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IMPACTS OF FIRE AND VERTEBRATE HERBIVORES ON PLANT COMMUNITY CHARACTERISTICS AND SOIL PROCESSES IN A COASTAL MARSH OF EASTERN LOUISIANA, USA

A Dissertation

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

in

The Department of Plant Biology

by

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ABSTRACT

Both vertebrate herbivores and fire have long been known to have dramatic and important effects on wetlands. In the first part of this study, conducted in the Pearl River Basin coastal marshes of Louisiana, the interaction between the effects of mammalian herbivores, especially nutria and wild boar, and fire was examined in three marsh community types: those dominated by *Sagittaria lancifolia*, *Panicum virgatum*, or *Spartina patens/Scirpus americanus*. Overall, above-ground biomass was reduced by burning but increased by fencing. Richness only increased in plots that were both burned and fenced. In the three communities, only *Scirpus americanus* cover was enhanced by fencing. Fencing reduced *Spartina patens* cover in the *Panicum* and *Sagittaria* marshes. Cover of *Panicum virgatum* in the *Panicum* marsh and *Sagittaria lancifolia* and *Vigna luteola* in the *Sagittaria* marsh were all enhanced by burning. Therefore, burning shifts the communities from *S. patens* to *S. lancifolia*, *V. luteola*.

In the second part of this study, exclosures were used in conjunction with feldspar and benchmark techniques to measure the effects of herbivore exclusion on vertical soil accretion, marsh elevation changes, and litter production. Overall, vertical soil accretion appears to be contributing sufficient material to offset the effects of subsidence in both the grazed and ungrazed plots. However, the examination of the root zone over time indicates that not only is this layer expanding and contracting, but it appears that it also is contributing to soil elevation change.
The third part of this study was conducted in order to assess the impact of herbivores on plant biomass, cover, and species richness. Biomass was four times as great in exclosed plots for both *Spartina patens* and *Scirpus americanus* compared to the control plots. A detrended correspondence analysis revealed that exclusion of grazers resulted in overall shifts in community composition. Species richness increased in the grazed plots after fifteen months and decreased in the ungrazed plots, with a total difference in richness of two species. Overall, the results suggest that grazing in the system selectively alters species composition and increases species diversity.
CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

BACKGROUND INFORMATION

Global warming, sea level rise and the loss of wetlands worldwide have captured the attention of scientists, governments, businesses and the population in general. This dissertation starts with a review of the literature concerning both natural and human-influenced impacts, which increase these processes and result in major changes to our planet. Additionally, background information on coastal wetlands and the animals that live there is discussed. Included in this review is an inspection of the potential influences of large exotic mammals called nutria (Myocastor coypus Molina), which were released into coastal Louisiana in the late 1930's and who many people feel are a threat to the Louisiana wetlands. Results of several experiments on the impacts of nutria on coastal marshes, as well as their interaction with natural forces such as fire, are presented in the following chapters.

Our nations wetlands are in danger. Wetland loss in the United States is estimated near 141,640 ha per year and the rate of loss in the coast of Louisiana is one of the highest in the world, at roughly 65 km² per year (Dunbar, et al. 1992). Wetland functions include flood water storage, filtration of surface water, aquifer recharge and important habitat for both resident and migrating species of animals. Many aquatic animals, such as fish and shrimp, use wetlands during part of their life.
cycle. Loss of wetlands will result in diminished water quality, a decrease in the multi-million dollar fishing industry, a loss of habitat essential to the fur trapping industry and as winter homes for many species of migrating waterfowl. Losses in revenue to states in terms of reduced hunting, fishing and other recreational activity incomes could be dramatic. Coastal marshes also help to protect inland areas from surges related to hurricanes. Some of the trends we currently are witnessing are likely irreversible.

Numerous activities and processes cause wetland loss. In addition to human activities, such as filling, development, dredging of canals and the restriction of sediment input to marshes due to levees, many natural influences such as rising sea level and subsidence of marsh soils have also been shown to contribute to wetland loss. Although much has been written about herbivory and fires in marshes, there is little data to indicate their potential effects on marsh loss.

CLIMATE

Currently, there is much discussion about the greenhouse effect and global warming. While some critics claim that there is no evidence to support the existence of a global warming trend, data indicates that mean temperatures worldwide have risen 0.2 to 0.3°C during the past 100 years (IPCC 1992). Warming has not been consistent, though, as rapid warming took place until the mid-1940's, after which a cooling phase occurred until early in the 1970's. Since 1980, the trend reversed again and rapid warming is being recorded (Pirazzoli 1990).
Increased carbon dioxide in the atmosphere is believed to be the primary cause of increased temperatures. Since the start of the industrial revolution, carbon dioxide levels have increased 25% (Schneider 1989). Roughly 50% of the increases in carbon dioxide levels are due to the burning of fossil fuels and the clearing of forests (Schneider 1989). To some degree of the greenhouse effect is beneficial. Titus et al. (1987), estimate that the Earth's temperature would be 33°C less than it is today, without the greenhouse effect. The IPCC (1992) further predicts that temperatures will rise between 1.2 and 4.5°C over the next century as a direct result of greenhouse warming, if carbon dioxide doubles (Jelgersma 1990). With present rates of emission a large buildup of CO₂ seems certain and may exceed levels of the last interglacial period, based on air bubble analysis of Antarctic ice. If fossil fuel consumption continues to increase at its present rate, it is estimated that carbon dioxide in the atmosphere will double by the year 2100 A.D. In addition, methane gas (CH₄) is also believed to be contributing to global warming. Wetlands, much of which may be lost as a result of global warming and resulting seal level rise, may be a major source of methane gas.

In spite of some predictions, the cause and effect relationship of increased carbon dioxide levels and global warming is poorly understood. The primary question at present is not if temperatures will continue to rise, but to what extreme or whether or not increases documented are a result of normal random fluctuations. Schneider (1989) contends that current models are too coarse to detect small natural
fluctuations. When compared to the past 100 years of data, models predict temperatures approximately 1°C warmer than have been measured (Schneider 1989).

SEA LEVEL RISE

Sea level increases vary regionally. Gornitz et al. (1982) and DeLaune et al. (1990) report a 23.0 cm increase on the Gulf of Mexico coast over the past 100 years, while Titus et al. (1987) claim a 30 cm increase. In the Chesapeake Bay, Froomer (1980) reports 27.4 cm of increase in the past century. According to Kilge (1990), sea level worldwide increased 12 cm during the same time period. Peltier and Tushingham (1989) report a current worldwide increase of 2.4 mm per year.

Although sea level rise continues, Russell (1957) claimed that there had been no significant change in the past 5000 years. Contrary to this belief, radiocarbon dated marsh and peat deposits in Chesapeake Bay indicate a rapid rise in sea level in the past few centuries (Froomer 1980), which appear to take place in sharp jumps (Jelgersma 1990). From 900 to 1300 A.D., global temperatures were approximately 2.5°C warmer than present and sea level was 0.5 m higher than it is today. The net rise during that time is comparable to the rise in sea level taking place in the late 20th century (Fairbridge and Jelgersma 1990).

Sea level increases alone don't provide an accurate picture of possible water depths in coastal marshes. More important is relative sea level rise, which is eustatic sea level rise, the rise worldwide due to natural effects, plus submergence of soils, which is called subsidence. Numerous factors contribute to relative sea level rise. In addition to eustatic sea level rise, which is mediated by glacial melt and expanding
ocean volumes, subsidence, crustal downwarping, tectonic deformation and soil compaction also contribute to relative sea level rise. Submergence of marshes in Connecticut is 2.6 mm per year (Harrison and Bloom 1977), while the Louisiana coastal deltaic marshes are submerging at the rate of 1.1 cm per year (Nyman 1990). Submergence rates may be biased due to compaction of sediments by the weight of the gauges and be underestimated because of the depth of poles supporting gauges (Cahoon et al. 1995), indicating a higher sea level rise than actual (DeLaune et al. 1990). Therefore, Pirazzoli (1990) believes that predicting sea level rise in the next century will be difficult. Others disagree, with predictions on sea level rise ranging from 23 to 96 cm in the next century (IPCC 1995) to 50-200 cm in the same time interval (Salinas et al. 1986). Predictions for the deltaic coast of Louisiana are 1.2 cm per year (Salinas et al 1986, Reed 1989) to 1.23 cm per year (Baumann et al. 1984).

Sedimentation negates some of these effects by elevating the marsh surface though the exact cause and effect has been the subject of some debate (Russell 1957). Sedimentation adds height to the marsh surface. If sedimentation does not offset relative sea level rise, then marsh soil elevation decreases relative to sea level. Compaction of sediments, due to the weight of the soil on itself, dewatering, and the settling of soils is a major cause of subsidence. Subsidence rates at Grand Isle in Louisiana are 0.91 cm per year (Penland et al. 1989). Crustal downwarping, which is cause by the weight of the soil as a single unit, is another important process in subsidence, but acts too slow to be of much concern to us (Fairbridge and Jelgersma 1990) in the time scale of a single human life.
Changes in total ocean volume, which is a result of both additional water from surface and groundwater sources and the thermal expansion of the oceans, contribute to sea level rise (Fairbridge and Jelgersma 1990). Groundwater is added through its pumping out and use on the surface. Gornitz et al. (1982) feel that most of sea level rise is due to thermal expansion.

Small glacier melt is considered another major cause of sea level rise. Since the last ice age, global ice cover has declined from 27% to 10% and small glacier melt is believed to be responsible for an approximate increase in sea level of 150 m (Titus et al. 1987, Russell 1957). Like ocean expansion, glacial melt is a result of rising global temperatures (Titus et al. 1987). If carbon dioxide increases cause temperatures to continue to increase to a level of 0.6 to 1.0°C by the year 2050 A.D., ocean volume should expand resulting in a 4 to 8 cm increase in eustatic sea level rise (Wigley and Raper 1987). From 1880 to 1985, world average sea level rose between 2 to 5 cm, with glacial melt believed responsible for 2.5 cm out of every 10 to 15 cm of rise (Wigley and Raper 1987). Rates of sea level rise due to small glacier melt recently range from 0.46 cm per year (Wigley and Raper 1987) to 0.52 cm per year (Meier 1984). Titus et al. (1987) and Gornitz et al. (1982) predict small glaciers will contribute 70 cm to sea level rise by the year 2050 A.D., providing that small glacier melt continues at its current rate. Jelgersma (1990) predicts an increase of nearly 140 cm in the next one hundred years. Only half of small glacial melt might be contributed to global warming. The other half is believed by some to be due to volcanic activity.
(Oerlemans 1988). Peltier and Tushingham (1989) disagree, feeling that there is strong evidence showing that as much as 75% of sea level rise may be a result of small glacial melt.

