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Impacts of vertebrate herbivores and Hurricane Georges on densities of belowground plant material on shallow mudflats in the active Mississippi River Delta

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IMPACTS OF VERTEBRATE HERBIVORES AND HURRICANE GEORGES ON DENSITIES OF BELOWGROUND PLANT MATERIAL ON SHALLOW MUDFLATS IN THE ACTIVE MISSISSIPPI RIVER DELTA

A Thesis

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 Master of Science

in

The School of Renewable Natural Resources

by
Scotland Talley
B.S.F.R., University of Georgia, 1996
December 2002
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For all the helpful discussions, assistance in the field and lab, and most of all friendship, I am grateful to the many folks I have come to know during my tenure at LSU. Although there are too many to name, I am especially indebted to fellow students M. Anteau, F. Bolduc, G. Holm, J. Jones, R. Olson, J. Pahl, B. Perez, B. Peterson, K. Richkus, W. Robinson, L. Stanton, N. Walters, and C. Walther. Dr. David White of Loyola University graciously provided reprints and data from his work in the Mississippi River Delta, as well as informative and helpful discussion. I thank Dr. Bill Hohman for providing me the opportunity to conduct this study. The United States Fish and Wildlife Service provided funding and logistic support for this project. James Harris, Mike Guidry, Chris Bly, and Jim Graham of the USFWS made this project possible with their support and hard work; I could not be more appreciative of their assistance and patience. I thank Graduate Coordinator Dr. Allen Rutherford for his friendship and all his help negotiating the bureaucratic intricacies of graduate education. Dr. Charles Sasser and Dr. Robert Downer served on my graduate committee and improved my thesis with their helpful commentary, for which I am grateful. I am very thankful that Dr. Robert Chabreck agreed to serve as major professor for one final graduate student. His encouragement and support were a key to the completion this project. Finally, the love and support of my family, made it possible for me to pursue this project.
# TABLE OF CONTENTS

Acknowledgements...........................................................................................................ii

Abstract.............................................................................................................................iv

Chapter 1. Introduction.......................................................................................................1

Chapter 2. Belowground Production and Vertebrate Herbivore Use of
*Schoenoplectus* and *Sagittaria* Communities...............................................................6
  Methods............................................................................................................................8
  Statistical Analysis..........................................................................................................9
  Results.............................................................................................................................10
    Analysis of 1998-1999 Season..................................................................................10
    Analysis of 1999-2000 Season..................................................................................13
    Analysis of 1998-2000 Seasons................................................................................17
  Discussion......................................................................................................................17

Chapter 3. Belowground Production of *Schoenoplectus* and *Sagittaria*
Communities Following Disturbance by Hurricane Georges..............................................26
  Methods..........................................................................................................................29
  Statistical Analysis........................................................................................................31
  Results...........................................................................................................................31
    Belowground Biomass 1998-1999 Season.................................................................31
    Aboveground Biomass Summer 1999.......................................................................33
    Belowground Biomass Fall 1999...............................................................................33
  Discussion......................................................................................................................37

Chapter 4. Summary..........................................................................................................44

Literature Cited...................................................................................................................47

Vita.....................................................................................................................................51
ABSTRACT

Delta National Wildlife Refuge (DNWR) is located in the active Mississippi River Delta (MRD). Resource managers at DNWR are implementing a marsh creation program that consists of dredging crevasses (openings) in the natural or man-made levees of major distributaries to divert sediment rich waters in to open bays. The mudflats thus created are colonized by stands of delta duck-potato (*Sagittaria platyphylla*) and delta three-square (*Schoenoplectus deltarum*). These plant communities stabilize the mudflats and provide high quality habitat for wintering waterfowl and nutria. Two challenges for the maintenance of these plant communities is disturbance from tropical storms and intense winter grazing. Objectives for my study were to measure initial (fall) density of belowground biomass in tropical storm impact vs. non-impact years and quantify herbivore use of belowground biomass.

My study was conducted in 1998-2000 following disturbance by Hurricane Georges in September 1998. Exclosures were used to prevent all grazing or limit grazing to nutria only in two treatments. The third treatment was unrestricted grazing. Twelve replicates were distributed over four crevasse/mudflat complexes. Soil cores were collected in November, January, and March to assess production and use of belowground biomass. A mixed model (PROC MIXED, SAS 1996) was used to analyze treatment effects.

Production in November 1998 was less than in November 1999 in both communities. In March of 1999 and 2000 belowground biomass in no grazing treatments was different from open grazing and nutria only grazing treatments, but the open grazing and nutria only grazing treatments did not differ.
Disturbance from Hurricane Georges did reduce belowground production in 1998 and winter grazing further depleted belowground biomass, but belowground production in 1999 was greater than 1998. The productivity of these plant communities were capable of sustaining heavy reduction in belowground biomass, yet return to high levels of productivity in the following year.
CHAPTER 1. INTRODUCTION

The active Mississippi River Delta (MRD), approximately 140,000 ha (Chabreck and Palmisano 1973) in size, was formed in the past 700 years by the deposition of sediments carried by the Mississippi River (Kolb and Van Lopik 1966). The MRD is comprised of a complex of sub-deltas that originate from crevasses or openings in the natural levees of the main distributary channels. Where these crevasses occur, sediment laden river water is diverted into an open bay where the water velocity is reduced and sediments accumulate. As these sediments accumulate, a mouth bar forms and bifurcates the channel. This process builds subaqueous mudflats and subaerial splays separated by distributary channels that in turn build mouth-bars and create new mudflats and splays (Welder 1959).

The mudflat/splay complexes are colonized by emergent plants that stabilize the sediments and create new marsh. As these marshes build, they require rapid accumulation of sediments to offset rapid natural land subsidence rates and eustatic sea level rise (Boesch and Levin 1983, Turner 1987). Relative sea level rise, a combination of land subsidence and eustatic sea level rise, is currently estimated to be 1.2 cm/yr (Day and Templet 1989).

Subdelta systems generally have a period of active development for approximately 100 years, after which loss of advantageous hydrologic gradient reduces sediment inputs (Coleman et al. 1969). In much of the MRD, anthropogenic alteration of hydrologic cycles has resulted from canal and levee construction disrupting sediment supplies and contributing to marsh loss (Turner 1987). Other causes of marsh loss include damage from catastrophic storms (Chabreck and Palmisano 1973) and subsurface
fluid withdrawals (Boesch and Levin 1983). As a result, large areas of marsh have subsided due to reduced sediment deposition creating large open water bays (Turner 1997). Since the mid-1950s, about 51% of marshes in the active MRD have been converted to large open water ponds (Boesch and Levin 1983). The MRD is composed largely of freshwater marshes with a narrow band of brackish marshes at the interface with the Gulf of Mexico. The freshwater marshes are composed of large stands of common reed (*Phragmites australis*) intermixed with mudflats dominated by delta duck-potato (*Sagittaria platyphylla*) and delta three-square (*Schoenoplectus deltarum*). Higher levees and spoils banks are dominated by black willow (*Salix nigra*) and rattlebox (*Sesbania drummondii*). Nomenclature of plant species follows the National PLANTS Database (USDA, NRCS 1999).

Delta National Wildlife Refuge (DNWR) is located on the MRD and encompasses 19,749 ha that include subdelta marshes formed at an 1862 crevasse known as Cubits Gap. Cubits Gap gives origin to four main distributary channels: Main Pass, Octave Pass, Brant Pass, and Raphael Pass. Like all marshes of the MRD, the Cubits Gap sub-delta is experiencing rapid deterioration and loss of its constituent marshes. In 1978 high waters created several natural crevasses and diverted sediments into open bays. New marshlands grew rapidly at these crevasses and in 1983, the U. S. Fish and Wildlife Service (USFWS) began constructing artificial crevasses to mimic the marsh building processes observed at the natural crevasses. The mudflat/splay complexes averaged 4.7 ha/year/crevasse in accreted marshland (Boyer et al. 1997) and were vegetated primarily by delta duck-potato and delta three-square. An extensive discussion of the crevasse
construction project can be found in Boyer et al. (1997), and White (1993) provides a thorough discussion of plant community development.

