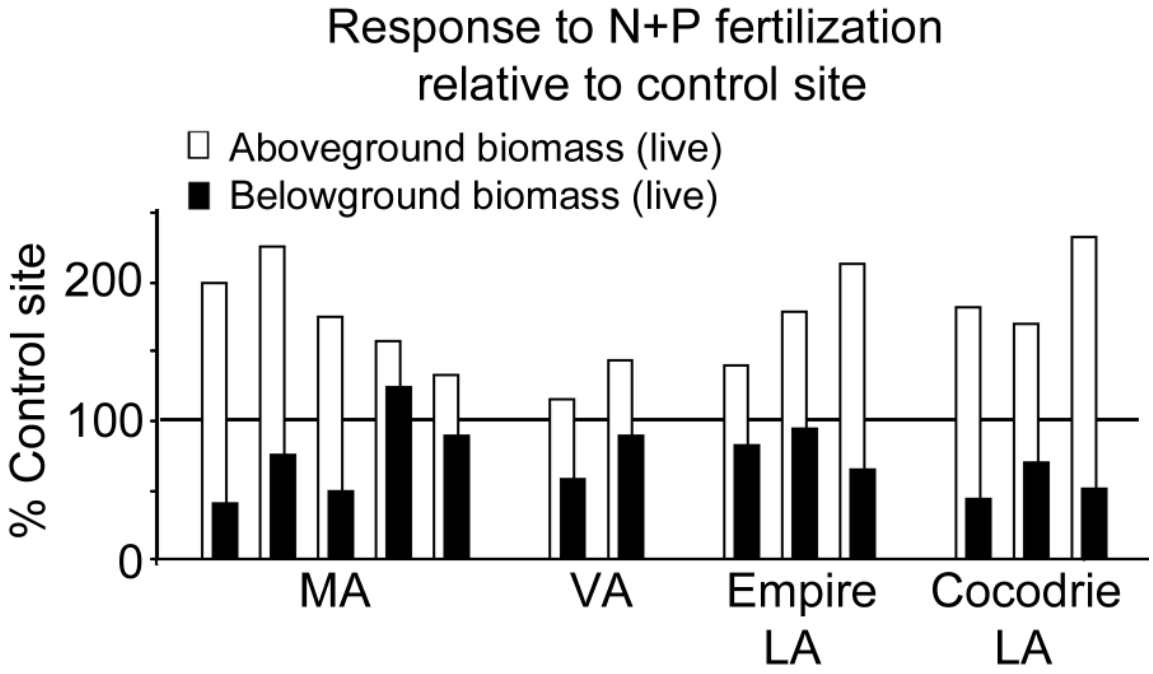


Fig. 5.1. The changes in live above- and belowground biomass at the end of the growing season expressed as a percentage of the live biomass in replicated fertilized plots relative to the control sites. Nitrogen and phosphorus was added simultaneously at all sites to the surface of the marsh. The first three results from Massachusetts are from Valiela et al. (1976).

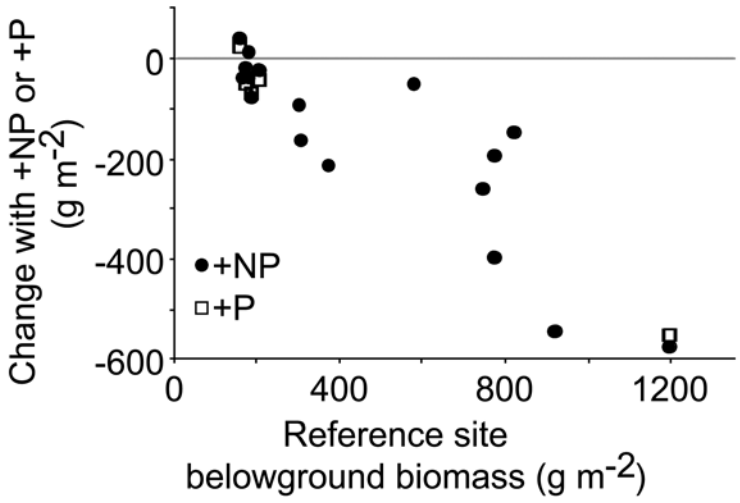


Fig. 5.2. The relationship between the change in live belowground biomass after fertilization for several months (harvest at the end of the growing season) and the live belowground biomass in the reference sites (paired samples).