Large and seemingly permanent glaciers don’t seem to be contributing to sea level rise. During the last warm period, which was 5000 years before present (YBP) and 1°C warmer than current temperatures, no melt is believed to have taken place. Although a break up is possible, there are no data to support this theory (Gornitz et al. 1982). Cycles of freezing and thawing are on a frequency of about 100,000 years. The last de-glaciation was 6,000 YBP (Titus et al. 1987, Peltier and Tushingham 1989, Jelgersma 1990) with shorter cycles of sea level rise superimposed on the larger ones (Hicks 1981, Jelgersma 1990). Without long term data, changes in the cycles of either freezing or thawing may be minor fluctuations and may not indicate possible long term effects. Also, a time lag of 18 years exists between temperature increases and sea level rise, making it difficult to attribute current climate conditions with expect sea level changes (Gornitz et al. 1982, Pirazzoli 1990).

COASTAL WETLAND LOSS

Approximately 40% of all coastal wetlands in the contiguous United States of America are in Louisiana (Sasser et al. 1986, Baumann et al. 1984) with 65% of Gulf of Mexico coastal marshes occurring in Louisiana (Degan 1984), comprising 3.2 million ha (Hatton et al. 1983). Craig et al. (1979) reports that 18% of these marshes have fresh water plant communities, while Nyman (1990) claims a higher number at 30%. Mesohaline plant communities reportedly make up 49% of the coastal marsh...
(Craig et al. 1979). Most of the coastal wetlands are in the Mississippi River deltaic plain (MRDP), which has experienced cycles of building, abandonment, and deterioration in 1000 to 2000 year intervals for nearly 7000 YBP (Penland et al. 1989).

The retreat of the coastline of Louisiana has been recorded since 1812 (Bird 1985). Presently, the rate of submergence in the deltaic plain is greater that during the late Holocene (DeLaune et al. 1983). In 1913, 17.35 km² of deltaic shoreline were disappearing annually. By the year 1980, 102 km² (Gagliano et al. 1981) of the coast were disappearing each year, including the barrier islands. In 1990, 65 km² of the coast were disappearing yearly (Dunbar et al. 1992). The maximum loss rate of 10,200 ha per year (Gagliano et al. 1981, Sasser et al. 1986) was high compared to the rest of the United States (Gosselink and Baumann 1980). Loss rates translate to 0.20% from 1945 to 1956 A.D., 0.32% until 1969 and 1.49% up until 1980 (Sasser et al. 1986).

Many factors contribute to marsh loss. Filling of wetlands for development or building of spoil banks during canal construction is one cause of loss (Craig et al. 1979). Erosion, caused by boat wakes in both natural water systems and canals, can cause extensive shoreline loss (Morgan 1963, 1977; Craig et al. 1979, Salinas et al. 1984). Land reclamation, which has been taking place since the early 18th century has claimed much of the marsh, mostly through draining for agricultural purposes. From the year 1910, marshes have been drained for urban and industrial uses (Craig et al. 1979, Salinas et al. 1984). With a similar effect, fluid withdrawal of ground
water from the marshes has contributed to marsh loss by allowing salt water intrusion, which accelerates deterioration of the plant communities (Craig et al. 1979, Salinas et al. 1984).

One of the most widespread activities which directly destroys many hectares of marsh is the dredging of canals for oil fields and navigation (Craig et al. 1979, Baumann et al. 1984, Salinas et al. 1984). Besides converting active marsh to open water, dredging fills in marsh with the building of dredge spoil banks and allows salt water to intrude into what would otherwise be less saline systems (Hatton et al. 1983, Sasser et al. 1984, Degan et al. 1986). The marsh management practice of flooding marshes for waterfowl habitat also directly converts these systems to open water (Craig et al. 1979).

Submergence, which is a combination of sea level rise and subsidence, is another major factor contributing to marsh loss (DeLaune et al. 1983, Baumann et al. 1984, Salinas et al. 1986). Subsidence can be divided into two broad types: deep and shallow. Deep subsidence is primarily a result of regional crustal downwarping, a long-term effect which is caused by the weight of the delta sediments, which can be up to 100 m thick in the Mississippi River Delta (Craig et al. 1979, Hatton et al. 1983, Degan et al. 1984). Shallow subsidence is due to several factors, such as dewatering, degassing and the compaction of soils. For the Gulf of Mexico coast, the Barataria Basin of Louisiana is experiencing the worst compaction near the coast (Kolb and Van Lopik 1958, DeLaune et al. 1990). This is because the basin is in the youngest lobe of the Mississippi River Delta Plain (MRDP) (Hatton et al. 1983). This
process, like regional crustal downwarping, is due to the weight of sediments settling under their own weight (Sasser et al. 1986). The weight of artificial and natural levees and barrier beaches add to the compaction problem (Craig et al. 1979).

Overwhelmingly, lack of soil accretion seems to be the primary cause of submergence of coastal lands. Soil accretion is the buildup of sediments and organic matter. Prior to the leveeing of the Mississippi River by the United States Army Corps of Engineers, the river would seasonally flood, resulting in a major annual input of mineral sediments rich in nutrients (Craig et al. 1979, DeLaune et al. 1983, Degan et al. 1984). Levees also limit tidal inputs. In Delaware Bay, diked marshes suffered greater subsidence than undiked marshes (Phillips 1986). Unless river sediments are reintroduced, subsidence will eventually lead to open water (Baumann et al. 1984). Removal of plant biomass, either by grazing or for waterfowl management, can result in less sediment capture (Phillips 1986).

Subsidence rates are highly variable between sites (Ohlson and Dalhberg 1991), but only slightly different between seasons (DeLaune et al. 1989). Inland marsh areas accrete slower than streamside (Hatton et al. 1983, Salinas et al. 1986). In Connecticut a high marsh accretes at 2 to 6.6 mm per year, while a drier Phragmites marsh of higher elevation accretes at the rate of 17.1 mm per year, mostly due to a very high rate of plant biomass production (Harrison and Bloom 1977). On Long Island, salt marsh accretion is an average 2.5 mm per year, with a maximum of 4.7 mm per year (Flessa and Cushman 1977). Due to slow decomposition or organic matter, low compaction and low dewatering, Chesapeake Bay has been accreting at the rate of 0.18
to 0.74 cm per year over the past 190 years (Kearney and Ward 1986). Previous to 1940
A.D., soil accretion was 0.04 cm per year. Since then, sediments have accreted at the
rate of 1.04 to 1.38 cm per year, believed to be due to the introduction of regular tides
(Orson et al. 1990) and accelerated sea level rise. On the Louisiana Gulf of Mexico
coast, the accretion rate has been 0.74 cm per year, slowing to 0.67 cm per year from
1963 to 1978 A.D. (DeLaune et al. 1989). Currently, the source of some sediments may
be entirely from within the marshes (DeLaune et al. 1989, Baumann et al. 1984; Nyman
et al. 1990). Storms are believed to be the main cause of marsh sediment resuspension
(Reed 1989).

Organic matter is the controlling factor in accretion in sediment starved
marshes (Gagliano et al. 1981). The volume of the soil, which is more important than
the weight, contributes the most to sustaining soil elevation. Peat, which is 75% organic
matter, occupies more volume than mineral matter in all except the salt marsh (Nyman
Rates of peat accumulation vary due to variation in production rates among species
found in each marsh type (DeLaune et al. 1983, Ohlson and Dahlberg 1991), with
*Phragmites* having the highest rates (Phillips 1986). Compaction in peat occurs rapidly,
reported to take place in less than 50 years in Swedish mires. Upper anaerobic
processes and plant species have strong influences on the compaction rates of peat
(Ohlson and Dahlberg 1991). Water content by percent volume, can be 80% in peats in
the upper 20 cm of the marsh (Kearney and Ward 1986). Therefore, dewatering during
periods of drawdown, which occurs both naturally and through human influences,
can contribute to the loss in soil elevation directly and by increasing decomposition rate through increased aerobic activity of decomposers exposed to the atmosphere.

Roots and rhizomes are also an important component of the organic layer (Nyman et al. 1990). Most below ground organic matter is believed to originate from below ground biomass production (Nyman et al. 1990). In order to offset the submergence rate of 1.2 cm per year, it is believed that input of both above and below-ground biomass production to the peat layer is needed (Nyman et al. 1990). Currently, there are no data with which to evaluate this hypothesis.

**HERBIVORE EFFECTS**

Herbivory can have profound negative effects on plant communities where herbivore densities are high. Although herbivores can have high consumption rates in certain circumstances, it is estimated that they only eat about an average of 10% of the net primary productivity (NPP) (Crawley 1983). Grazing can have numerous effects including increasing primary production (Mc Naughton 1979), allowing an increase of surface soil temperatures when standing crops are removed, which in turn increases decomposition, and creating local heterogenieties by eating over a large area and defecating in a small area (Crawley 1983).

Symptoms of heavy grazing can include reduced plant growth rate in the spring, reduced winter survival, shortened internode length, reduced leaf width, and depleted carbohydrates (Crawley 1983). Removal of leaves before senescence may reduce litter production (Nicholson et al. 1970). Defoliation can stop root growth, decrease root respiration and nutrient uptake within 48 hours (Troughton 1957, Ryle...
1970, Davidson 1979). In grasses, time of defoliation can affect production yield (Binnies et al. 1980). In Carex, high herbivory intensity can result in mortality up to 95% (Chapman and Slack 1979). In sugar beets, 50% leaf loss was reported to result in a 5% root reduction and 100% leaf loss resulted in a 30% root reduction (Bardner and Fletcher 1974).