While the primary objective of the USFWS project was to promote marsh building, the splays also provide abundant high quality wildlife habitat, particularly for wintering waterfowl (Boyer et al., 1997). These splays support high densities of delta duck-potato and delta three-square, as well as Walter’s millet (*Echinochloa walteri*), disk waterhyssop (*Bacopa rotundifolia*), various sedges (*Cyperus* spp.), and panic grasses (*Panicum* spp.), all preferred waterfowl foods (McAtee 1939, Martin et al. 1951, Chabreck et al. 1983, Alisauskas et al. 1988, Bielefeld and Afton 1992).

The value of these marshes as wintering waterfowl habitat is of special interest because of their location. The Gulf Coastal Plain is one of nine critical waterfowl regions identified in the North American Waterfowl Management Plan (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1984). NAWMP goals for the Gulf Coast Joint Venture call for the protection, restoration, and enhancement of 710,000 ha of waterfowl habitat: however, as of 1999, only 423,600 ha of this goal had been reached (GCJV Progress Report 1999). The Mississippi River Delta is an important component of the GCJV area that has supported thousands of wintering waterfowl in the past. Access to high quality winter habitat is an important factor for survival (Reinecke et al. 1987) and increasing reproductive success in the following spring (Ankney and Macinnes 1978, Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Raveling and Heitmeyer 1989, Krapu and Reinecke 1990).

Waterfowl and nutria (*Myocastor coypus*) were found to reduce the density of delta duck-potato tubers on these mudflats in a previous study (Chabreck et al. 1983), but
the study did not include delta three-square rhizomes. Bielefeld (1993) investigated differences in densities of tubers and rhizomes between mudflats and open ponds on MRD, and recorded differences in canvasback activity budgets between these habitats. Bielefeld (1993) reported a positive correlation between food densities and foraging time on mudflats.

In addition to herbivory, plant communities on the mudflats are affected by tropical storms. Hurricane Camille passed within 80 km of the MRD in August of 1969, and a storm surge of 3 m above mean sea level (MSL) and winds in excess of 100 kts were reported (Hsu 1970). Vegetative cover prior to the storm was estimated at 81.1% of the marsh, 3 weeks after the storm vegetative cover was reduced to 56.6%, yet one year later vegetative cover had increased to 75.2% (Chabreck and Palmisano 1973). Changes in the species composition and relative abundance of marsh vegetation were noted, including the loss of some species and the introduction of others. Wright et al. (1970) found that the root mat was intact in much of the marsh and provided for the restoration of species capable of regenerating from rhizomes and tubers. Most of the damage was attributed to the physical effects of wind and water, because salinities did not remain high after the storm-waters receded.

Hurricane Opal occurred October 4, 1995 and brought a storm surge of about 2.4 m above MSL and sustained winds of 64 kts. Although not as powerful as Camille, Hurricane Opal nevertheless removed most aboveground vegetation from the mudflats. Waterfowl counts during the winter following Hurricane Opal were reduced from previous years and lead refuge managers to hypothesize that the storm might have significantly reduced belowground food resources.
On September 27, 1998 Hurricane Georges passed on the east side of the MRD and brought a 2.7 m storm surge and sustained winds in excess of 50 kts. This storm also removed much of the aboveground vegetation and provided an opportunity to study the impact of a tropical storm event on plant-herbivore interaction on these MRD mudflats.

A study was already planned for the winter of 1998-99 with the following objectives: to quantify belowground production of tubers and rhizomes and there use by vertebrate herbivores. After Hurricane Georges, the objectives were modified to include tropical storm effects on belowground production and herbivore effects on the recovery of vegetation. Thus specific objectives for the study were updated: 1) Measure belowground production of tubers and rhizomes in tropical storm impact vs. non-impact years, 2) Quantify vertebrate herbivore use of belowground material, 3) Investigate tropical storm impacts on plant-herbivore interaction and plant productivity.
CHAPTER 2. BELOWGROUND PRODUCTION AND VERTEBRATE HERBIVORE USE OF *SCHOENOPECTUS* AND *SAGITTARIA* COMMUNITIES

This study was conducted on Delta National Wildlife Refuge (DNWR) in the active Mississippi River Delta (MRD) to assess the production and use of belowground plant biomass that is an important food resource for wintering waterfowl. DNWR contains 19,749 ha and encompasses a subdelta formed by an 1862 crevasse or levee opening known as Cubits Gap. The Cubits Gap sub-delta is experiencing rapid deterioration and loss of its constituent marshes. In 1978 high waters created several natural crevasses and diverted sediments into open bays on DNWR. At each crevasse, a “splay” developed which was a complex of mudflats and inter-distributary channels. New marshlands grew rapidly at these crevasses and in 1983, the USFWS began constructing artificial crevasses to mimic the marsh building processes observed at the natural crevasses. The mudflats associated with these crevasses averaged 4.7 ha/year/crevasse in accretion (Boyer et al. 1997) and were vegetated primarily by delta duck-potato (*Sagittaria platyphylla*) and delta three-square (*Schoenoplectus deltarum*). An extensive discussion of the crevasse construction project can be found in Boyer et al. (1997), and White (1993) provides a thorough discussion of plant community development.

While the primary objective of crevasse construction was to promote marsh building, a secondary benefit that the splays created was abundant high quality wildlife habitat, particularly for wintering waterfowl (Boyer et al., 1997). Splays created by crevasse construction supported high densities of delta duck-potato and delta three-square, as well as Walter’s millet (*Echinochloa walteri*), disk waterhyssop (*Bacopa rotundifolia*), various sedges (*Cyperus* spp.), and panic grasses (*Panicum* spp.) all

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Waterfowl and nutria (Myocastor coypus) reduced the density of delta duck-potato tubers on mudflats in a previous study (Chabreck et al. 1983), but the study did not include delta three-square rhizomes. Bielefeld (1993) investigated differences in densities of tubers and rhizomes between mudflats and open ponds, and recorded differences in canvasback activity budgets between these habitats. Bielefeld (1993) reported a correlation between higher food densities and greater foraging time on mudflats. On the Atchafalaya Delta, Evers et al. (1998) found that herbivory reduced belowground biomass of Sagittaria dominated communities, and contributed to
conversion of *Sagittaria* communities to bare mudflats. The objective of my study was to estimate belowground production of *Sagittaria* tubers and *Schoenoplectus* rhizomes and to estimate their utilization by wintering waterfowl and nutria.

**METHODS**

My experiment compared three grazing treatments in two plant communities. *Schoenoplectus deltarum* was the dominant species of one community, and *Sagittaria platyphylla* was the dominant species in the other community. The two communities were very distinct and nearly complete monocultures. *Schoenoplectus deltarum* produces belowground rhizomes that were heavily grazed by geese and nutria. *Sagittaria platyphylla* produces tubers that were grazed by geese, ducks, and nutria.

Four different crevasses were randomly selected and exclosures were constructed in each community on three mudflats within each crevasse/splay complex for twelve replicates of three grazing treatments. Grazing treatments applied to each community were non-grazed plots (NG) with exclosures that prevented grazing by any vertebrate herbivores, nutria only plots (NO) with exclosures that discouraged waterfowl while permitting grazing by nutria, and openly grazed plots (OG). This methodology was adapted from previous work on the Mississippi River Delta by Chabreck et al. (1983) and on the Atchafalaya Delta by Evers et al. (1998). The experimental design utilized contained 4 splayes (blocks), 3 mudflats within each splay (whole plots), 2 communities within each mudflat (split plots), and 3 grazing treatments within each community. The no grazing (NG) exclosures were constructed from a 2m X 2m PVC pipe frame with 40mm mesh vinyl coated wire attached. This mesh panel was then staked down horizontally on the surface to prevent access from geese or nutria. The waterfowl (NO)
Exclosures were constructed from four 1m X 2m panels with vinyl coated wire mesh, but the panels were left open at the bottom 20cm. These four panels were then attached at the corners and staked out. Nutria were able to access the interior, but waterfowl were unable to enter the exclosures. A 2m² plot was marked by a PVC pole for the open grazing (OG) plot.