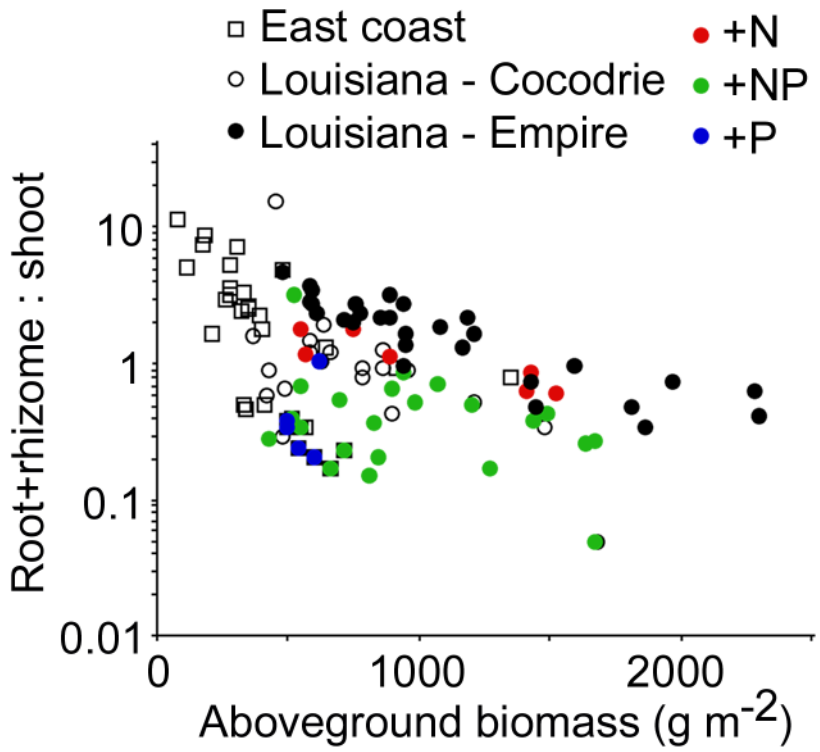


Fig. 5.3. The ratio of the belowground live biomass (roots and rhizomes) : live aboveground biomass in different salt marshes with and without additions of N, N+P, or P (red, green and blue, respectively). Data are from this study, and from literature sources described in the text. The squares and circles are measurements from salt marshes on the east coast US or Louisiana, respectively. The data are for the end of the growing season.

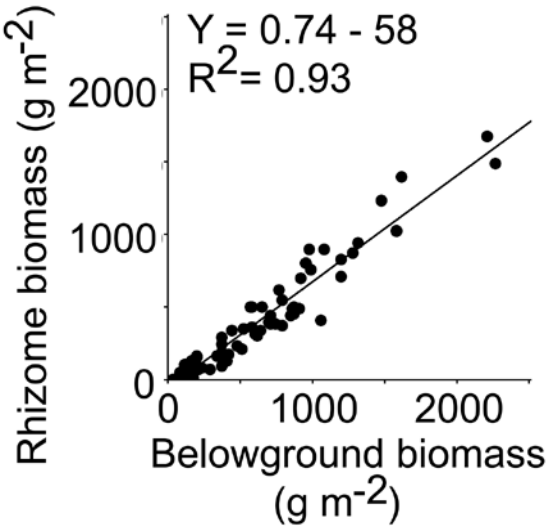


Fig. 5.4. The relationship between the biomass of live rhizomes and the total belowground biomass (g $m^{-2}$). The data are for the end of the growing season.

experimental artifact and that cross-system comparisons are valid.

The effect of fertilization is to reduce the amount of the total plant biomass that is belowground (Fig. 5.5). The effect of a changing standing stock on the total below- or aboveground biomass *production*, however, depends on how much biomass production there is per standing biomass throughout the year.