Standing biomass, which includes dead stems, does not equal available food (Crawley 1983), because herbivores prefer green tissues to old (Arnold 1964). Also, when food is scarce, animals will spend more time grazing. For example, sheep feeding on Phalaris grazed for 7 hours a day when the crop was at 2,200 kg/ha and for 10 hours a day when the crop was at 700 kg/ha (Arnold 1964). Herbivores tend to aggregate in areas of more attractive foods, with poor areas becoming even less preferred for feeding (Arnold 1964).

In the Louisiana marshes, there are many herbivores. Small mammals, such as mice, are not believed to consume large amounts of plant biomass (Abernathy et al. 1985) though they may be important seed harvesters. Since Louisiana is at the southern end of the Mississippi flyway, wintering waterfowl are one of the major herbivores. For example, nearly one million gadwalls (Anas strepera) wintered in Louisiana in 1980 (Paulus 1982). Snow geese (Chen caerulescens) have been known to eat an entire marsh, breaking the soil to a depth of 20 cm, consuming tubers and rhizomes and discarding ten times as much biomass from above-ground as was eaten (Lynch et al. 1947). Thousands of geese feeding two times daily can denude a marsh
in several weeks. As an example, Lynch et al. (1947) reported that 10,000 geese consumed 2 ha of marsh, leaving the entire area bare of vegetation.

Another major herbivore, the muskrat (*Odontra zibethica*), which was called musquash by the indigenous Cree people (Lynch et al. 1947), is believed to originally be an exotic species in coastal Louisiana. None were reported by John Audubon in 1850 A.D., although there were unconfirmed reports of dense populations in the Barataria Basin as early as 1840 A.D. In 1870 A.D., the first confirmed sighting was reported in Grand Cheniere (O'Neil 1949).

*Scirpus americanus* Pers. is the primary food of muskrats, making up 80 to 90% of their food. Muskrats, which begin to eat at the age of one month, can defoliate a *S. americanus* marsh, in an event called an "eatout", in as short as three months or as long as four years. Revegetation can occur in as little as one year, but usually takes several years (Lynch et al. 1947, O'Neil 1949). Muskrat herbivory includes eating the base of plants and root systems, often breaking the marsh to a depth of 50 cm. If the marsh is broken into many small vegetation islands, which are then consumed, the marsh can become a mudflat.

In order for a marsh to recover from an eat out, the rhizomes must be intact or there must be viable seeds that can germinate on the floating mats of left over vegetation (Lynch et al. 1947). Roots typically take 3 to 10 weeks to bind in the floating mats. If this does not occur in time, storms can wash vegetation out of the marsh (Lynch et al. 1947). If the water level remains high, recovery will be slow to non-existent, in which case open water will be the end result. Salt water can
intrude after an eat out, stressing the plant community. If drawdown occurs after salt water intrudes, salt concentrations in the soil may inhibit seed germination (Lynch et al. 1947).

In the fresh marsh, Typha and Scirpus species are preyed upon by muskrats. In floating marsh, which are called flotant, many muskrats can be produced yearly. High muskrat populations may produce what is called a hidden eatout, where the plant biomass and cover is strongly reduced, but mudflats do not occur. Climax in the marsh community may be premature from the muskrats eating desired species leaving undesired later successional species without competition. Additional muskrat activities which affect the marsh are tunneling in peat when the marsh is dry, using vegetation for mounds, which are often homes, or defecating on a specific site, thus relocating nutrients to a small area (Lynch et al. 1947).

Occupying a niche similar to the muskrat is Myocastor coypus. In Latin Myocastor coypus literally means mouse-beaver, which refers to its mouse-like appearance and beaver-like size. In England, they are known as coypu, which is an Araucanian word for watersweeper, referring to the action of its tail (Lowery 1974, Wilner 1982). In the United States M. coypus is known as the nutria. With valvular mouth lips that close behind their incisors (Wilner 1982), the nutria have been described as stunted beavers with teeth that can easily pierce a boat paddle (Kays 1956). However, there is no report of this occurring. Nutria are not native to North America. McIlhenny, of Tabasco fame, brought 50 nutria from Argentina to Avery Island, New Iberia, Louisiana in 1937 to raise for their fur. Accounts of how the
nutria were introduced to the wild are conflicting. Gainey (1949), Ashbrook (1948) and Kays (1956) write that some may have escaped by digging under the fences of their cages. Other reports claim that McIlhenny may have intentionally released some to help control the water hyacinth problem (Norris 1966, Lowery 1974). As many as 150 were reported to have either escaped during a hurricane or were released because of the flooding associated with that hurricane (Kays 1956).

Although trapping pressure nearly wiped out nutria in Argentina (Kays 1958), demand in Louisiana was low and the population spread rapidly (Laurie 1946, O’Neil 1949, Gainey 1949, Brown 1975). They produce litters at the average rate of 5 every 2 years with an average of 5 per litter. The number of offspring per litter ranges from 2 to 11 (Kays 1956, Lowery 1974, Wilner 1982). Additionally, predation pressure has little effect on populations. Predators include alligator (Alligator mississippiensis), the gar (Lepisosteus sp.), cottonmouths (Agkistrodon piscivorus), redshouldered hawks (Buteo lineatus) and feral dogs (Canis lupis) (Wilner 1982). But these apparently do not feed on nutria in sufficient numbers to control the population.

Initially, it was believed that nutria and muskrats would occupy different habitats, with the nutria living in fresh marshes and muskrat living in more saline marshes (Gainey 1949, Lowery 1974). Although Kinler (1978) reported that nutria populations were highest in the fresh marsh, by 1956, nutria numbers exceeded the muskrat population (Kays 1956), with approximately one million nutria living in coastal Louisiana. Due to a decrease in the demand for fur worldwide, trapping of nutria in Louisiana declined from a high of 986,014 animals harvested in 1986 to
171, 470 in 1994-1995 (Louisiana Department of Wildlife and Fisheries). This seems to have resulted in an increase in nutria population (personal observation). Numbers have reached a level such that nutria have become a nuisance, consuming rice fields parts of the state, undermining roads and burrowing through canal embankments in the suburbs of New Orleans, limiting the regeneration of baldcypress (*Taxodium distichum*), and consuming vast hectares of marsh along the coast.

**DISSERTATION OBJECTIVES**

It has been hypothesized by some that nutria may be contributing to wetland loss through their destructive habits. This dissertation reports on two separate exclosure experiments which were conducted to determine impacts of nutria and other herbivores on coastal marshes, specifically at the Pearl River in southeastern Louisiana. The first experiment examined the interaction of fire and herbivory on plant biomass, cover, and species richness in three plant community types. Results from the second experiment are presented in two parts. Chapter 3 presents results on the impacts of nutria on soil accretion, shallow subsidence, soil elevation changes, soil bulk density and organic matter content changes, root and rhizome biomass production, and litter production. Chapter 4 presents results on plant biomass, the frequency of occurrence of species and community composition changes over the course of two growing seasons, and light levels at the soil surface. It is hoped that these studies will help answer questions related to nutria's role in changes to the Louisiana marshes and their influence on wetland loss.
CHAPTER 2

INTERACTIVE EFFECTS OF FIRE AND VERTEBRATE HERBIVORY
IN A COASTAL MARSH IN LOUISIANA

INTRODUCTION

Vertebrate herbivores have been shown to have a significant impact on Gulf of Mexico coastal wetlands (Chabreck 1959, Linscombe et al. 1981, Wright and Bailey 1982). Among the most intense examples of herbivore effects reported are those dealing with muskrat (*Ondatra zibethica*), nutria (*Myocastor coypus*) and snow geese (*Chen caerulescens*). In 1949, O’Neil reported a large scale defoliation called an “eatout” in Southwestern Louisiana that resulted in a complete and permanent replacement of marsh by open water. In 1954, a 15-acre eatout by snow geese led to the permanent loss of marsh in Cameron Parish, Louisiana (Adams 1956). Experimental studies of snow geese in Canadian salt-marsh (Bazely and Jefferies 1986) have shown that protection of vegetation from herbivory resulted in increased plant diversity, increased number of dicot species, changes in species composition, and initial increases in total standing crop (reviewed in Westoby 1989). Studies conducted in the recently emerging islands of the Atchafalaya Delta in Louisiana have shown that high densities of nutria lead to significant changes in plant community composition (Fuller *et al.* 1985, Rejmanek *et al.* 1990, Shaffer *et al.* 1990, and Visser 1991). Chabreck (1959) found that mesohaline marsh plots that were protected from herbivory possessed 40% greater standing crop than unprotected plots. For three community types in the coastal marshes...
marshes of the Pearl River in Louisiana, above-ground biomass was found to be 30% less in unprotected plots versus plots protected from nutria (Taylor et al. 1995). Although Nyman et al. (1993) found that nutria populations on Marsh Island in Louisiana had a negative effect on plant species richness, at the Pearl River Taylor and Grace (1995) found no significant effect on richness caused by nutria.

The effects of herbivores on coastal wetlands have been shown to depend on a number of factors. It has been shown that species that are not preferred food tend to dominate areas of herbivory while species that are preferred will dominate areas protected from herbivory, with both richness and evenness increasing in protected plots (Shaffer et al. 1992). Linscombe et al. (1981) reported that as the density of nutria decreased in the mesohaline marsh of Vermilion Bay, Louisiana, biomass of Spartina patens (Aiton) Muhl decreased while Scirpus americanus Pers. (formerly Scirpus olneyi Gray), which is a preferred food of nutria, increased. In the Atchafalaya Delta, cover of vegetation decreased while diversity increased in areas of intense herbivory that were also exposed to prolonged flooding (Shaffer et al. 1992).

In a study of Marsh Island, Louisiana, Nyman et al. (1993) found evidence that muskrat herbivory tended to increase richness while nutria herbivory decreased richness. Grace and Ford (1996) found that there were no long-term effects of episodic flooding and salinity stress on Sagittaria lancifolia L. unless herbivory also became a factor; the combination of all three factors resulted in death of S. lancifolia individuals. Marsh community type can also be a factor affecting herbivore impacts. Taylor and Grace (1995) found no significant difference in the effects of herbivores in fresh, oligohaline,
and mesohaline marshes at the Pearl River; however, the responses by individual species varied from community to community. Fire has been shown to alter effects of herbivory in some marsh types (Smith and Kadlec 1985). However, in a study of interactive effects of herbivory and fire in an oligohaline marsh, Taylor et al. (1994) found no interaction between herbivore and fire effects.