Exclosures were constructed in first week of November 1998 and initial samples collected. Two samples were collected from each plot and consisted of soil cores 10.7 cm in diameter and 40 cm in depth. Samples were collected again in mid-January 1999 and the first week of March 1999. The following fall and winter sampling was conducted in mid-November 1999, mid-January 2000, and the last week of March 2000. Samples were washed through a 0.8 cm sieve, and tubers or rhizomes were frozen and returned to the lab for analysis. Samples were dried to constant mass at 60° C and weighed to the nearest 0.001g on a Metzler H80 balance.

**Statistical Analysis**

The design of the experiment was a split plot randomized block. A mixed model analysis of variance was used to analyze treatment effects on biomass (PROC MIXED, SAS Institute 1996). In this model the splays (blocks) and splay*mudflat (block*whole plot) interaction were random effects. Fixed effects were mudflat and treatment.

Treatment effects within sampling periods were tested using the split-plot model for each sampling period. Tukey’s LSD test was used to determine individual treatment differences when an overall treatment effect was detected. Model based means ± SE were used to describe biomass. Each year was analyzed independently and both years combined were analyzed.
RESULTS

Analysis of 1998-1999 Season

Analysis of *Sagittaria* tuber biomass for the 1998-1999 season indicated an overall treatment effect (Table 2.1). A Tukey’s LSD test of treatments revealed that the biomass of non-grazed (NG) plots was greater than the biomass of open grazed (OG) plots \( t = -2.65, \text{d.f.} = 90, P = 0.0258 \). Nutria only (NO) plots did not differ from NG plots \( t = 2.30, \text{d.f.} = 90, P = 0.0608 \) or from OG plots \( t = -0.35, \text{d.f.} = 90, P = 0.9364 \).

Analysis by sampling period indicated no difference in initial tuber biomass in November sampling (Figure 2.1). Mean tuber biomass \( \text{(g/m}^2 \text{)} \) for all treatments was 55.47 ± 3.09 (mean ± SE) in November 1998.

In January, no treatment difference was detected \( F = 2.06, \text{d.f.} = 2, 18, P = 0.1569 \), but biomass had been reduced 28% in NO plots and 23% in OG plots (Figure 2.1).

In March, a treatment effect was detected \( F = 4.25, \text{d.f.} = 2, 18, P = 0.0309 \). Tukey’s LSD test for tuber biomass in March indicated that reduction was greater in the OG plots than that in the NG plots \( t = -2.82, \text{d.f.} = 18, P = 0.0290 \). In March, tuber biomass in NG plots \( 56.28 \pm 4.69 \) was similar to November at 61.21 ± 5.73 while biomass was not reduced from January in NO plots. Biomass in OG plots was reduced 22% from January.

Analysis of *Schoenoplectus* rhizome biomass for the 1998-1999 winter season detected an overall treatment effect (Table 2.1). A Tukey’s LSD test of treatments revealed that the biomass of NG plots was greater than the biomass of OG plots \( t = 3.27, \text{d.f.} = 90, P = 0.0043 \). NO plots did not differ from NG plots \( t = 1.20, \text{d.f.} = 90, P = 0.4556 \) or from OG plots \( t = -2.07, \text{d.f.} = 90, P = 0.1016 \).
Table 2.1. Split-plot mixed model analysis for biomass of *Sagittaria* tubers and Schoenoplectus rhizomes for the 1998-99 season including a Tukey’s LSD test for treatments.

**Sagittaria**

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*Tukey’s LSD Test for treatment*

**Schoenoplectus**

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<th>Grouping*</th>
<th>LS Mean</th>
<th>Treatment</th>
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<td>0.6757</td>
<td>Open Grazing</td>
</tr>
</tbody>
</table>

*Tukey’s LSD Test for treatment*

*Treatment means with the same letters do not differ at $\alpha = 0.05$ level*
Figure 2.1. Mean belowground biomass for the *Sagittaria* community subjected to no grazing (NG), nutria only grazing (NO), and open grazing (OG) during 1998-1999.

Figure 2.2. Mean belowground biomass for the *Sagittaria* community subjected to no grazing (NG), nutria only grazing (NO), and open grazing (OG) during 1999-2000.
Analysis of treatment means by sampling period did not differ in November, but the range was much greater than in *Sagittaria* plots (Figure 2.3). Mean November biomass was highest in NO plots at 127.81 ± 4.12 and lowest in NG plot at 94.79 ± 4.12. Mean biomass (g/m²) for all treatments was 112.30 ± 3.01 in November 1998.

In January, a treatment difference was detected (F = 4.15, d.f. = 2, 18, \( P = 0.0329 \)). A Tukey’s LSD test of treatments revealed that the biomass of NG plots was greater than the biomass of OG plots (t = -2.84, d.f. = 18, \( P = 0.0278 \)). January rhizome biomass in NG plots was similar to fall at 84.29 ± 4.98 while biomass was reduced 37% in NO plots and 55% in OG plots (Figure 2.2).

In March, a treatment effect was detected (F = 10.00, d.f. = 2, 18, \( P = 0.0012 \)). Tukey’s LSD test revealed that the biomass of NG plots was greater than the biomass of OG plots (t = -4.42, d.f. = 18, \( P = 0.0009 \)) and NO plots (t = 2.81, d.f. = 18, \( P = 0.0294 \)). Spring rhizome biomass in NG plots was similar to fall at 87.97 ± 4.61 while biomass was reduced 54% in NO plots and 66% in OG plots.

**Analysis of 1999-2000 Season**

Analysis of *Sagittaria* tuber biomass for the 1999-2000 winter season detected an overall treatment effect (Table 2.2). A Tukey’s LSD test of treatments revealed that NG plots differed from OG plots (t = -2.72, d.f. = 90, \( P = 0.0213 \)) and NO plots (t = 3.00, d.f. = 90, \( P = 0.0097 \)).

Biomass of *Sagittaria* tubers in November did not show a treatment effect (F = 0.57, d.f. = 2, 18, \( P = 0.5732 \)). The range of initial tuber biomass was higher November of 1999 than 1998. Biomass in NG plots was 131.04 ± 6.45, in NO plots 125.38 ± 6.45,
and in OG plots 159.64 ± 6.45. Average biomass for all treatments in November was 137.91 ± 4.91.

In January, a treatment effect was detected ($F = 4.01$, d.f. = 2, 18, $P = 0.0364$). Tukey’s LSD test indicated that tuber biomass in January was greater in NG than in NO plots ($t = 2.53$, d.f. = 18, $P = 0.0522$). NG and OG plots did not differ, but were very close to the 0.05 level ($t = -2.36$, d.f. = 18, $P = 0.0721$). Biomass in NG plots was similar to November at 137.16 ± 6.23, and was reduced 52% in NO plots and 49% in OG plots (Figure 2.3).

There was little change in March biomass, and differences between NG plots and both OG plots ($t = -3.90$, d.f. = 18, $P = 0.0029$) and NO plots ($t = 3.03$, d.f. = 18, $P = 0.0188$) were detected.

Analysis of *Schoenoplectus* rhizome biomass for the 1999-2000 winter season detected an overall treatment effect (Table 2.2). A Tukey’s LSD test of treatments revealed that NG plots differed from OG plots ($t = -5.95$, d.f. = 90, $P = 0.0001$) and NO plots ($t = 5.28$, d.f. = 90, $P = 0.0001$).

Biomass of *Schoenoplectus* rhizomes in November did show a treatment effect carrying over from the previous year ($F = 4.56$, d.f. = 2, 18, $P = 0.0249$). Biomass in NG plots was greater than that in NO plots ($t = 2.51$, d.f. = 18, $P = 0.0548$) and OG plots ($t = -2.71$, d.f. = 18, $P = 0.0361$). Biomass in NG plots was 317.55 ± 3.99, and 36.6% greater than that of NO plots, and 39.1% greater than that of OG plots (Figure 2.4).