Belowground Production

The production : standing stock ratio (P : SS; end of summer values) is not expected to be the same for above- and belowground production or across the distributional range of *S. alterniflora*. The belowground production of salt marshes can be estimated using any one of three basic methods, and all three have been applied at several locations for more than one year at the same location. The' Smalley' method uses differences in the standing stocks of live and dead material throughout a growing season to estimate a minimum amount production necessary to account for the observed changes in dead and live biomass pools (Dame and Kenny 1986). The 'Max-Min' method uses the maximum difference in live biomass throughout a growing season. Blum (1993) used a third approach. She made monthly measurements of root biomass accumulation bimonthly, root growth in growth chambers, and root decomposition in litter bags to estimate annual belowground plant production. Although each method used to estimate belowground production has its faults and advantages, each has higher production per unit belowground standing stock of live material (Fig. 5.6), and the data derived from them can be used to calculate a relative production rate per unit biomass ratio (PB) along a latitudinal gradient. These data also demonstrate the variability in production between years, suggesting that edaphic factors are an important influence.

The PB ratio is highest at the warmer end of the latitudinal distribution of *Spartina alterniflora* (Fig. 5.7). The significance of these results is that the highest production rates per

unit biomass is in Gulf of Mexico salt marshes, and that belowground production is proportional, albeit in some still-incompletely measured way, to the standing stock of live belowground plant material. The logical conclusion is that eutrophication will result in lower belowground production, especially in the Gulf of Mexico. The more oligotrophic system, in other words, will have the greatest amount of belowground production and are most sensitive to changes in nutrient supply. Louisiana marshes have an aboveground P : SS ratio of 2.25 (Kaswadji et al. (1990) and a belowground P : SS ratio of > 10. The effect of eutrophication is, therefore, to result in a lower total salt marsh plant production there.

Soil Biogeochemistry

The average soil Eh at 10 cm depth was directly related to the R&R : S ratio in 12 triplicate treatment plots at Cocodrie, LA (Fig. 5.7). The average Eh decreased as the R&R : S ratio increased. The sites with the highest belowground biomass have a more aerated soil system. Soil Eh could decline at these sites because of greater respiratory demand, but not from increased flooding, because the control and fertilized sites were located within 15 m of each other in a marsh that appeared homogenous. This result implies that soil respiration is higher in the fertilized sites compared to the control sites, as Morris and Bradley (1999) describe in a more inorganic-rich South Carolina salt marsh. One consequence of the lower Eh in the fertilized plots is to increase the likelihood that sulfide will form during flooding, which may result in the catastrophic demise of the plant (Mendelssohn et al. 1981). Dissolved sulfide concentrations in *S. alterniflora* marshes, for example, have been shown to be negatively correlated with above-ground production (King et al. 1982).

Management Implications

The consequences of higher nutrient loading to salt marshes will not be equally distributed across the salt marsh landscape. The belowground plant biomass among locations

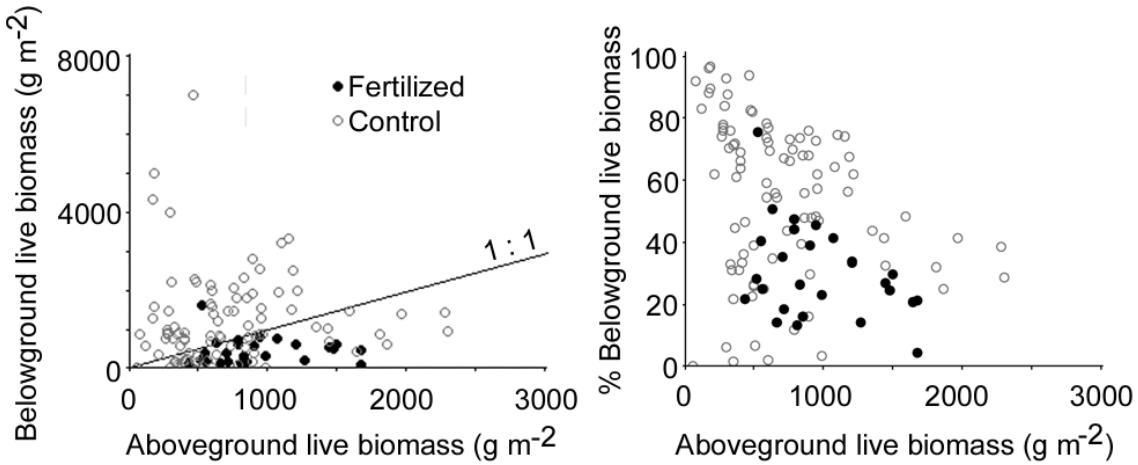


Fig. 5.5. The relationship between the above- and belowground live biomass for fertilized and control sites. The data are for the end of the growing season. The data are from this study and from the literature cited in the text.