In Louisiana, coastal marshes burn for a variety of reasons. Fire has long been a natural force affecting wetlands (Lynch 1941, Wright and Bailey 1982, Mitsch and Gosselink 1986, Chabreck 1988, Kirby et al. 1988). Historical records indicate that native Americans traditionally set fires for a variety of purposes and likely increased the frequency above natural levels (Duever et al. 1986). There is a widespread belief that fire promotes high population densities of wildlife (Chabreck 1982, 1988). Records for Louisiana indicate that hunters and trappers have regularly set fires in the marshes for at least the past 100 years (Lowery 1981). At present, fires are common, particularly winter fires set by wildlife managers, trappers and hunters. Literature suggests that fire may favor plant species that are beneficial to muskrat and nutria. For example, Mendelssohn et al. (1988) found that burning favored Scirpus americanus by suppressing growth of its competitors (particularly Spartina patens). Chabreck (1982) found autumn burns acted to favor Scirpus americanus over Spartina patens. These studies are significant for herbivory studies because in the case of nutria, muskrat, and snow geese, Scirpus americanus is considered to be a very important food species in mesohaline marshes (O'Neil 1949, Linscombe et al. 1981, Chabreck 1988).
Relatively few studies have examined the interactive effect of fire and herbivory in wetlands. In the Great Salt Lake Marsh, fire enhanced the degree of herbivory. Protein increased in vegetation after fire and preferential grazing was observed occurring (Smith and Kadlec 1985). In an oligohaline marsh of coastal Louisiana, effects of fire and herbivory on biomass and species richness were examined by Taylor et al. (1994). Herbivory reduced biomass of both Spartina patens and Scirpus americanus while biomass was increased for Cyperus flavescens L. and C. odoratus L. Fire significantly reduced biomass for Spartina patens and Bacopa monnieri (L.) Pennell, but not for other species. Richness was not effected by herbivory or fire. No interaction was detected between factors for biomass or richness. Our understanding of the interactive effects of fire and herbivory are currently limited by the small number of such studies and their limited scope. This paper reports results of a two year study of the effects of herbivory and fire on three contrasting marshes of the lower Pearl River system: a Panicum virgatum marsh, a Sagittaria lancifolia marsh, and a Scirpus americanus marsh. The study site for this work was the Pearl River basin in Louisiana (Taylor and Grace 1995). The Pearl River drains about 2.3 million ha from south central Mississippi into the extreme southeastern part of Louisiana. Study sites for this research were chosen to represent three community types based on the dominant vegetation.

METHODS

In order to ensure each community type was represented, in fall 1992 five sample sites were arbitrarily selected in each of the plant communities with the provision that no two be closer than 100 m. Within each plot, 2 m X 2 m subplots were
established and one subplot was randomly selected to be fenced by using plastic coated weldwire of 5 cm mesh and 0.6 cm rebar as corner posts. The other subplot was simply marked with rebar. Bailing wire was fashioned into U-shaped pieces and inserted through the fencing into the ground to discourage animals from burrowing under the fences. Within each 2 m X 2 m subplot, the inner 1 m² was designated for study with the remaining perimeter area reserved as a buffer (Fig. 2.1). Fire breaks 2 m wide were cut in the vegetation to both protect the plots and to define their boundaries. Fire breaks were maintained throughout the study.

Plots were censused in fall 1992 for areal cover of all species. One randomly selected plot at each site was burned and the other was left unburned. All plots were censused in fall 1993 and then the plots originally burned were reburned. In fall 1994, 0.25 m² subplots within each plot were harvested. Cover was estimated and plants were harvested for dry weight data for all species.

Statistical Analysis

Data analyses were performed by using SAS (SAS Institute, Cary, NC). The dependent variables (final biomass, species cover and species richness) were examined for univariate normality and homogeneity of variances prior to analysis of variance. Normality of residuals was evaluated using the Wilks-Shapiro test (Sokal and Rohlf 1981). Homogeneity of variances was evaluated using discriminant function analysis on the model residuals with a chi-square test criterion (SAS Institute, Cary, NC). Final biomass was transformed to ln(biomass + 1) in order to achieve normality and
Panicum marsh

Sagittaria marsh

Spartina marsh

3 marsh types
5 sites at each marsh
plots are burned or unburned
subplots are fenced or not

Figure 2.1. Experiment design and layout of plots and treatments for fire/herbivory interaction study.
homogeneity of variances for the analysis. Values were detransformed for presentation (Sokal and Rohlf 1981). Species cover and richness were found to be normal and homoscedastic.

The basic experimental design was a split-split plot design with 10 m X 10 m plots within each of the five sample sites representing the first split and 2 m X 2 m subplots representing the second split. Analyses were conducted using the GLM procedure in SAS (SAS Institute, Cary, NC). For final biomass and species richness, the main factor- differences between marshes were tested using the MARSH BY SITE interaction term, the effect of burning and the interaction between marsh and burning were tested by using the MARSH BY BURN BY SITE interaction term, and effects of fencing and interactions between fencing and higher terms were tested using the total error term. A posteriori tests for differences between marshes were accomplished by using the Tukey's HSD test (SAS Institute, Cary, NC). Data on species coverage for the most abundant species in each community were tested for treatment effects separately for each marsh because of limited overlap in dominant species. Following the recommendation of Yoccoz (1991), an alpha level of 0.10 was used to evaluate hypothesis with primary emphasis placed on magnitude of effect as indicative of biological significance.

RESULTS

Burning significantly reduced above-ground biomass for all community types (p=0.003); on average biomass was reduced by a third (Fig. 2.2 and Table 2.1). This
Figure 2.2. Effects of burning and fencing on biomass for the Sagittaria, Panicum and Spartina communities. Error bars represent ± 1 standard error.
Table 2.1. ANOVA values for of the log normal transformed biomass data.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>MARSH</td>
<td>2</td>
<td>5.89</td>
<td>0.0165</td>
</tr>
<tr>
<td>BURN</td>
<td>1</td>
<td>13.24</td>
<td>0.0034</td>
</tr>
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<td>MARSH*BURN</td>
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<td>0.30</td>
<td>0.7452</td>
</tr>
<tr>
<td>FENCE</td>
<td>1</td>
<td>53.86</td>
<td>0.0001</td>
</tr>
<tr>
<td>BURN*FENCE</td>
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<td>0.1239</td>
</tr>
<tr>
<td>MARSH*FENCE</td>
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<td>2.20</td>
<td>0.1346</td>
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<td>MARSH<em>BURN</em>FENCE</td>
<td>2</td>
<td>1.07</td>
<td>0.3602</td>
</tr>
</tbody>
</table>
effect held true for both fenced and unfenced plots. Fencing, however, significantly increased biomass. There was no significant interaction between the treatments.

Species richness at the beginning of the study (1992) was greatest in the
Sagittaria community with an average value of 8.15±0.32 (± 1 standard error)
compared to means of 6.55±0.04 for the Panicum community and 6.20±0.28 for the
Scirpus community. By the end of the study (1994), richness in untreated plots
(unfenced and unburned) had increased by an average of approximately 1.8±0.8 species
in the Panicum community (Fig. 2.3); however, in the other communities, there was no
significant change over time in untreated plots. ANOVA results (Table 2.2) indicated
that there was a significant interactive effect of burning and fencing on richness. In all
three communities, the biggest increase in richness occurred in plots that were burned
and fenced (Fig. 2.3). The response to this treatment combination was most dramatic in
the Sagittaria community where species increased by an average of nearly 4 per plot.
In both the Scirpus and Panicum communities, plots that were burned and fenced
increased in richness by approximately 2.4 species on average. In the Sagittaria and
Scirpus communities, all other treatments had no effect on richness. In the Panicum
community, both burned and unburned plots which were unfenced showed a tendency to
increase in richness during the experiment, perhaps because of between-year effects.

Burning had an effect on cover for all three dominant species in the Sagittaria
lancifolia community: Sagittaria lancifolia (p=0.0560), Spartina patens (p=0.0706)
and Vigna luteola (Jacquin) Bentham (p=0.0267) (Table 2.3 and Fig. 2.4). Cover for
S. patens was reduced by burning, while cover for both Sagittaria lancifolia and
Figure 2.3. Effects of burning and fencing on change in plant species richness for the Sagittaria, Panicum and Scirpus communities. (b=burned, n=unburned) Error bars represent ± 1 standard error.
Table 2.2. ANOVA values for the changes in richness (Figure 2.2).

<table>
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<tr>
<td>MARSH</td>
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<td>0.4896</td>
</tr>
<tr>
<td>BURN</td>
<td>1</td>
<td>8.05</td>
<td>0.0150</td>
</tr>
<tr>
<td>FENCE</td>
<td>1</td>
<td>4.45</td>
<td>0.0465</td>
</tr>
<tr>
<td>BURN*FENCE</td>
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</tr>
<tr>
<td>MARSH*BURN</td>
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<td>MARSH*FENCE</td>
<td>2</td>
<td>2.72</td>
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Table 2.3. ANOVA values for cover data of the split-split plot design in a *Sagittaria lancifolia* dominated marsh with *Spartina patens* and *Vigna luteola*.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. lancifolia</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BURN</td>
<td>1</td>
<td>5.01</td>
<td>0.0556</td>
</tr>
<tr>
<td>FENCE</td>
<td>1</td>
<td>0.06</td>
<td>0.8072</td>
</tr>
<tr>
<td>BURN*FENCE</td>
<td>1</td>
<td>1.19</td>
<td>0.3063</td>
</tr>
<tr>
<td><em>S. patens</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BURN</td>
<td>1</td>
<td>4.35</td>
<td>0.0706</td>
</tr>
<tr>
<td>FENCE</td>
<td>1</td>
<td>0.37</td>
<td>0.5619</td>
</tr>
<tr>
<td>BURN*FENCE</td>
<td>1</td>
<td>1.68</td>
<td>0.2310</td>
</tr>
<tr>
<td><em>V. luteola</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BURN</td>
<td>1</td>
<td>7.34</td>
<td>0.0267</td>
</tr>
<tr>
<td>FENCE</td>
<td>1</td>
<td>4.21</td>
<td>0.0744</td>
</tr>
<tr>
<td>BURN*FENCE</td>
<td>1</td>
<td>4.21</td>
<td>0.0744</td>
</tr>
</tbody>
</table>
Figure 2.4. Effects of burning and fencing on plant cover of *Spartina patens*, *Sagittaria lancifolia* and *Vigna luteola* in the *Sagittaria* community. (b=burned, n=unburned) Error bars represent ± 1 standard error.
*V. luteola* was dramatically increased (Fig. 2.4). There was no significant effect of fencing on any of the dominant species.