In January, biomass was reduced in all treatments: 13% in NG plots, 29% in NO plots, and 32% in OG plots. The biomass of NG plots was greater than that of NO plots
Table 2.2. Split-plot mixed model analysis for biomass of *Sagittaria* tubers and *Schoenoplectus* rhizomes for the 1999-2000 season including a Tukey’s LSD test for treatments.

### *Sagittaria*

<table>
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<tr>
<th>Source</th>
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<th>DDF</th>
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<th>Pr &gt; F</th>
<th>Grouping*</th>
<th>LS Mean</th>
<th>Treatment</th>
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<td>1.05774</td>
<td>Open Grazing</td>
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*Treatment means with the same letters do not differ at $\alpha = 0.05$ level

### *Schoenoplectus*

<table>
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<tr>
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<th>DDF</th>
<th>Type III F</th>
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<th>Grouping*</th>
<th>LS Mean</th>
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<td>1.46551</td>
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Figure 2.3. Mean belowground biomass for the *Schoenoplectus* community subjected to no grazing (NG), nutria only grazing (NO), and open grazing (OG) during 1998-1999.

Figure 2.4. Mean belowground biomass for the *Schoenoplectus* community subjected to no grazing (NG), nutria only grazing (NO), and open grazing (OG) during 1999-2000.
(t = 2.67, d.f. = 18, P = 0.0392) and OG plots (t = -3.06, d.f. = 18, P = 0.0177).

In March, biomass was once again reduced in all treatments: 37% in NG plots, 49% in NO plots, and 51% in OG plots. The biomass of NG plots was greater than that of NO plots (t = 3.28, d.f. = 18, P = 0.0110) and OG plots (t = -3.74, d.f. = 18, P = 0.0041).

**Analysis of 1998-2000 Seasons**

Analysis of *Sagittaria* tuber biomass for the 1998-2000 seasons indicated an overall treatment effect (Table 2.3) as well as a difference between years (F = 93.56, d.f. = 1, 195, P = 0.0001). A Tukey’s LSD test of treatments indicated that the biomass of NG plots was greater than the biomass of NO plots (t = 3.72, d.f. = 195, P = 0.0007) and OG plots (t = -3.70, d.f. = 195, P = 0.0008).

Analysis of *Schoenoplectus* rhizome biomass for the 1999-2000 winter season indicated an overall treatment effect (Table 2.4) as well as a difference between years (F = 150.57, d.f. = 1, 195, P = 0.0001). A Tukey’s LSD test of treatments indicated that the biomass of NG plots was greater than the biomass of OG plots (t = -6.35, d.f. = 195, P = 0.0001) and NO plots (t = 4.44, d.f. = 195, P = 0.0001).

**DISCUSSION**

Most of the reduction of belowground biomass occurred during late fall between early November sampling and January sampling. After January, there was little biomass reduction in OG plots and no reduction in the NO plots. This corresponds well with aerial survey estimates of wintering waterfowl on the refuge (USFWS, unpublished data). An aerial survey was flown on 12 December 1998, and the number of waterfowl was estimated to be 104,000 ducks and 40,000 geese.
Table 2.3. Split-plot mixed model analysis for biomass of *Sagittaria* tubers for all sampling periods including a Tukey’s LSD test for treatments.

<table>
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*Treatment means with the same letters do not differ at $\alpha = 0.05$ level
Table 2.4. Split-plot mixed model analysis for biomass of *Schoenoplectus* rhizomes for all sampling periods including a Tukey’s LSD test for treatments.

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</tbody>
</table>

*Treatment means with the same letters do not differ at $\alpha = 0.05$ level
On 4 January 1999, another estimate was made and was down to 28,800 ducks and 29,500 geese. These estimates were well below the average for all 1991-2000 aerial survey data, but not as low as the estimates from the 1995-96 season following Hurricane Opal. Peak waterfowl numbers occurred in mid-December to early January and counts diminished in late January to early February for all years that survey data were available. This pattern was particularly noticeable in ducks, which feed more in the *Sagittaria* community, than geese, which feed more in the *Schoenoplectus* community.

Grazing reduced tuber biomass in the OG plots by about one-third during late fall, which may be an indication that 30-40 g/m² is the point at which searching for tubers becomes energetically inefficient for waterfowl. Tuber biomass in the NO plots was reduced by one-fifth, but nutria had other resources available. Nutria populations may have been reduced by the storm surge associated with Hurricane Georges, further reducing grazing pressure.

In November 1999, tuber biomass was consistent with that reported by Bielefeld (1993) in the fall of 1990, and no treatment effect from the previous year was apparent. The effect of Hurricane Georges and the previous winter’s grazing of tubers did not prevent the *Sagittaria* dominated community from recovering well in one growing season. Waterfowl population estimates in aerial surveys also recovered to near the 10-year average. With peak estimates of 167,850 ducks in November dropping off in January to 57,620, the year followed the pattern of peak populations in November and December and a decline in January.

Grazing reduced tuber biomass by one-half during the 1999-2000 in both NO and OG plots, and again much of this reduction occurred between November and January.
sampling periods. When final samples were taken in March the mean tuber biomass in OG plots exceeded the initial biomass of the 1998 season. The fact that tuber biomass was reduced by one-half, yet still exceeded the previous year’s production, indicates that sufficient food resources were still available for ducks, and other factors contributed to the timing of migration.

Previous measurement of rhizome biomass for *Schoenoplectus* dominated communities in the MRD was unavailable for comparison. However, rhizome biomass during the fall 1998 was probably less than would be expected without Hurricane Georges. Palmisano (1967) reported wet (fresh) mass of a closely related species, *Schoenoplectus americanus*, in the Chenier Plain of Louisiana to be 3400 to 5600 g/m². Dry mass was not reported, but Alisauskas et al (1988) reported dry mass of rhizomes to be 21% of wet mass; therefore, the dry mass of the Palmisano (1967) sample would have been 714 to 1176 g/m². In the East Texas Chenier Plain, 1,073.7 g/m² dry mass for *S. americanus* was reported by Singleton (1951). This very high production on the Chenier Plain may not be attainable in the more dynamic deltaic environment, but does give an idea of the potential productivity of *Schoenoplectus* in Gulf Coast marshes. A study in the Fraser River Delta in British Columbia, Canada reported fall rhizome biomass of 500 g/m² in low marsh and 1000 g/m² in high marsh (Karagatzides and Hutchinson 1991), but in the St. Lawrence estuary of Quebec, Canada, Giroux and Bedard (1988) report estimates of 174-234 g/m² using several different core sizes and shapes. These marshes have shorter growing seasons and different physiography, which makes comparison difficult, but it seems likely that MRD marshes would be as productive with the semi-tropical climate and nutrient rich waters of the Mississippi River. Hurricane Georges’
impact on the MRD removed the aboveground portion of plants before the development of rhizomes was complete and created a situation whereby *Schoenoplectus* was resprouting in fall further reducing belowground biomass at the end of the growing season.

The reduction of belowground biomass by grazing occurred throughout the winter. Grazing reduced rhizome biomass by about two-thirds and by March estimates of biomass in OG plots were 30-40 g/m², and in NO plots were 40-50 g/m². Most of the reduction occurred between November sampling and January sampling, but after January, there was still 15% reduction in OG and NO plots. This is consistent with less rapid decline in goose numbers and the fact that geese have fewer alternative resources than ducks. Estimates of goose numbers were below the 10-year average in the 1998-1999 season, but not as much as ducks.

In November 1999, rhizome biomass was much greater than the previous year, but there was a treatment effect. Biomass was tripled in the NG plots, but was less than doubled in the NO and OG plots. The effect of Hurricane Georges and the previous winter’s grazing of rhizomes appeared to retard the full recovery of *Schoenoplectus* communities. Waterfowl estimates in aerial surveys also recovered to near the 10-year average.

In both NO and OG plots rhizome biomass was reduced by one-half, and again much of this reduction occurred between November and January sampling periods. When final samples were taken in March the mean tuber biomass in NO and OG plots was similar to the initial biomass in the 1998 season. As with the *Sagittaria* community,
the amount of *Schoenoplectus* biomass available in March indicates that factors other than the available food resources contribute to the timing of migration.