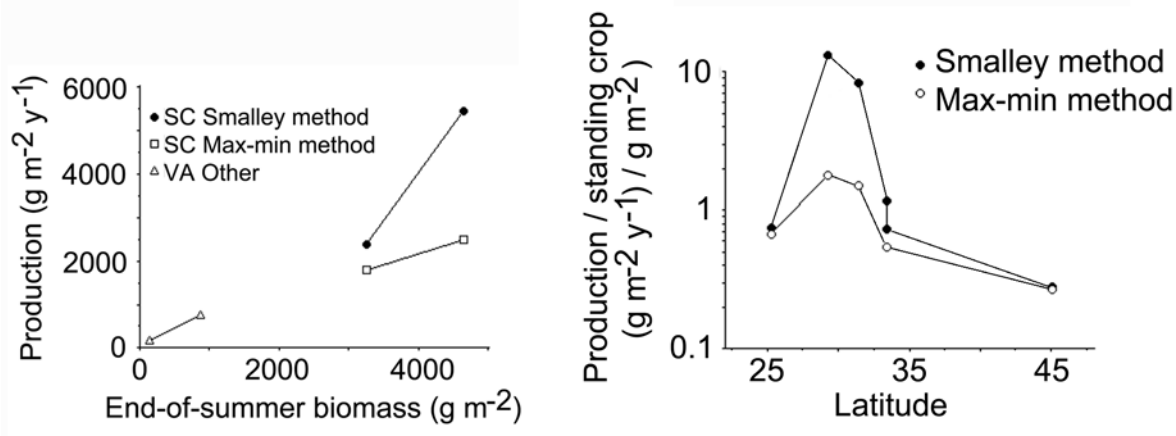


Fig. 5.6. The relationships between belowground production and standing stock of biomass at the end of summer (left) and the production per unit biomass (right). Estimates are based on data in Conner and Chmura (2000; Nova Scotia, Canada), Blum and Christian (2005; VA), Dame and Kenny (1986; SC), Ornes and Kaplan (1989; SC), Schubenhauer and Hopkinson (1984; GA), Darby and Turner (this study), and Lana et al. (1991; Brazil).

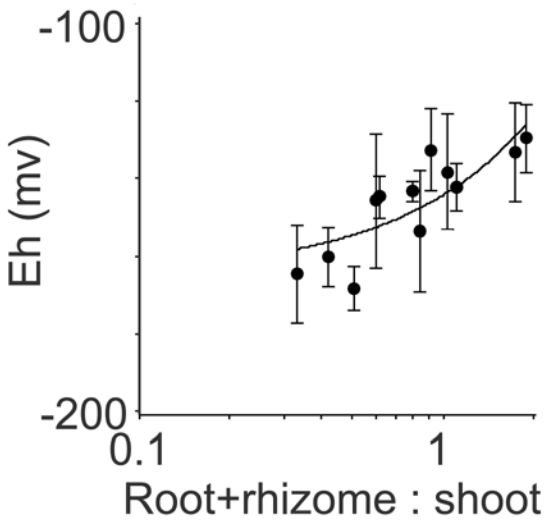


Fig. 5.7. The relationship between soil Eh at 10 cm and the root+rhizome : shoot ratio (live biomass) in experimental plots at Cocodrie, LA, 3 Sept. 2004. The bars are +/- 1 Std. error. The curve is a simple linear regression of the untransformed data.

reflects the relative ease with which the plant scavenges nutrients from the soil and moves them to the aboveground biomass. Nutrients loaded to a wetland do not necessarily become available to the plant because of *in situ* soil processes, e.g., redox reactions transforming nitrogen from an available form to another, toxics such as sulfides, or immobilization (iron phosphates) (Howes et al. 1981, 1985). There is no apparent within-estuary geographic gradient in the belowground biomass of *S. alterniflora*, but there are limits to the distribution of salt marshes across hydrologic regimes. It is at these limits that new stressors, or the multiple effects of increased stressors, will probably affect the salt marsh ecosystem the most. These general observations about the effect of nutrient enrichment on plant belowground biomass may also apply to coastal marsh communities exposed to low salinities.