In the *Panicum virgatum* community, cover of *S. patens* was significantly reduced in burned plots (Fig. 2.5 and Table 2.4). Burning increased *P. virgatum* cover, but significance was marginal (p=0.1027). Fencing had no significant effect on *S. patens* but had a marginal effect on *P. virgatum* (p=0.0630).

In the *Scirpus americanus* community, burning had no significant effect on percent cover of either *S. americanus* or *S. patens* (Fig. 2.6 and Table 2.5). Only *S. americanus* was affected by fencing, which dramatically increased cover from approximately 20% to between 50% and 55% (Fig. 2.5).

Although burning reduced biomass overall (Fig. 2.1) and reduced cover of *S. patens* in *S. lancifolia* and *P. virgatum* communities, there was no effect on cover of any of the dominant species in the *S. americanus* community (Figs. 2.4, 2.5 and 2.6). Though overall biomass was reduced, cover for *S. lancifolia* and *V. luteola* was enhanced (Fig. 2.4) in the *Sagittaria* community. Fencing increased overall biomass, but had no effect on cover of *S. patens, P. virgatum, S. lancifolia, or V. luteola* in any community (Figs. 2.4, 2.5, and 2.6). Only *S. americanus* cover was enhanced by fencing, relative to biomass increase (Fig. 2.6).

**DISCUSSION**

In this study, fencing increased biomass by approximately two fold in the three marsh community types (Fig. 2.2). Herbivory has been well documented to have strong effects on wetland vegetation. Herbivory on 200 one-year-old seedlings of
Figure 2.5. Effects of burning and fencing on plant cover of *Spartina patens* and *Panicum virgatum* in the *Panicum* community. (b=burned, n=unburned) Error bars represent ± 1 standard error.
Table 2.4. ANOVA values for cover data of the split-split plot design in a *Panicum virgatum* dominated marsh with *Spartina patens*.

<table>
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<tbody>
<tr>
<td><em>P. virgatum</em></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>BURN</td>
<td>1</td>
<td>3.39</td>
<td>0.1027</td>
</tr>
<tr>
<td>FENCE</td>
<td>1</td>
<td>4.66</td>
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</tr>
<tr>
<td>BURN*FENCE</td>
<td>1</td>
<td>0.22</td>
<td>0.6484</td>
</tr>
<tr>
<td><em>S. patens</em></td>
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<td>0.1785</td>
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<tr>
<td>BURN*FENCE</td>
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<td>6.87</td>
<td>0.0306</td>
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</table>
Figure 2.6. Effects of burning and fencing on plant cover of *Spartina patens* and *Scirpus americanus* in the *Spartina* community. (b=burned, n=unburned) Error bars represent ± 1 standard error.
Table 2.5. ANOVA values for cover data of the split-split plot design in a *Spartina patens* dominated marsh with *Scirpus americanus*.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>DF</th>
<th>F Value</th>
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</tr>
<tr>
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<td>BURN*FENCE</td>
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<td>0.7356</td>
</tr>
<tr>
<td><em>S. americanus</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BURN</td>
<td>1</td>
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baldcypress, *Taxodium distichum* (L.) Rich. resulted in 100% mortality in only two years in Manchac Marsh of Lake Pontchartrain (Myers *et al.* 1995). In the recently emergent delta islands of Louisiana, Visser (1991) showed that high densities of nutria can lead to significant reductions of plant biomass. After excluding herbivores for two years, biomass of *Sagittaria lancifolia* and *Ammannia coccinea* Rottboell increased significantly on the Atchafalaya Bay islands (Fuller *et al.* 1985). Results from exclosure studies conducted in mesohaline marshes by Chabreck (1959) indicated that plots protected from herbivory possessed 40% greater standing crop than unprotected plots. In an earlier study of the Pearl River (Taylor and Grace 1995), biomass increased 30% in plots protected from herbivory in fresh, oligohaline and mesohaline marshes. Since that earlier study, which took place in 1990-91, our observations indicated that populations of nutria and wild boar (*Sus scrofa*) have increased substantially. I hypothesized that the increase in nutria has resulted from decreased trapping. Wild boar appear to be recently introduced to the Pearl River, and it is possible that their increased activity is associated with a post-introduction population increase. Regardless of the cause, it appears that the impact of herbivores has tripled (based on the percentage of biomass increase resulting from fencing) in the Pearl River marshes.

The primary effect of fencing on species cover was a dramatic increase in *Scirpus americanus* in the *S. americanus* community (Fig. 5). This finding is consistent with the results of several other studies which indicate that *Scirpus americanus* is the preferred food of nutria (Linscombe *et al.* 1981), muskrat (O' Neil 1949), and snow
geese (Lynch et al. 1947). Thus, while the overall effect of herbivores in the Pearl River is a general reduction for all dominant species, they reduce *Scirpus americanus* to a greater extent.

Comparatively few studies have documented the effects of burning on Gulf coastal marshes (Chabreck 1982, Mendelssohn et al. 1988). In this study, burning led to a one-third reduction in biomass, much of which appeared to result from removal of senescent tissues and litter. This effect was markedly similar across habitats even though fire intensity varied among communities. In addition to a general effect on community biomass, burning had a significant effect on the cover of dominant species in the *Sagittaria lancifolia* and *Panicum virgatum* communities. In the *Sagittaria* marsh, *S. patens* cover was reduced while cover of *S. lancifolia* and *V. luteola* dramatically increased (Fig. 2.4). Mendelssohn et al. (1988) found that burning could suppress one species, particularly *S. patens*, while allowing a species that was an inferior competitor to increase. While it was expected that burning might increase herbivory due to a preference by herbivores for regrowth (Lynch 1941, Kays 1956, Smith and Kadlec 1985), there is no indication of such an effect in this study.

Richness was enhanced primarily by the combination of burning and fencing (Fig. 2.3). The greatest increase took place in the *Sagittaria lancifolia* community where richness increased from 8 to 13 species (Fig. 2.3 and Table 2.2). Taylor et al. (1994) found no significant effect of herbivory or fire richness in a degenerating mesohaline marsh. In contrast to our results, they found no interactive effect on richness.
coastal marshes. Schmalzer et al. (1991) found that species richness increased one year after fires in *Juncus roemerianus* Scheele and *Spartina bakeri* Merr. marshes. This change was primarily due to an increase in minor species. Such a result is not surprising since fire opens up the canopy, increases nutrient cycling (Hoffpauir 1961, Vogel 1977, Wright and Bailey 1982), removes litter, increases ash deposits, has little negative impact on seed survival and, therefore, often initiates or stimulates new growth (Kays 1956, Vogel 1977, Wright and Bailey 1982). In this case, limiting herbivory in burned areas may have created a special set of conditions suitable for enhanced species richness.

Overall, both fire and herbivory, common features of the Pearl River marshes, resulted in reduced biomass of all species. Grazing clearly led to a preferential reduction in *Scirpus americanus* but had few additional effects on species composition. Burning, in contrast, had more widespread effects on species composition by tending to reduce the prevalence of *Spartina patens* in all communities, though not always to a great degree. These results, therefore, are consistent with the hypothesis that burning acts to reduce the dominance of *Spartina patens*, a species generally regarded as unpalatable to most wildlife (Lynch et al. 1947, Kays 1956, Linscombe et al. 1981, Love 1985, Chabreck 1988). In addition to affecting biomass, burning (in the absence of grazing) led to a substantial increase in species richness which did not occur when grazing was permitted. Similar to the findings by Taylor et al. (1994), burning neither caused a major increase in the effects of grazing, nor promoted eatouts.
CHAPTER 3

EFFECTS OF HERBIVORES ON VERTICAL SOIL ACCRETION, SHALLOW SUBSIDENCE, AND SOIL ELEVATION CHANGES IN COASTAL LOUISIANA

INTRODUCTION

Vertebrate herbivores have been shown to have significant impacts on Gulf of Mexico coastal wetlands. Among the most intense examples of herbivore effects reported are those dealing with muskrat (*Ondatra zibethica*), nutria (*Myocastor coypus*) and snow geese (*Chen caerulescens*). It has been argued that vertebrate herbivores, particularly nutria, may constitute a threat to Louisiana coastal marshes (Chabreck 1988). In 1949, O'Neil reported a large scale eatout by muskrat in Southwestern Louisiana that resulted in a complete and permanent replacement of marsh by open water. During the winter of 1939-40, several square kilometers of *Typha* marsh of the Delta Refuge were consumed by geese. Unwanted plants were pulled up and tossed aside, tops and roots of food plants were discarded and rhizomes were dug up, cut into pieces and eaten. The marsh soil was broken to a depth of 13-20 cm (Lynch *et al.* 1947). In 1954 a 6 hectare eatout by snow geese led to the permanent loss of marsh at the Rockefeller Wildlife Refuge in Cameron Parish, Louisiana (Adams 1956). Studies conducted in the recently emerging islands of the Atchafalaya Delta in Louisiana have shown that high densities of nutria lead to significant changes in plant community composition (Fuller *et al.* 1985, Rejmanek *et al.* 1990, Shaffer *et al.* 1990, and Visser 1991). Chabreck (1959) found that mesohaline marsh plots that were protected from
herbivory possessed 40% greater standing crop than unprotected plots. However, in three community types in the coastal marshes of the Pearl River in Louisiana, above ground biomass was found to be 30% less in unprotected plots versus protected plots (Taylor and Grace 1995). Ford (1996) reported roughly a 50% reduction in biomass due to herbivory in *Sagittaria lancifolia, Panicum virgatum* and *Spartina patens* communities.