In both years and in both communities, the model indicated differences between NG plots and both NO and OG plots, but no difference was found between NO and OG plots. The mean biomass for each treatment was consistently greatest in NG plots, followed by NO plots, OG plots had the lowest mean biomass.

While this supports the conclusion that nutria are the primary consumer of belowground plant material, I do not have confidence in the effectiveness of the NO exclosures in preventing waterfowl grazing. Although I never observed waterfowl inside the NO exclosures, on several occasions while collecting samples, I observed evidence (feces or footprints) of waterfowl within the NO exclosures.

Nutria were routinely observed feeding on mudflats, but generally alone or in pairs. Occasionally, an adult female was observed with several young. By contrast, waterfowl were observed feeding in large flocks. The flock size of ducks ranged widely, but was usually greater than 20 birds and rarely more than 100 birds. Geese were commonly observed in much larger flocks, generally several hundred birds and often several thousand birds.

Another indication that waterfowl are the primary consumers of belowground plant material is the fact that most reduction occurred between November and January sampling when waterfowl numbers were greatest. Nutria may also of been attracted to the exclosures due to the cover they provided, thus exaggerating their contribution to the removal of belowground material. Regardless, the impact of nutria in the MRD does not appear to significantly reduce habitat quality for waterfowl.
My findings are somewhat different from what has been reported on the Atchafalaya and Wax Lake Deltas (Evers et al. 1998). They reported that vertebrate herbivores were able to convert previously vegetated mudflats to bare mudflats. Furthermore, they reported that the Atchafalaya Delta wintered only a few snow geese, which are an important grazer in the MRD. There are a number of important differences in the two areas. The genesis of these mudflats is quite different. The Wax Lake and Atchafalaya Deltas are in the early stages of formation, while the MRD is a fully mature delta and the splay restoration projects are within the context of a much larger delta. The authors also point out that the Atchafalaya Delta, where the most destructive grazing occurred, consists of islands separated from the mainland. The Wax Lake portion of their study area was closer to the mainland and did not suffer as much damage. The nutria on the Wax Lake Delta were closer to alternative feeding sites, much like nutria in the MRD, which have access to many more feeding sites.

On the MRD, I observed geese feeding almost exclusively on the larger dense stands of *Schoenoplectus*, while ducks preferred the *Sagittaria* dominated areas. This is consistent with their respective feeding behavior and food habits (Millet 1995, Bielefeld and Afton 1992, Alisauskas et al. 1988, Smith and Odum 1981). According to White (1998), the stands dominated by *Schoenoplectus* are found on splays with more efficient distributary channels, while *Sagittaria* dominates in areas where the channels are breaking down and flow is reduced. In these areas, sediment inputs are less and consolidation and subsidence are progressing faster.

If managers wish to increase food availability for geese, maintaining the depth and velocity of the crevasse and interdistributary channels should favor large stands of
Schoenoplectus. Sagittaria communities on the other hand are best produced by allowing crevasses and interdistributary channels to silt in, thus providing habitat more attractive to ducks.

Although geese feed almost exclusively by grubbing for tubers and rhizomes, duck also feed on seeds, aquatic vegetation, and invertebrates. Research is needed to investigate the availability and use of these resources as well to provide managers with data needed for decision-making. Research on the importance of seedbanks on the annual regeneration of Schoenoplectus and Sagittaria stands is also needed to improve our understanding of how these highly productive and valuable communities function.
CHAPTER 3. BELOWGROUND PRODUCTION OF SCHOENOPLECTUS AND SAGITTARIA COMMUNITIES FOLLOWING DISTURBANCE BY HURRICANE GEORGES

Delta National Wildlife Refuge (DNWR) is 19,749 ha of marsh encompassing a subdelta of the Mississippi River Delta formed at an 1862 crevasse known as Cubits Gap. The MRD consists of a complex of sub-deltas created by the deposition of sediments and building of a mouth-bar that bifurcates the channel. This process builds subaqueous mudflats and subaerial splays separated by distributary channels that in turn build new mouth-bars and create new mudflats and splays (Welder 1959). The mudflat/splay complexes are colonized by emergent plants that stabilize the sediments and create new marsh. These freshwater marshes are composed of large stands of common reed (*Phragmites australis*) intermixed with mudflats dominated by delta duck-potato (*Sagittaria platyphylla*) and delta three-square (*Schoenoplectus deltarum*), and higher levees and spoil banks dominated by black willow (*Salix nigra*) and rattlebox (*Sesbania drummondii*). Nomenclature of plant species follows the National PLANTS Database (USDA, NRCS 1999).

Like all the marshes of the MRD, the Cubits Gap sub-delta was experiencing rapid deterioration and loss of its constituent marshes because of natural factors such as subsidence and eustatic sea level rise (Boesch and Levin 1983, Turner 1987, Day and Templet 1989), as well as anthropogenic factors, such as canal construction and levee building (Turner 1987). In 1978 high waters created several natural crevasses diverting sediments into open bays. New marshlands grew rapidly and in 1983, the USFWS began constructing artificial crevasses to mimic the marsh building processes observed at the natural crevasses. The mudflat/splay complexes average 4.7 ha/year/crevasse in
accretion (Boyer et al. 1997) and are initially dominated by delta duck-potato and delta
three-square. An extensive discussion of the crevasse construction project can be found
in Boyer et al. (1997), and White (1993) provides a thorough discussion of plant
community development.

While the primary objective of crevasse construction was to promote marsh
building, the splays created abundant high quality wildlife habitat, particularly for
wintering waterfowl (Boyer et al., 1997). These splays support high densities of delta
duck-potato and delta three-square, as well as Walter’s millet (*Echinochloa walteri*),
waterhyssop (*Bacopa rotundifolia*), various sedges (*Cyperus* spp.), and panic grasses
(*Panicum* spp.) all preferred waterfowl foods (McAtee 1939, Martin et at. 1951,

The value of these marshes as wintering waterfowl habitat is of special interest
because of their location. The Gulf Coastal Plain is one of nine critical waterfowl regions
identified in the North American Waterfowl Management Plan (U.S. Fish and Wildlife
Service and Canadian Wildlife Service 1984). NAWMP goals for the Gulf Coast Joint
Venture call for the protection, restoration, and enhancement of 710,000 ha of waterfowl
habitat: however, as of 1999, only 423,600 ha of this goal had been reached (U.S. Fish
and Wildlife Service 1999). Access to high-quality winter habitat is an important factor
for survival (Reinecke et al.1987) and increasing reproductive success in the following
spring (Ankney and Macinnes 1978, Heitmeyer and Fredrickson 1981, Kaminski and

Waterfowl and nutria have been found to reduce density of delta duck-potato
tubers of these mudflats in a previous study (Chabreck et al. 1983), but the study did not
include delta three-square rhizomes. Bielefeld (1993) investigated differences in
densities of tubers and rhizomes between mudflats and open ponds, and recorded
differences in canvasback activity budgets between these habitats. Bielefeld reported a
correlation between higher food densities and greater foraging time on mudflats.

In addition to herbivory, plant communities on the mudflats are affected by
tropical storms. Hurricane Camille passed within 80 km of the MRD in August of 1969.
Meteorological reports indicate a storm surge of 3 m above mean sea level (MSL) and
winds in excess of 100 kts (Hsu 1970). Vegetative cover prior to the storm was estimated
at 81.1% of the marsh, 3 weeks after the storm vegetative cover was reduced to 56.6%,
yet one year later vegetative cover had increased to 75.2% (Chabreck and Palmisano,
1973). There were some changes in the species composition and relative abundance of
marsh vegetation, including the loss of some species and the introduction of others.
Wright et al. (1970) found that the root mat was intact in much of the marsh providing for
the restoration of species capable of regenerating from rhizomes and tubers. Most of the
damage was attributed to the physical effects of wind and water, as salinities did not
remain high after the storm waters receded.