The eutrophication of estuaries may have hidden consequences (belowground) to salt marshes that may not appear for years if the accretionary processes are affected. The paradigm that salt marshes are "nitrogen limited" is true in terms of the aboveground biomass (Visser et al. 2006), but not the belowground biomass. Not only *S. alterniflora* roots and rhizomes, but also the salt marsh soil microbial community is limited primarily by phosphorus, not nitrogen (Sundareshwar et al. 2003; Huang and Morris 2005). Restoration monitoring valuations based on higher aboveground plant biomass may be fatally-flawed if they value higher aboveground biomass rather than either belowground biomass or plant cover. More plant production aboveground can be roughly assumed to result in less belowground production, which is not a desirable management goal for organic-rich coastal marshes. Restoration strategies meant to increase nutrient delivering to coastal wetlands by means of river diversions, which add to the predominately rainfall-supplied nutrient sources, may have no impact or even a negative impact on the marsh ecosystem. These diversions are not a trivial economic endorsement of the 'nutrient enhancement" restoration paradigm of coastal restoration. The two largest river

diversions in Louisiana are at Caenarvon in Breton Sound and at Davis Pond, in the Barataria Bay estuary. The Caenarvon diversion cost $26 million to construct. The initial cost of the Davis Pond diversion was $87 million and later became $120 million; another $100 million is now needed for engineering modifications to compensate for the unanticipated collection of floating marsh mats at the out-flow channel weirs.

Reducing nutrient loadings to coastal systems will simultaneously favor coastal wetland conservation and be consistent with the science supporting the Action Plan for Reducing, Mitigating, and Controlling Hypoxia in the Northern Gulf of Mexico (Mississippi River/Gulf of Mexico Watershed Nutrient Task Force 2001). This "Dead Zone" annually forms off the Louisiana coast and its size appears to be directly related to nitrogen loading by the Mississippi River, although phosphorus and silica are also important factors (Rabalais and Turner 2001; Turner et al. 2003, 2006). A single-nutrient management strategy for ecosystem management is, once again, shown to be a falsely-narrow approach to water quality problems, and should be replaced by an integrated strategy designed to reduce nutrient loadings.

## LITERATURE CITED


BERTNESS, M. D., P. J. EWANCHUK, AND B. R. SILLIMAN. 2002. Anthropogenic modification of New England salt marsh landscapes. *Proceeding of the National Academy of Sciences (USA)* 99:1395-1398.

BLUM, L. K. 1993. *Spartina alterniflora* root dynamics in a Virginia marsh. *Marine Ecology Progress Series* 102:69-178.

BLUM, L. K. AND R. R. CHRISTIAN. 2005. Belowground production and decomposition along a tidal gradient in a Virginia salt marsh. p. 47-74. *In* The Ecomorphology of Tidal Marshes. S. Fagherazzi, M. Marani, and L. K. Blum (eds.). American Geophysical Union, Washington, D.C.

CHAPIN, F. S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* 11:233-260.

CLOERN, J. E. 2001. Review. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210:223-253.

CONNER, R. AND G. L. CHMURA. 2000. Dynamics of above- and belowground organic matter in a high latitude macrotidal saltmarsh. *Marine Ecology Progress Series* 204:101-110.

DAME, R. F. AND P. D. KENNY. 1986. Variabiliity of *Spartina alterniflora* primary production in the euhaline North Inlet estuary. *Marine Ecology Progress Series* 32:71-89.

GILL, R. A. AND R. B. JACKSON. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147:13-31.

GOSSELINK, J. G., R. HATTON, AND C. S. HOPKINSON. 1984. Relationship of organic carbon and mineral content to bulk density in Louisiana marsh soils. *Soil Science* 137:177-180.

HOWARTH, R. W. AND R. MARINO. 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: Evolving views over three decades. *Limnology and Oceanography* 51:364-376.

HOWES, B. L., R. W. HOWARTH, J. M. TEAL, AND I. VALIELA. 1981. Oxidation-reduction potentials in a salt marsh: Spatial patterns and interactions with primary production. *Limnology and Oceanography* 26:350-360.

HOWES, B. L., J. W. H. DACEY, AND J. M. TEAL. 1985. Annual carbon mineralization and belowground production of *Spartina alterniflora* in a New England salt marsh. *Ecology* 66:595-596.