The effects of herbivores on coastal wetlands have been shown to depend on a number of factors. Linscombe *et al.* (1981) reported that as the density of nutria decreased in the brackish marsh of Vermilion Bay in Louisiana, *Spartina patens* (Aiton) Muhl cover decreased while *Scirpus americanus* Pers. (formerly *Scirpus olneyi* Gray), which is a preferred food of nutria, increased in cover. In the Atchafalaya Delta, area of cover of vegetation decreased while diversity increased in areas of intense herbivory that were also exposed to prolonged flooding (Shaffer *et al.* 1992). Ford (1996) reports richness significantly increased overall, in three communities of the Pearl River, when exposed to herbivory, while cover was significantly reduced only for *Vigna luteola, Panicum virgatum* and *Scirpus americanus*. Grace and Ford (1996) found that there were no long term effects of episodic flooding and salinity stress on *Sagittaria lancifolia* L. unless herbivory also became a factor; the combination of all three factors resulted in death of *S. lancifolia* individuals. Marsh community type can also be a factor in herbivore impacts. Above-ground biomass of *Panicum virgatum* L. was found to be significantly reduced by grazing in a fresh community while significantly increased in an oligohaline community (Taylor and Grace, 1995).
The long term consequences of herbivory for Gulf coast marshes is affected by the vulnerability of this region to wetland loss. Loss rates as high as 90.39 km² per year have been reported along the Louisiana Gulf coast (Gagliano et al. 1981). This loss is partially due to human influences, such as canal dredging, which directly replaces marsh with open water, and spoil bank building, which directly fills wetlands and alters sheet flow of water across the marsh. Additionally, natural factors contribute to the problem. Eustatic sea level rise, which is global sea level rise, is partially responsible for the problem. Small glacier melt and thermal expansion of oceans, both of which are a result of an overall increase in Earth's atmosphere temperature, contribute to eustatic sea level rise. Currently, the rate of eustatic sea level rise is 1.8 mm per year (EPA 1995). If the soil building processes cannot keep pace with sea level rise, coastal lands will eventually submerge.

Vertical soil accretion, which is the vertical dimension of marsh soil development, integrates both mineral and organic processes occurring on and within the uppermost part of the marsh substrates and is essential for maintaining marsh soil elevation. Rates of mineral sedimentation vary throughout the Louisiana coast. Seasonal riverine flooding, which is a source of sediment input, is severely inhibited by artificial levees constructed along the rivers. Locally, as the distance from the edge of a river or stream increases, the amount of mineral sediment deposited decreases (Baumann 1980). Geographically, as the distance from the mouth of major rivers increases, sediment loads carried by rivers into wetlands decreases. Some of the lowest rates of soil accretion in Louisiana occur between the mouths of the Mississippi and
Atchafalaya Rivers in the Barataria and Terrebonne basins (Baumann et al. 1984, DeLaune et al. 1990, Cahoon 1994, Cahoon and Reed 1995). Far from riverine sources, these areas rely on the resuspension of existing sediments in water bottoms adjacent to marshes and the subsequent deposition on the marsh surface as a source of mineral sedimentation (Wang et al. 1993, Reed 1989). Winter storms and summer tropical cyclones, such as hurricanes, are important mechanisms for mobilizing sediments in these areas (Baumann et al. 1984, Reed 1989, Wang et al. 1993, Cahoon et al. 1995).

Organic input to the soils is also an important component of soil accretion (DeLaune et al. 1990, Nyman et al. 1990). As much as 1,523 g/m² organic material per year is estimated as necessary to maintain soil elevation in the Mississippi River Deltaic Plain (Nyman et al. 1990), compared to 1,798 g/m² of mineral matter per year.

Subsidence, which is the sinking of land, can be broken down into two types. Regional subsidence is the change in elevation of an entire coast region relative to a stationary datum caused by secondary consolidation of deltaic sediments and tectonic processes, such as downwarping and faulting of tectonic plates. Shallow subsidence occurs through the reduction in volume of recently formed, surficial sediments in response to mechanical loading, compaction (dewatering and degassing), and decomposition of refractory organic material (Penland et al. 1989). Subsidence rates are relatively similar along the Gulf of Mexico coast of Louisiana with measurements of 1.29 cm per year at Grand Isle (Sasser et al. 1986), 1.11 cm per year average along the Louisiana coast (Nyman et al. 1990) and 1.2 cm per year in East Cove marshes near the Louisiana-Texas state line (Salinas et al. 1986).
There exist a number of possible mechanisms whereby herbivores can influence soil accretion and marsh loss. Removal of plant structures can result in increased erosion. Grubbing by herbivores tears up the root zone, which leaves the soils structurally vulnerable to erosion during storms. Reallocation of nutrients from the roots to rebuild above-ground structures can lead to less root biomass production and therefore a diminished contribution of the roots to the below-ground organic accretion. Trampling by animals directly contributes to the physical compaction of soils, at least in the top several centimeters. Ranwell (1964) reported that mineral sedimentation rates tend to be highest where plant density is the greatest, however Cahoon et al. (1995) reported the highest rate of vertical accretion was at Bayou Chitigue, which was the most deteriorated of three sites examined in that study. In areas of intense herbivory where eatouts occur, vertical soil accretion may be inhibited, erosion (Visser 1994) and subsidence could possibly increase resulting in an elevation deficit, which the loss of soil surface elevation (Cahoon et al. 1995); thus, increasing the rate of wetland loss. Additionally, it is believed that root zone may be expanding as biomass is produced in the growing season and contracting as plant subterranean structures deteriorate over winter. To date there have been no studies designed to examine the mechanism whereby herbivores affect soil building processes in the Gulf coast. This study examines the effects of large mammals on vertical soil accretion, shallow subsidence and soil elevation changes in a brackish marsh in areas of intense animal activity.
Study Site

The study site for this work was the Pearl River basin in Louisiana (Taylor and Grace 1995). The Pearl River drains about 2.3 million ha from south-central Mississippi into the extreme southeastern part of Louisiana. Study sites for this research were located near the mouth of the Pearl River, south of highway U.S. 90 in Louisiana, along the main channel of the river and a passage known as North Pass, which flows out of Little Lake. Marsh vegetation indicates a mesohaline community dominated by *Spartina patens* and *Scirpus americanus*, with river salinities ranging from 0 to 14 ppt yearly. Muskrat, rabbit (*Sylvilagus palustris*) and raccoon (*Procyon lotor*) are all common in the marsh, but observations indicate that these species appear to have minor impacts on plants and soils in the community. Exotic mammals such as nutria and wild boar (*Sus scrofa*) are present in large numbers and appear to be having an intense physical effect in the community.

METHODS

In order to document extreme impacts of nutria and wild boar herbivory on marsh soils and the plant community, ten eatout sites were selected in the brackish marsh during the spring of 1993. Fenced exclosures 4 m X 6 m were erected to establish the ungrazed treatment. Plastic coated 1.2 m wide garden fence with 2.5 cm² openings was buried in trenches 30 cm deep, with the intent of discouraging burrowing by animals. Boards 2.4 m long and 5 m X 10 cm thick were inserted into the soil to act as corner posts and to support the fences along the six meter sides. Gateways were cut in the middle of each fence to aid with entry into the exclosures and metal clips...
fashioned from bailing wire held the fence gates closed. Boardwalks were placed inside the exclosures, 1.5 m from the midline between treatment plots and parallel to the fence line. Boardwalks were set up in the grazed treatment in positions which mirrored the ungrazed treatment. These were used to limit impacts on the marsh soil surface during sampling. Boardwalk cross overs were erected between treatments, perpendicular to treatment boardwalks. These were elevated one meter above the marsh surface. Fence posts 1.8 m long with 5 cm X 10 cm cross braces were used as bases for all boards, which were 5 cm X 24.5 cm X 245 cm. Sampling started in June 1993, over a month after the sites were established, and was continued quarterly until June 1995. High water in September 1994 prevented most data collection during this month. Above-ground biomass was estimated nondestructively using regression in permanent 1 m² vegetation plots.

Vertical soil accretion was measured using a soil marker technique. An artificial soil-marker horizon of feldspar clay was laid down on the soil surface in June of 1993 in 0.25 m² plots, which were marked with 2.54 cm diameter PVC poles. The accuracy of this technique is adequate to detect seasonal changes in vertical soil accretion in marshes (Baumann et al. 1984, Cahoon and Turner 1989, and Cahoon 1994). Quarterly samples were collected from August 1993 until March 1995. The intent was to collect data for two years, however intense animal activity resulted in the premature destruction of all accretion plots in fall of 1994.

Accretion soil cores were collected with a cryogenic coring probe (Cahoon et al. in press), consisting of a copper tube with a 30 caliber bullet in the end, which was
inserted into the ground. Liquid nitrogen was piped through a hose from a 25 liter pressurized dewar flask into the probe until the soil core was frozen. This method eliminates compaction of the soil core during sampling. Cores were extracted and scraped clean to expose the feldspar layer. The distance from the top of the feldspar layer to the top of the new soil surface was measured using calipers. Up to four measurements were made on each core (Knaus and Cahoon 1990). Cores were replaced in sample holes and allowed to thaw, thus preventing sediment trapping by sample holes. Used cores were marked with orange metal surveying flags so that they could be avoided in future samplings.

Aluminum irrigation pipes 7.62 cm wide and 6.3 m long were inserted vertically into the soil in the middle of each site. Roughly 30 cm of pipe was left exposed above the soil surface. Concrete was poured into each pipe filling within 2.5 cm of the top. Small notched adapter pipes were inserted into each irrigation pipe with the notches oriented so that a sediment-erosion table (SET) (Boumans and Day 1993) could be placed in two positions in both grazed and ungrazed treatments, for a total of four positions. The SET was set in the same place for each sampling event for the four positions with the aid of the notched adapter in each base. The arm is adjustable so that the device can be placed in the exact same position each time. A bubble level was used to verify the position of the SET. Nine pins were lowered through the plate, located at the end of the arm, until contact was made with the soil surface. The distance from the plate to the top of each pin was measured. If the distance increased, the marsh soil surface elevation was increasing. If the distance decreased, then surface elevation was
decreasing. Measurements were made in two positions in each treatment, with the SET moved 90 degrees at each measurement. SET data were collected through December 1995. However, due to high water in September 1995, SET data were instead collected in October 1995. Shallow subsidence was calculated as the difference between vertical accretion and surface elevation change (Cahoon et al. 1995).