Hurricane Opal on October 4, 1995 brought a storm surge of about 2.4 m above
MSL and sustained winds of 64 kts. While not as powerful as Camille, Hurricane Opal
nevertheless removed most aboveground vegetation from the mudflats. Waterfowl
counts during the winter following Hurricane Opal were reduced from previous years
leading refuge managers to hypothesize that the storm might have reduced belowground
food resources significantly.
On September 27, 1998 Hurricane Georges passed the east side of the MRD bringing a 2.7 m storm surge and sustained winds in excess of 50 kts. This storm also removed much of the aboveground vegetation providing an opportunity to study the impact of tropical storm events on plant-herbivore interaction on these MRD mudflats.

After Hurricane Georges, a study of tropical storm effects on belowground production and herbivore effects on the recovery of vegetation was initiated. The specific objectives for the study were to measure initial (fall) density of tubers and rhizomes in impact vs. non-impact years, and investigate tropical storm impacts on plant-herbivore interaction and plant productivity.

**METHODS**

I compared the effects of three grazing treatments on the recovery of marsh vegetation after a major disturbance in two plant communities. *Schoenoplectus deltarum* was the dominant of the *Schoenoplectus* community, and *Sagittaria platyphylla* was the dominant species of the *Sagittaria* community. The belowground production of *S. deltarum* consists of rhizomes that are heavily grazed by geese and nutria. *Sagittaria platyphylla* produces tubers that are grazed by geese, ducks, and nutria.

Four different splays were randomly selected and exclosures were constructed in each community on three mudflats within each splay complex for twelve replicates of three grazing treatments. Grazing treatments were applied to each community: non-grazed plots with exclosures that provided complete protection from vertebrate herbivores, nutria only plots with exclosures that discouraged waterfowl while permitting grazing by nutria, and openly grazed plots.
This methodology was adapted from previous work on the Mississippi River Delta by Chabreck et al. (1983) and on the Atchafalaya Delta by Evers et al. (1998). The experimental design utilized contained 4 splays, 3 mudflats within each splay, 2 communities within each mudflat, and 3 grazing treatments within each community.

The non-grazed exclosures were constructed from a 2m X 2m PVC pipe frame with 40mm mesh vinyl-coated wire attached. This mesh panel was then staked down horizontally on the surface to prevent grazing by geese or nutria. The nutria only plots were constructed from four 1m X 2m panels with vinyl-coated wire mesh, but the panels were left open at the bottom 20cm. These four panels were then attached at the corners and staked out. Nutria were able to access the interior, but waterfowl were unable to enter the exclosures. A 2m² plot was marked by a PVC pole for the open grazing plot.

Exclosures were constructed during the first week of November 1998 and initial samples were collected. Two samples were collected from each plot and consisted of soil cores 10.7 cm in diameter and 40 cm in depth. Samples were collected again in mid-January and the first week of March 1999, and the following fall in mid-November 1999. Samples were then washed through a 0.8 cm sieve, and tubers or rhizomes were frozen and returned to the lab for analysis. Samples were dried to constant mass at 60° C and weighed to the nearest 0.001g on a Metzler H80 balance.

Aboveground biomass was sampled in June, July, and August. A 25cm X 25cm PVC frame was randomly placed in each treatment, and aboveground plant material was harvested by clipping all vegetation to the soil surface. This material was bagged and stored on ice for return to the lab where samples were stored at 10° C. Samples were
dried to constant mass at 60° C and weighed to the nearest 0.01g on an Allied Fischer Scientific Model 8206A balance.

**Statistical Analysis**

The design of the experiment was a split plot randomized. A mixed model analysis of variance was used to analyze treatment effects on biomass (PROC MIXED, SAS Institute 1996). In this model the splays (blocks) and splay*mudflat (block*whole plot) interaction were random effects. Fixed effects were mudflat and treatment. Treatment effects within sampling periods were tested using the same model, but replacing the repeated statement with a by statement. Where an overall treatment effect was detected a Tukey adjusted LSD pairwise comparison test was used to determine differences between the three grazing treatments. Model based least squares means ± SE were used to describe biomass.

**RESULTS**

**Belowground Biomass 1998-1999 Season**

Tuber biomass (g/m²) for all treatments was 55.47 ± 3.09 (mean ± SE) in *Sagittaria* communities in the fall of 1998. This was the total tuber production for the 1998 growing season. In the spring of 1999, a treatment effect was detected (Table 3.1). Tuber biomass in non-grazed (NG) plots was similar to fall at 61.21 ± 5.73, and biomass was reduced in nutria only (NO) plots 29% and in open grazing (OG) plots 40%. Spring tuber biomass differed between NG and OG plots (t = -2.82, d.f. = 18, P = 0.0290). No difference was detected between NG and NO plots (t = 2.04, d.f. = 18, P = 0.1305) or NO and OG plots (t = -0.78, d.f. = 18, P = 0.7214). Average biomass of individual *Sagittaria platyphylla* tubers was 0.45 ± 0.07g in the 1998-99 season.
Table 3.1. Split-plot mixed model analysis for biomass of *Sagittaria* tubers and Schoenoplectus rhizomes for spring 1999 including a Tukey’s LSD test for treatments.

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<th>Pr &gt; F</th>
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<td>0.3880</td>
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<td>0.08851</td>
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### *Sagittaria*

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<td>Open Grazing</td>
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</table>

* *Tukey’s LSD Test for treatment* *(α = 0.05)*

*Treatment means with the same letters do not differ at $\alpha = 0.05$ level*
Rhizome biomass (g/m²) for all treatments was 112.30 ± 3.01 in *Schoenoplectus* communities in the fall of 1998. This was the total rhizome production for the 1998 growing season. In the spring of 1999, a treatment effect was detected (Table 3.1). Spring 1999 rhizome biomass in NG plots was similar to fall at 87.97 ± 4.61 while biomass was reduced in NO plots 55% and in OG plots 66%. NG plots differed from NO plots (t = 2.81, d.f. = 18, P = 0.0294) and OG plots (t = -4.42, d.f. = 18, P = 0.0009), but no difference was detected between NO and OG plots (t = -1.60, d.f. = 18, P = 0.2703).

**Aboveground Biomass 1999**

In the *Sagittaria* community, no difference was detected in end of season aboveground biomass among treatments (Table 3.2). Aboveground biomass measured in June was 106.28 ± 14.06 in NG plots, 89.71 ± 14.06 in NO plots, and 31.36 ± 14.06 in OG plots (Figure 3.1). In August, aboveground biomass had increased 440% in NG plots and NO plots, but in OG plots the increase was 1200%.

In the *Schoenoplectus* community, a difference was detected in end of season biomass among treatments (F = 12.74, d.f. = 2,90, P = 0.0001). Aboveground biomass measured in June was 360.05 ± 35.48 in NG plots, 171.32 ± 35.48 in NO plots, and 124.95 ± 35.48 in OG plots (Figure 3.2). In August, aboveground biomass had increased 215% in NG plots, 321% in NO plots, and in OG plots the increase was 338%.

**Belowground Biomass Fall 1999**

Biomass of *Sagittaria* tubers in the fall of 1999 followed the trend of aboveground biomass and did not show a treatment effect (Table 3.3). Biomass in OG plots was slightly higher than NG and NO plots. Biomass in NG plots was 131.04 ± 6.45,
Table 3.2. Split-plot mixed model analysis for aboveground biomass of *Sagittaria* and *Schoenoplectus* summer 1999 including a Tukey’s LSD test for treatments.