HUANG, X. AND J. T. MORRIS. 2005. Distribution of phosphatase activity in marsh sediments along an estuarine salinity gradient. *Marine Ecology Progress Series* 292:75-83.

KASWADJI, R., J. G. GOSSELINK, AND R. E. TURNER. 1990. Estimation of primary production using five different methods in a *Spartina alterniflora* salt marsh. *Wetlands Ecology and Management* 1:57-64.

KING, G. M., M. J. KLUG, R. G. WIEGERT, AND A. G. CHALMERS 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* productivity in a Georgia salt marsh. *Science* 218:61-63.

LANA, P. DA CUNHA, C. GUISS, AND S. T. DISARÓ. 1991. Seasonal variation of biomass and production dynamics for above- and belowground components of a *Spartina alterniflora* marsh in the euhaline sector of Paranaguá (SE Brazil). *Estuarine, Coastal and Shelf Science* 32:231-241.

MENDELSSOHN, I. A. 1979. The influences of nitrogen level, form, and application method on the growth response of *Spartina alterniflora* in North Carolina. *Estuaries* 2:106-112.

MENDELSSOHN, I. A., K. L. MCKEE, AND W. H. PATRICK, Jr. 1981. Oxygen deficiency in *Spartina alterniflora* roots: Metabolic adaptation to anoxia. *Science* 214:439-441.

MEULEMAN, A. F. M., J. P. BEEKMAN, AND J. T. A. VERHOEVEN. 2002. Nutrient retention and nutrient-use efficiency in *Phragmites australis* stands after wastewater application. *Wetlands* 22:712-721.

MISSISSIPPI RIVER/GULF OF MEXICO WATERSHED NUTRIENT TASK FORCE. 2001. Action Plan for Reducing, Mitigating, and Controlling Hypoxia in the Northern Gulf of Mexico. Office of Wetlands, Oceans, and Watersheds, U.S. Environmental Protection Agency, Washington, D.C.

MORRIS, J. T. 1991. Effects of nitrogen loading on wetland ecosystems with particular reference to atmospheric deposition. *Annual Review of Ecology and Systematics* 22:257-279.

MORRIS, J. M. AND P. BRADLEY. 1999. Effects of nutrient loading on the carbon balance of coastal wetland environments. *Limnology and Oceanography* 44:699-702.

NATIONAL RESEARCH COUNCIL [NRC Committee on the Causes and Management of Coastal Eutrophication; Ocean Studies Board and Water Science and Technology Board] 2000. Clean Coastal Waters. Understanding and Reducing the Effects of Nutrient Pollution. National Academy Press, Washington, D. C. 393 pp.

ORNES, W. H. AND D. I. KAPLAN. 1989. Macronutrient status of tall and short forms of *Spartina alterniflora* in a South Carolina salt marsh. *Marine Ecology Progress Series* 55:63-72.

PALUDAN, C. AND J. T. MORRIS. 1999. Distribution and speciation of phosphorus along a salinity gradient in intertidal marsh sediments. *Biogeochemistry* 45:197–221.

RABALAIS, N. N. AND R. E. TURNER (eds.). 2001. Coastal Hypoxia: Consequences for Living Resources and Ecosystems. Coastal and Estuarine Studies Series Vol. 58, American Geophysical Union. Washington, D. C. 463 pp.

RABALAIS, N. N. 2002. Nitrogen in aquatic ecosystems. *Ambio* 31:102-112.

ROOTH, J. E. AND J. C. STEVENSON. 2000. Sediment deposition patterns in *Phragmites australis* communities: Implications for coastal areas threatened by rising sea-level. *Wetlands Ecology and Management* 8:173–18.

SCHUBENHAUER, J. P. AND C. S. HOPKINSON. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnology and Oceanography* 29:1052-1063.

SUNDARESHWAR, P. V., J. T. MORRIS, E. K. KOEPFLER, AND B. FORMWALT. 2003. Phosphorus limitation of coastal ecosystem processes. *Science* 299:563-565.

TILMAN, D. AND D. WEDIN. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72:685-700.