Bulk density samples were collected using an acrylic coring tube 10 cm in diameter and 0.5 m long (Hargis and Twilley 1994). The coring tube had a sharpened metal edge to aid with cutting through the soils. Samples were collected quarterly, starting in June 1993 and ending in June 1995. The samples were sectioned into 5 cm segments. Potting soil was placed in sample holes to reduce sediment trapping. Samples were placed in resealable plastic bags and returned to the laboratory where they were dried at 80°C until they reached a constant weight. Densities were calculated from weight and volume measurements. Percent mineral and organic matter were estimated by ashing sub-samples of the bulk density cores at 550°C for 24 hours.

Root and rhizome biomass production was estimated by collecting roots and rhizomes bi-monthly. Cores were established by taking soil cores in the same manner as the bulk density cores, however the soils were discarded and clean sand was placed in 30 cm deep holes. Every other month, cores were extracted and cut into 5 cm sections. Fresh clean sand was replaced in the core holes. Samples were placed in labeled resealable plastic bags and returned to the laboratory where they were frozen until they could be processed. Samples were thawed and washed over a fine mesh sieve. Roots and rhizomes were separated and picked out from miscellaneous debris in glass pans.
with forceps. Samples were then dried at 80°C for 48 hours and weighed to the nearest tenth of a gram. Dead tissues were originally separated from live, but this consistently amounted to less than 0.01 g of material, so the practice was not continued after the first sampling period.

The thickness of the root zone was measured using a variation of the SET technique. A PVC plate with the same dimensions as the SET head was placed in the ground under the root zone directly below the position of the SET head half the distance between the SET measuring positions for each treatment. A notch was cut in the soil the same size as the PVC plate, then a slit was cut below the root zone, which is approximately 30 cm thick. The PVC plate was inserted into the slit (Fig. 3.1). The plates were allowed to settle from October 1993 until December 1993 when the first measurements were made. Long pointed pins were used to pierce the soil until they made contact with the buried PVC plate. Root zone thickness was calculated using the following equation and by measuring pin height and the height of the SET head then subtracting pin height, SET head height and SET head thickness from the pin length:

\[
\text{Pin length} - \text{Pin height} - \text{SET head thickness} - \text{SET plate height} = \text{Root zone thickness.}
\]

Measurements were made at the same quarterly intervals as all other quarterly measurements.

In August 1994, nutria invaded a fenced exclosure by digging under the buried fence. Virtually all vegetation was consumed within 48 hours. Within 2 months, 7 out of 10 exclosures had been breached. Therefore, only data for the first year of sampling
Figure 3.1. Schematic of SET and PVC plate in soil for measuring of root zone expansion.
were used to compare treatments. Data collection continued in the grazed treatment for another year since this treatment had not been altered from its natural state.

**Statistical Analysis**

Data analyses were performed using SAS (SAS Institute, Cary NC). The experimental design was randomized block with grazed and fenced (ungrazed) treatments located as natural pairs at each of ten sites with the marsh. Dependent variables (litter, biomass, soil elevation, vertical soil accretion and subsidence) were examined for univariate normality and homogeneity of variance prior to analysis of variance. Normality of residuals was evaluated using the Wilk-Shapiro test (Sokal and Rohlf 1981). Homogeneity of variances were evaluated using discriminant function analysis on the model residual with a chi-square test criterion (SAS Institute, Cary, NC). Subsidence values were transformed to \( \ln(\text{subsidence}+25) \) in order to achieve normality and homogeneity of variances for the analysis. Values were detransformed for presentation (Sokal and Rohlf 1981). Other variables were found to be normal and homoscedastic. Following the recommendation of Yoccoz (1991), an alpha level of 0.10 was used to evaluate hypothesis with primary emphasis placed on magnitude of effect as indicative of biological significance.

**RESULTS**

Herbivory significantly reduced plant biomass by the end of one year \((p=0.0002)\). Roughly four times as much biomass grew inside the ungrazed plots \((330.37 \, \text{g/m}^2)\) as in the grazed \((85.00 \, \text{g/m}^2)\) for *Spartina patens*. Nearly six times as
much biomass grew inside the ungrazed (172.40 g/m²) plots as in the grazed plots (27.32 g/m²) for *Scirpus americanus* (see also chapter 4).

Dead biomass, which included both plant litter on the soil surface and senescent structures still on plants, varied between treatments. At the end of one year, 58% more dead biomass of plant material (*p*=0.0828) was collected in the grazed plots (1063.20 g/m²) than in the ungrazed plots (614.09 g/m²) (Fig. 3.2).

Marsh vertical soil accretion was found to be comparable between grazed and ungrazed plots at the end of one year (Fig. 3.3, *p*=0.6022). In the grazed plots an average of 2.48 cm of soil accreted while an average of 1.82 cm accreted in the ungrazed plots (Table 3.1). Subsidence was calculated to be greater in the grazed plots (2.26 cm) than in the ungrazed (1.07 cm), resulting in an increase in soil elevation (relative to the fixed SET pipe) of 0.75 cm in ungrazed plots, but only 0.22 cm in grazed plots (Fig. 3.4). Subsidence of the marker horizon was calculated to be 12.64 mm per year, while subsidence of the PVC plate was measured to be 21.21 mm per year (Fig. 3.5), between December 1993 and December 1994. Rates of subsidence varied seasonally with the greatest difference between the subsidence of the marker horizon and the PVC plate occurring between March and June 1994 (Fig. 3.5).

Both subsidence and soil elevation changes varied with time (Fig. 3.6). The difference between elevation and vertical soil accretion is subsidence. Vertical accretion was sufficient in both treatments to offset subsidence. For the first year, there appeared to be little difference between treatments in the amount of change of soil elevation. From June 1994 until December 1995, soil elevation decreased 10 cm, then
Figure 3.2. Biomass of litter for permanent 1 m² plots for both grazed and ungrazed treatments at the end of one year. Error bars represent ± 1 standard error.
Figure 3.3. Vertical soil accretion rates for both grazed and ungrazed treatments over one year.
Table 3.1. ANOVA values for accretion measurements of herbivory treatments in grazed and ungrazed plots.

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Figure 3.4. Summary of vertical soil accretion, shallow subsidence and soil elevation changes for both grazed and ungrazed treatments at the end of one year.
Figure 3.5. Absolute values for subsidence of the feldspar marker horizon and PVC plate, by months, for one year.
Figure 3.6. Quarterly soil elevation and subsidence mean values for (A) ungrazed plots and (B) grazed plots over two years. Error bars represent ± 1 standard error.
Table 3.2. ANOVA values for soil elevation measurement averages of herbivory treatments in grazed and ungrazed plots.

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increased approximately 20 cm, then decreased 10 cm again in the grazed plots (p=0.0379. Table 3.2). Due to intense animal activity, soil accretion plots were destroyed in the grazed areas, therefore, no data are available to measure subsidence beyond December 1994. The large increase in elevation in the spring of 1995 may be due to sedimentation from a large flood event which took place in the area and which resulted from nearly 12 cm of rain falling in a 36 hour period (Fig. 3.6).

Though bulk densities for the 0-5 cm increment in the upper 15 cm of the soil were consistently greater for the grazed plots than for the ungrazed (Fig. 3.7), the differences were not significant (p=0.3028. Table 3.3). Bulk density of the upper 5 cm of soil ranged from 0.13 to 0.32 g cm$^{-3}$ between treatments (Fig. 3.7A). During the study, only the June 1994 0-5 increment showed marginally significant differences in the means (p=0.0829, Table 3.3). In the 5-10 cm increment, bulk densities ranged from 0.18 to 0.38 g cm$^{-3}$ between treatments. Differences were significant between grazed and ungrazed plots (p=0.0123, Table 3.3) at the end of this portion of the study in December 1994. For the 10-15 cm increment, bulk densities ranged between 0.18 and 0.49 g cm$^{-3}$ and differences between plots were significant for the December 1994 sampling period (p= 0.0024, Table 3.3).

Percent organic matter was consistently greater in the ungrazed plots than in the grazed plots for all 5 cm increments in the upper 15 cm of the soil (Fig. 3.8). In the upper 5 cm of soil, values ranged between 60% and 37% in the ungrazed plots and between 62% and 31% in the grazed plots (Fig. 3.8A). Mean differences were significant at the March 1994 sampling (p=0.0330) but were not by the end of the study...
Figure 3.7. Bulk density means for grazed and ungrazed treatments in 5 cm increments to a depth of 15 cm. Error bars represent ± 1 standard error.
Table 3.3. ANOVA values for average soil bulk density measurements of herbivory treatments in grazed and ungrazed plots.

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Figure 3.8. Percent organic matter means for grazed and ungrazed treatments in 5 cm increments to a depth of 15 cm. Error bars represent ± 1 standard error.
Table 3.4. ANOVA values for average percent organic matter measurements of herbivory treatments in grazed and ungrazed plots.

<table>
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<td>0.00</td>
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<td>10-15 cm</td>
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<td>1994</td>
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<td></td>
<td></td>
</tr>
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</tr>
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<td>10-15 cm</td>
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<tr>
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<td>2.14</td>
<td>0.1606</td>
</tr>
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<td></td>
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(p=0.1606, Table 3.4). For the 5-10 cm increment, percent organic matter ranged between 60% for both set of plots to 28% in the ungrazed and 25% in the grazed plots (Fig. 3.8B). Mean differences were not significant (p=0.6434, Table 3.4). In the 10-15 cm increment, percent organic matter ranged between 58% and 25% in the ungrazed plots and between 59% and 26% in the grazed plots (Fig. 3.8). Mean differences between plots were significant during the June 1994 sampling (p=0.0853), but were not by the end of the study (p=0.8402, Table 3.2).