<table>
<thead>
<tr>
<th>Source</th>
<th>NDF</th>
<th>DDF</th>
<th>Type III F</th>
<th>Pr &gt; F</th>
<th>Grouping*</th>
<th>LS Mean</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mudflat</td>
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<td>6</td>
<td>0.49</td>
<td>0.6326</td>
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<tr>
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<td>16.64222</td>
<td>Nutria Only</td>
</tr>
<tr>
<td>Mudflat*Treatment</td>
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<td>90</td>
<td>0.31</td>
<td>0.8685</td>
<td>A</td>
<td>14.00778</td>
<td>Open Grazing</td>
</tr>
</tbody>
</table>

*Tukey’s LSD Test for treatment*

<table>
<thead>
<tr>
<th>Source</th>
<th>NDF</th>
<th>DDF</th>
<th>Type III F</th>
<th>Pr &gt; F</th>
<th>Grouping*</th>
<th>LS Mean</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
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</tr>
<tr>
<td>Mudflat*Treatment</td>
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<td>1.17</td>
<td>0.3316</td>
<td>B</td>
<td>16.03139</td>
<td>Open Grazing</td>
</tr>
</tbody>
</table>

*Treatment means with the same letters do not differ at $\alpha = 0.05$ level*
Figure 3.1. Mean aboveground biomass for the *Sagittaria* community subjected to no grazing (NG), nutria only grazing (NO), and open grazing (OG) during Summer 1999.
Figure 3.2. Mean aboveground biomass for the *Schoenoplectus* community subjected to no grazing (NG), nutria only grazing (NO), and open grazing (OG) during Summer 1999.
in NO plots 125.38 ± 6.45, and in OG plots 159.64 ± 6.45. Average biomass of individual *Sagittaria platyphylla* tubers was 0.59 ± 0.07g in the fall of 1999. This differs from the average biomass of tubers in 1998 (t = -3.2722, d.f. = 174, P = 0.0013).

Biomass of *Schoenoplectus* rhizomes did show a treatment effect (Table 3.3). Biomass in NG plots differed from NO plots (t = 2.51, d.f. = 18, P = 0.0548) and OG plots (t = -2.71, d.f. = 18, P < 0.0361), but NO and OG plots did not differ (t = -0.21, d.f. = 18, P > 0.9763). Biomass in NG plots was 317.55 ± 3.99, in NO plots 200.84 ± 3.99, and in OG plots 193.33 ± 3.99.

**DISCUSSION**

Hurricane Georges appears to have reduced belowground biomass in the fall of 1998. Below ground biomass of *Sagittaria* was less than one-half the 123.7 ± 2.9 reported by Bielefeld (1993) in fall of 1990 for the MRD. The mean dry mass of individual tubers in 1998 was similar to Bielefeld’s report of 0.47 ± 0.10. Annual productivity on mudflats in the MRD is highly variable. White (1999) found a strong negative relationship between end of season aboveground biomass and average daily flow (CFS) of the Mississippi River during spring (March – May) over a 14 year period from 1984 to 1998. Average March – May flow was approximately 850,000 CFS in 1990 and 1998 and end of season aboveground biomass for *Sagittaria* was approximately 200-250 g/m² in both years.

Giroux and Bedard (1988) also found belowground production to be highly correlated with end of season aboveground biomass for both *Sagittaria* and *Schenoplectus*. On that basis, one would expect similar belowground production in 1990 and 1998.
Table 3.3. Split-plot mixed model analysis for biomass of *Sagittaria* tubers and *Schoenoplectus* rhizomes for fall 1999 including a Tukey’s LSD test for treatments.

<table>
<thead>
<tr>
<th>Sagittaria</th>
<th>Tukey’s LSD Test for treatment</th>
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</thead>
<tbody>
<tr>
<td>Source</td>
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</tr>
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<td>Mudflat</td>
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</tr>
<tr>
<td>Treatment</td>
<td>2</td>
</tr>
<tr>
<td>Mudflat*Treatment</td>
<td>4</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Schoenoplectus</th>
<th>Tukey’s LSD Test for treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Source</td>
<td>NDF</td>
</tr>
<tr>
<td>Mudflat</td>
<td>2</td>
</tr>
<tr>
<td>Treatment</td>
<td>2</td>
</tr>
<tr>
<td>Mudflat*Treatment</td>
<td>4</td>
</tr>
</tbody>
</table>

*Treatment means with the same letters do not differ at \( \alpha = 0.05 \) level.
Previous measurement of rhizome biomass for *Schoenoplectus deltarum* dominated communities in the MRD was unavailable for comparison. However, belowground biomass in fall 1998 was probably lower than would be expected without Hurricane Georges. Some research has been conducted on a closely related species, *Schoenoplectus americanus*, on the Gulf Coast and in Canada. Palmisano (1967) reported wet (fresh) mass of *S. americanus* rhizomes in the Chenier plains of Louisiana to be 3400 to 5600 g/m², dry mass was not reported, but Alisauskas et al (1988) reported dry mass of rhizomes to be 21% of wet mass yielding 714 to 1176 g/m². In the East Texas Chenier plain, 1,073.7 g/m² dry mass was reported by Singleton (1951). This very high production on the Chenier plain may not be attainable in the more dynamic deltaic environment, but does give an idea of the potential productivity of *Schoenoplectus* in Gulf Coast marshes. A study in the Fraser River Delta in British Columbia, Canada reported fall rhizome biomass of 500 g/m² in low marsh and 1000 g/m² in high marsh (Karagatzides and Hutchinson 1991), but in the St. Lawrence estuary of Quebec, Canada, Giroux and Bedard (1988) report estimates of 174-234 g/m² using several different core sizes and shapes. These marshes have shorter growing seasons and different physiography, which makes comparison difficult, but it seems likely that MRD marshes should be at least as productive.

While grazing further reduced belowground biomass over the winter, the reduction did not appear to be biologically significant. In *Sagittaria* communities, aboveground production in grazed plots initially lagged behind NG plots, but plant growth was vigorous and this difference was not detected later in the summer. August 1999 sampling showed all three treatments exceeding 350 g/m² in aboveground biomass,
which was similar to that found elsewhere in the MRD (White 1999), in the Pearl River area (Ford and Grace 1998), and in the Atchafalaya Delta (Visser 1989, Evers et al. 1998).

Over-winter grazing of *Schoenoplectus* plots reduced belowground biomass in NO and OG plots, and this reduction did appear to affect regeneration the following growing season. Plant growth was vigorous in all plots, but aboveground biomass was greater throughout the growing season in NG plots. August 1999 aboveground biomass in NG plots was at the high end of the range reported by White (1999) and Karagatzides and Hutchinson (1991), and exceeds reports by Ford and Grace (1998) and Giroux and Bedard (1988). Aboveground biomass in OG and NO plots is similar to the highest values reported by Ford and Grace (1998) and Giroux and Bedard (1988), and is similar to the lower values reported by White (1999) for the MRD and Karagatzides and Hutchinson (1991) in the Fraser River Delta. While herbivory had a significant impact on aboveground production, grazed areas still recovered well from storm impacts.

Fall 1999 belowground biomass in *Sagittaria* communities was not different among treatments and was similar to that reported by Bielefeld in 1990. This indicates that the effects of tropical storm disturbance did not prevent recovery by the highly productive *Sagittaria* marshes on the mudflats. The lack of difference among treatments may be due to the very low initial belowground biomass after Hurricane Georges. This differs somewhat from the results of studies in the Atchafalaya Delta (Evers et al. 1998) where the impact of herbivory was much greater and led to the conversion of *Sagittaria* marsh to bare mudflat. Nutria populations in the MRD may have been reduced by the storm surge associated with Hurricane Georges, thus reducing grazing pressure. In
addition, wintering waterfowl numbers declined in the 1998-1999 winter similar to the declines seen in the winter of 1995-1996 after the passage of Hurricane Opal (USFWS, unpublished data).

The greater aboveground production in *Schoenoplectus* NG plots was reflected in belowground production in the fall of 1999, but belowground biomass for all treatments was still very low compared to the very high estimates reported by Palmisano (1967) and Singleton (1951) on the Chenier plain and Karagatzides and Hutchinson (1991) on the Fraser River Delta. The NG plots exceeded estimates of Giroux and Bedard (1988) for the St Lawrence Estuary, but OG and NO plots were in the range of their estimates. In the *Schoenoplectus* community, the combination of herbivory and tropical storm disturbance appears to have had an additive effect on belowground biomass, although OG and NO plots produced much more rhizome biomass in the fall of 1999 than in the fall of 1998. While grazing did seem to retard the recovery of *Schoenoplectus* stands, there did not appear to be any risk of conversion to open mudflats.