TURNER, R. E. AND N.N. RABALAIS.1999. Suspended particulate and dissolved nutrient loadings to Gulf of Mexico estuaries. p. 89-107. *In* T. S. Bianchi, J. R. Pennock and R. W. Twilley (eds). Biogeochemistry of Gulf of Mexico Estuaries. J. Wiley & Sons, Inc. New York.

TURNER, R. E. AND N.N. RABALAIS. 2003. Linking landscape and water quality in the Mississippi River Basin for 200 years. *BioScience* 53:563-572.

TURNER, R. E., N. N. RABALAIS, AND D. JUSTIC. 2006. Predicting summer hypoxia in the Northern Gulf of Mexico, Riverine N: P and Si loading. *Marine Pollution Bulletin* 52:139-148.

TURNER, R. E., E. M. SWENSON, AND C. S. MILAN 2001. Organic and inorganic contributions to vertical accretion in salt marsh sediments. p. 583-595. *In* M. Weinstein and K. Kreeger (eds.). Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishing, Dordrecht, Netherlands. 864 pp.

TURNER, R. E., E. M. SWENSON, C. MILAN, J. M. LEE, AND T. A. OSWALD. 2004. Belowground biomass in healthy and impaired salt marshes. *Ecological Research* 19:29-35.

VALIELA, I., J. M. TEAL, AND N. Y. PERSSON. 1976. Production dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. *Limnology and Oceanography* 21:245-252.

VALIELA, I. AND M. L. COLE. 2002. Comparative evidence that salt marshes and mangroves may protect seagrass meadows from land-derived nitrogen loads. *Ecosystems* 5:92-102.

VISSER, Y. M. AND C. E. SASSER. 2006. The effect of multiple stressors on salt marsh end-of-season biomass. *Estuaries and Coasts* 29:331-342.

WIGAND, C., R. A. MCKINNEY, M. A. CHARPENTIER, M. M. CHINTALA, AND G. B. THURSBY. 1993. Relationships of nitrogen loadings, residential development, and physical characteristics with plant structure in New England salt marshes. *Estuaries* 26:1494-1504.

# CHAPTER 6

# SUMMARY

The objectives of this study were to: 1) document the seasonal variability of the above- and belowground biomass of *Spartina alterniflora* in Louisiana salt marshes, 2) measure how the belowground biomass accumulation changed with nutrient additions, 3) test the usefulness and variability of three functional indicators of nutrient resorption: nutrient use efficiency, nutrient resorption efficiency, and nutrient resorption proficiency, and, 4) compare East coast and Gulf of Mexico salt marshes to compare the morphological responses to nutrient additions.

Chapter 1 is a general introduction to the salt marsh macrophyte *S. alterniflora*. *S. alterniflora* is a salt marsh macrophyte found from Canada to the Gulf of Mexico and which often provides the dominant plant cover. Although, *S. alterniflora* is well known for its high aboveground primary productivity, fifty to ninety percent of the annual production occurs belowground. The root and rhizome biomass contributes to the accumulation of organic matter thus maintaining the marsh's vertical position as sea level rises and the marsh soil compacts. The monthly variation of the below- and aboveground biomass of *S. alterniflora* was documented for a south Louisiana salt marsh in Chapter 2. The results indicated that the annual production rate above- and belowground was 1821 and 7887 g $m^{-2}$, respectively (Smalley method), which are highs along the latitudinal distributions of the plant's range. The belowground biomass was dominated by rhizomes, which declined precipitously in spring, and then rose to a seasonal high in the month before the late summer inflorescence. The average biomass of roots in a 30 cm soil profile was in the upper 10 cm, and in the 10 to 20 cm profile for rhizomes. The average root + rhizome : shoot ratio (R&R : S) was 2.6 : 1, which is lower than the R&R : S ratios of 4 to 5 : 1 reported for *Spartina sp.* marshes in the northeastern US. The maximum March biomass above- and belowground was four to five times that of the minimum biomass over the three sampling years. The average nitrogen : phosphorous molar ratios of 16: 1

aboveground and 37 : 1 belowground indicate N limitation of production aboveground and P limitation belowground.