Different patterns of grazing activity may explain why the effects of herbivory and tropical storm disturbance impacted *Schoenoplectus* more than *Sagittaria*. The *Schoenoplectus* marsh attracted large concentrations of lesser snow geese (*Chen caerulescens*) that grubbed intensively for rhizomes. Lesser snow geese wintering in the MRD were fewer in number following Hurricane Georges, but not as reduced as the numbers of wintering ducks (USFWS, unpublished data). The *Schoenoplectus* marshes were generally higher topographically and were grazed by geese whether dewatered or flooded.
The *Sagittaria* marshes were grazed by loose flocks of dabbling and diving ducks and the grazing activity was closely related to tides. *Sagittaria* marshes were grazed from the waterline to approximately 30 cm depth. This reduced the time available for grazing in certain portions of the marsh, particularly when northerly winds dewatered large areas. Pintails (*Anas acuta*) were the only duck species observed grubbing tubers above the waterline and their feeding was associated with wet depressions and standing water. Ducks do not rely exclusively on tubers and feed on seeds, submerged aquatic vegetation, algae, and invertebrates, which reduces feeding pressure on *Sagittaria* tubers. Nutria do feed on *Sagittaria* tubers, but appear to stay close to the higher, firmer areas near *Schoenoplectus* marshes and avoid the more frequently flooded portions of the mudflats.

Another factor contributing to the greater effect on *Schoenoplectus* marsh may have been the tendency of rhizomes to resprout. In the late October and early November *Schoenoplectus* shoots were observed on most of the mudflats and rhizomes collected in sampling had new shoots. *Sagittaria* tubers did not show a tendency to sprout during the fall and sprouting was not noted until the following spring. Because of the different sprouting dates, the timing of tropical storms could have different effects. Hurricane Georges was relatively late in September, but a storm in late July or early August might have a more harmful effect. The earlier removal of aboveground biomass would further reduce *Sagittaria* tubers and the ability to establish a new stand might be reduced. *Schoenoplectus* would establish a new stand, but depending on the timing and climactic conditions the new stand could be helpful or harmful. If a new stand grew quickly an
earlier winter might result in a net loss of stored energy, but a late onset of winter might allow for an increase in stored energy.

The productivity of the MRD marshes was able to overcome the impacts of both Hurricane Georges and the reduction in belowground biomass by nutria and waterfowl within one growing season. The reduction in belowground biomass was caused by fewer wintering waterfowl in the area, but the mass estimated from spring sampling was likely very near the minimum level that would support continued grazing. The small amount of belowground biomass remaining after winter was sufficient to generate what amounted to a fully stocked stand by the following August. One factor not accounted for in this study is the amount of regeneration resulting from seeds. Regeneration from seedbanks is frequently an important factor in the recovery of freshwater wetlands from disturbance (Keddy 2000). On the other hand, burial or sedimentation can reduce the effective germination rate of small seeded species (Keddy 2000) since these species lack sufficient energy reserves to emerge. The importance of seeds to the annual regeneration of these mudflats deserves attention, especially as it relates to recovery from disturbance.

The reduction in wintering waterfowl after a hurricane may be related to the reduced food resources available. The decline after Hurricane Georges was similar to the decline following Hurricane Opal (USFWS, unpublished data), but wintering waterfowl numbers after both storms recovered the next year indicating that late season hurricanes are a short-term problem. If an early season hurricane is more damaging to belowground reserves, then grazing might damage these mudflats and result in a longer recovery period, but there would have to be considerably less belowground biomass than that present during this study.
CHAPTER 4. SUMMARY

Belowground biomass in *Sagittaria* and *Schoenoplectus* dominated communities in the active Mississippi River Delta (MRD) is an important source of food for both resident nutria and wintering waterfowl. *Sagittaria* tubers and *Schoenoplectus* rhizomes also contribute to the annual regeneration of the marshes. My study found that this belowground biomass was significantly reduced over late fall and winter by waterfowl and nutria, yet this reduction did not prevent *Sagittaria* and *Schoenoplectus* dominated communities from regenerating during the following growing season.

Tropical storms also have the capacity to reduce the production of belowground biomass. The removal of aboveground biomass by the storm surge reduces the amount of energy that can be transferred and stored in tubers and rhizomes. This reduction in available resources may contribute to lower population estimates of wintering waterfowl.

With belowground production reduced by Hurricane Georges in November 1998, population estimates of wintering waterfowl were one-half of the ten-year average. Belowground biomass was reduced by one-half by winter grazing, yet sufficient material remained to regenerate the *Sagittaria* and *Schoenoplectus* communities during the summer 1999 growing season. Estimates of belowground biomass production in November 1999 was nearly double that of November 1998 in both communities.

Although production of belowground biomass increased, population estimates of wintering waterfowl also increased in 1999-2000. In March of 2000, belowground biomass was reduced by one-third, yet exceeded the belowground biomass estimate for November 1998 following Hurricane Georges. This suggests that the annual production of belowground biomass exceeds the requirements of wintering waterfowl.
Some difference was noted between the two community types. The *Sagittaria* community was grazed primarily by ducks, while the *Schoenoplectus* community was grazed primarily by geese. In addition, nutria were observed feeding in *Schoenoplectus* stands more frequently than in *Sagittaria* stands. Grazing by ducks was influenced by tidal fluctuations, which limited the area available for grazing, while geese fed in *Schoenoplectus* stands regardless of water levels. Belowground biomass estimates in November 1999 were higher in the no grazing (NG) treatments in the *Schoenoplectus* community, while there was no difference in estimates by treatment in the *Sagittaria* community. This suggests that grazing pressure may be higher on the *Schoenoplectus* community. Ducks and nutria have alternative resources available in the MRD, while geese feed nearly exclusively in the *Schoenoplectus* community. Geese also appeared to migrate several weeks later in the spring than ducks.

No difference was detected between open grazing (OG) treatments and nutria only (NO) grazed treatments. This does not necessarily indicate that nutria grazing is insignificant in the MRD. Nutria populations may have been reduced by Hurricane Georges, thus reducing grazing pressure. On the other hand, nutria have a number of alternate food sources on the willow (*Salix* spp.) dominated levees and spoil banks. Nutria may also suffer high predation rates. DNWR does not permit alligator (*Alligator mississippiensis*) harvest and many large alligators were observed sunning near study plots. The MRD also supports a large coyote (*Canis latrans*) population. I observed scattered, small areas heavily damaged by nutria, but no evidence of large eat-outs or conversion to bare mudflats reported in other marshes.
While belowground biomass is an important resource for wintering waterfowl, it is only a part of the total resource. Further study of seed production and use, as well as study of submerged aquatic vegetation production and use will provide a better picture of the abundance of food resources for wintering waterfowl.

Study of seed production will also provide needed insight into the regeneration of *Sagittaria* and *Schoenoplectus* dominated marshes each spring. During my study, the non-grazed plots produced aboveground vegetation nearly a month earlier than grazed treatments and biomass increased rapidly in summer 1999. By fall grazed treatments had nearly caught up with non-grazed plots, but I was unable to determine if regeneration from seed had a significant role.
LITERATURE CITED


VITA

Scotland Talley was born 28 September 1963, in Atlanta, Georgia. At the age of 6, the
family moved to St. Simons Island, Georgia, where his interests in woods and wetlands
were sparked. He graduated from Glynn Academy in 1981, and briefly attended Oxford
College of Emory University. After a hiatus from academic pursuits, he earned his
Bachelor of Science in Forest Resources degree (wildlife management concentration) at
the University of Georgia’s Warnell School of Forest Resources in 1996. As an
undergraduate, he participated in small mammal research conducted by the University of
Georgia Museum of Natural History in the Southern Appalachian Mountains. After
graduation, he was an assistant conservation biologist with the Joseph E. Jones
Ecological Research Center at Itchauway Plantation in Newton, Georgia. In 1997, he
moved to Louisiana to participate in research on waterbirds in the family Rallidae at the
Rockefeller Wildlife Refuge in Grand Chenier, Louisiana. He is currently a candidate for
the degree Master of Science in wildlife management at the Louisiana State University
School of Renewable Natural Resources.