The responses of *S. alterniflora* above- and belowground biomass to various combinations of N, P, and Fe were documented in a one seven month field experiment in a Louisiana salt marsh described in Chapter 3. Various combinations of N additions resulted in 18% to 138% more live aboveground biomass compared to the control plots, higher stem densities, and longer average stem lengths, but had no effect on the amount of live belowground biomass. The average root + rhizome : shoot (R& R : shoot) ratio was 0.9:1 for all treatments with added N. There was no change in the aboveground biomass when P was added, but there was a 40 to 60% decrease in the live belowground biomass, which resulted in an average R & R : shoot ratio of 0.5. The end-of-the-growing-season average N : P molar ratios in the above- and belowground tissues was 19.5 and 37, respectively, supporting the hypothesis that the accumulation of biomass aboveground was limited by N, and belowground by P. The addition of various combinations of multiple nutrients had a significant affect on the belowground biomass also indicating that the addition of P suppressed root foraging activity. I conclude that the aboveground biomass was limited by N, but not P, and that the belowground biomass was limited by P, but not N.

Four functional indicators of nutrient availability were examined in Chapter 4. These indicators were used to test the usefulness and variability: nutrient resorption efficiency, nutrient resorption proficiency, and nutrient use efficiency. The change in the three resorption indices with N additions, and the resorption values of P, and the other changes or lack of changes all indicate that accumulation of belowground biomass was limited by P. It appears that adding P stimulates greater resorption rates aboveground and lowers resorption rates belowground. Nitrogen additions did not change the resorption rates of N or P.

These functional indicators are shown to be useful tools in establishing and understanding nutrient availability and the role of plants as nutrients move through and within salt marshes. These indices do not always provide the same response, however, and so it may be necessary to explore new methods and to develop additional data to accurately evaluate nutrient resorption in wetland environments.

I conducted field experiments on a combination of geographically diverse and regionally-specific sampling of above- and belowground plant biomass in East coast and Gulf of Mexico salt marshes to understand if a similar morphological responses occurred in the dominant salt marsh plant, *S. alterniflora*. The results, described in Chapter 5, indicate that coastal eutrophication, which is widespread and continuing, will lead to lower root and rhizome biomass, belowground production, and organic accumulation. Higher soil respiration and a lower Eh are anticipated additional soil property changes. Phosphorus, more than nitrogen, seems to reduce root and rhizome biomass accumulation. The cumulative effects of increased nutrient loadings to salt marshes may be to decrease soil elevation and accelerate the conversion of emergent plant habitat to open water, particularly at the lower elevation range of the plant. The implications to management practices intended to conserve coastal marshes include: 1) reducing nutrient loading to coastal zones, and not diverting nutrients to coastal marshes, 2) solving water quality problems with a multiple nutrient approach, and 3) choosing monitoring metrics that are based not only on aboveground production, but also on belowground production of coastal marshes.

In summary, my results indicate that Louisiana salt marshes have the highest belowground biomass productivity within the latitudinal gradient over which it is found. There are seasonal patterns of translocation of resources in early spring before the onset of the live aboveground biomass growth, and in the late summer and fall. In addition, the N : P ratios

indicate that the aboveground accumulation of biomass was limited by N, and that the belowground accumulation of biomass was limited by P. When *S. alterniflora* is fertilized there is an increase in aboveground biomass with a corresponding decrease of belowground biomass. The observed changes in the three functional indicators are consistent with the above conclusion about aboveground N limitation and belowground P limitation. Eutrophication is detrimental to the long term sustainability of Louisiana's salt marshes, because it reduces the root and rhizome biomass that stabilizes marsh sediments and adds to organic matter accumulation.

# VITA

Faith Armand Darby was born in Marrero, Louisiana, Jefferson Parish, March 18, 1952, to Royal Joseph Armand and Gloria Weber Armand. Faith became an "on job trainee" in respiratory therapy in 1974. She attended Jefferson Parish Vocational Technical College in 1980, obtained a certificate, and became a supervisor at West Jefferson Medical Center. Faith was an adjunct faculty member at Nicholls State University and a clinical instructor at Jefferson Parish Vocational Technical College. She attended Our Lady of Holy Cross College in 1993, received an associate degree in allied health science, and became registered respiratory therapist. Faith attended the Pre-Doctoral Scholars Institute at Louisiana State University in the summer of 2000, She received a bachelor of science degree in biology from Our Lady of Holy Cross College in fall 2000 graduating *Suma Cum Laude*. After graduation Faith received the Board of Regents fellowship, to pursue doctoral studies at Louisiana State University in the fall of 2002.