Root biomass production overall was significant between treatments by the end of the study (p=0.0529, Table 3.5). Greater biomass was produced in the ungrazed plots than in the grazed plots, for the 0-5 cm increment in the upper 15 cm of the soil (Fig. 3.9). Mean biomass ranged between 0.04 and 2.1 g cm\(^{-3}\) in the ungrazed plots and between 0.2 and 1.3 g cm\(^{-3}\) in the grazed plots for the upper 5 cm increment (Fig. 3.9A). In the 5-10 cm increment mean root biomass ranged between 0.1 and 1.4 g cm\(^{-3}\) for the ungrazed plots and between 0.1 and 0.5 g cm\(^{-3}\) in the grazed plots (Fig. 3.9B). In the 10-15 cm increment, root biomass ranged between 0.1 g cm\(^{-3}\) for both sets of plots to 1.3 and 2.7 g cm\(^{-3}\) in the ungrazed and grazed plots, respectively (Fig. 3.9C).

From March to June 1994 root zone thickness decreased in the grazed treatments but increased in the ungrazed treatment (Fig. 3.10). Surface accretion and soil elevation changes in the grazed treatment are compared to root zone thickness changes in the grazed treatment in Figure 3.11. Surface accretion values represent actual amounts for the specific sampling times, instead of cumulative amounts presented above. From March to December 1994, soil elevation, accretion and root zone thickness changes
Table 3.5. ANOVA values for average root biomass production measurements of herbivory treatments in grazed and ungrazed plots.

<table>
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<td></td>
</tr>
<tr>
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<td>0-5 cm</td>
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</tr>
<tr>
<td></td>
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<tr>
<td></td>
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<td></td>
<td>all</td>
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</tr>
<tr>
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</tr>
<tr>
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<tr>
<td>1994</td>
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<td></td>
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</tr>
<tr>
<td>February</td>
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</tr>
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<td></td>
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<td></td>
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Figure 3.9. Root biomass means for grazed and ungrazed treatments in 5 cm increments to a depth of 15 cm. Error bars represent ± 1 standard error.
Figure 3.10. Difference of mean values of root zone thickness change for grazed and ungrazed treatments for March and June 1994.
Figure 3.11. Comparison of soil elevation, root zone thickness and soil accretion mean changes in grazed plots. Error bars represent ± 1 standard error.
increase and decrease with similar patterns. In June 1994, all three decrease and in December a large increase occurs in all three measurements. From December 1994 to March 1995, both the soil elevation and root zone thickness decrease similarly and between March and June 1995 both show a strong increase (Fig. 3.11).

DISCUSSION

In the Pearl River mesohaline marsh, herbivores had dramatic effects on both plants and soils. Biomass of *Spartina patens* was reduced by 75% and *Scirpus americanus* by 85% in grazed plots compared to ungrazed. Due to a decrease in demand for fur worldwide, trapping in Louisiana has declined from 986,014 animals harvested in 1986-1987 to 171,470 in 1994-1995 (Louisiana Wildlife and Fisheries Department). Field observations at the Pearl River during this time indicate that populations of nutria have increased substantially.

Organic input to the soil is an important component of soil accretion (DeLaune et al. 1990, Nyman et al. 1990). Removal of plant tissues before they become part of the litter layer may reduce litter production (Crawley 1983). Herbivores, however, can waste nearly ten times as much plant material as they consume (Crawley 1983). If nutria are increasing the rate of litter fall, as shown in this study, it is likely that this organic matter is becoming part of the surface accretion. In order to ascertain the amount of dead plant biomass available to marsh soils, both litter on the marsh surface and senescent tissues on standing plants were collected. Senescent structures, such as leaves or stems from both standing plants and litter on the soil surface, would potentially become part of the soil litter layer. However, by sampling once a month
throughout most of the year and twice a month in the fall, it is possible to miss some of
these structures as they fall. Also, if a sedimentation event occurred, then litter would
be buried and not counted in the litter measurement. Therefore, all biomass was
collected once tissues were visually determined to be senesced. Fences were examined
to determine if they were acting as barriers to the natural movement of litter with flood
surges. Virtually no plant material was found hanging on the fences or trapped at their
bases. Therefore, it was assumed that the fences were not acting as barriers to the
natural movement of litter across the soil surface. Nearly twice the amount of litter was
collected in the grazed treatment compared to the ungrazed treatment (Fig. 3.2).
Therefore, a greater amount of organic material, in the form of litter, was available to
be incorporated into the soil surface.

The sources of mineral sediments at the Pearl River were not examined,
however there are several possibilities. Sources of mineral sedimentation include:
suspended sediments from upstream erosion carried by river and bayou currents
(Templet and Meyer-Arendt 1988), resuspended bottom sediments from nearby rivers
and bayous (Wang et al. 1993), marine inputs from tidal flooding, the resuspension of
sediments within in a marsh during flood events (DeLaune et al. 1983), and from
resuspension of sediments from these sources during winter storms (Reed 1989) and
summer tropical cyclones (Baumann et al. 1984, Rejmanek et al. 1988, Wang et al.
1993). Whatever the source, though not significant, vertical soil accretion at the Pearl
River was nearly fifty percent greater in the grazed (2.48 cm) compared to the ungrazed
plots (1.82 cm) at the end of one year (Fig. 3.3). These findings are consistent with
Cahoon et al. (1995) who found the highest rate of vertical accretion in areas of low elevation relative to mean sea level in the most deteriorated marsh of that study.

Shallow subsidence was greater in the grazed plots (2.28 cm) compared to the ungrazed plots (1.07 cm) (Fig. 3.4). Herbivory can result in greater input of ambient light, which can increase surface temperatures and enhance root and rhizome decomposition. Also, herbivory causes a reallocation of effort for the re-growing of above ground structures, which can lead to less effort by plants in maintaining a healthy root system. Part of the explanation for such a strong effect may be because nutria tend to favor specific locations when they feed. Once they graze an area, they continue to feed there until all plants are gone or they are pushed out by other animals (Kays 1956, Ehrlich 1965, Willner 1982). This means that nutria will constantly be tracking over the same areas and soils can be locally compacted. Fuller et al. (1985) observed in the islands of the Atchafalaya Delta, that nutria caused damage in the form of trails. In the Pearl River marshes, trail depressions up to 1 cm deep were observed in areas of heavy nutria (and boar) activity. This form of physical compaction can contribute to shallow subsidence, which lowers the marsh soil surface. Areas of even slightly lower elevation are higher in sensitivity to flooding duration and frequency. Both autochthonous and allochthonous mineral sediments will collect and vertical soil accretion will increase during these flood events (Cahoon and Reed 1995). Soil elevation and hydroperiod can also influence above and below-ground biomass (Reed and Cahoon 1992), which will affect sedimentation rates. Overall, herbivore activity led to slightly more than three times as much shallow subsidence in the grazed plots than in the ungrazed plots.
Subsidence of the marker horizon and the PVC plate were compared. Between December 1993 and December 1994, the marker horizon was calculated to have subsided 12.46 mm. The PVC plate, which was positioned below the root zone, subsided 21.21 mm (Fig. 3.5). This indicates that subsidence, over the course of one year, occurred at a faster rate below the root zone. Though the mechanism is not clear, it appears that processes in the root zone may be slowing yearly subsidence rates. These rates varied seasonally as well. Between December 1993 and March 1994, subsidence rates between the marker horizon and the PVC plate were essentially the same. Between March and June 1994, at the start of the growing season, the PVC plate subsided 1 cm more than the marker horizon (Fig. 3.5). Most of the root zone is between the PVC plate and the marker horizon. It appears that processes in this zone are having a strong seasonal effect. Between June and December, the root zone subsided at a rate faster than the soils below the PVC plate, although the mechanisms causing this seasonal difference are not clear.

In spite of grazing effects, soil surface elevation increased with time for both treatments. Vertical soil accretion was sufficient to offset the effects of subsidence, even in areas where subsidence was enhanced by intense animal activity. The net result was an increase in soil elevation of 0.75 cm in the ungrazed treatment, but only 0.22 cm in the grazed. It is likely that both increased mineral sedimentation, as a result of a greater frequency and a longer duration of flooding in areas lowered by nutria and wild boar, and increased organic input from wasted plant matter, contributed to soil accretion. Thus, vertical soil accretion offset subsidence for both sets of plots, resulting
in an increase in soil elevation. The 2.2 mm increase in the grazed plots is roughly sufficient to keep pace with eustatic sea level rise.

Bulk density values were found to be greater than those reported by Cahoon and Turner (1989), DeLaune et al. (1989) and Nyman et al. (1990) in the Louisiana deltaic plain. Those areas are in a region of rapid degradation, largely due to restricted sedimentation as a result of the levee system preventing seasonal flooding. Soils at the Pearl River, however, receive nearly twice the sediment input than most of the deltaic plain (Hatton et al. 1983, DeLaune et al. 1990, Nyman et al. 1990). The only significant difference between treatments was in the 5-10 cm increment in December 1994 (Fig. 3.6), where the grazed treatment had a greater bulk density. Nyman et al. (1990) found that the network of organic material, which would be greatest in soils with the lowest bulk densities, was strongest in a zone from a few centimeters below the soil surface to a depth of approximately 10-20 cm. This is a common depth of the root zone in the deltaic marshes of Louisiana.

As plant mortality increases, the root network can degrade or be lost altogether, which can ultimately lead to soil disintegration. Organic matter contributes more to soil structure than a similar volume of mineral matter, because organic matter is living roots and rhizomes or plant structures that, though partially decomposed, still retain much of their structural integrity (Nyman et al. 1990). There was no significant difference in percent organic matter between treatments at any of the 5 cm increments for any of the sampling times. This is consistent with results found in the Mississippi Deltaic Plain (Nyman et al. 1990). However, percent organic matter was usually greater in the
ungrazed plots than in the grazed plots (Fig. 3.8). This supports data indicating lower bulk densities in ungrazed plots.

Roots, rhizomes and decomposing litter all contribute to the soil network (Nyman et al. 1990). Herbivory can result in lower root production. McNaughton and Georgiadis (1986) demonstrated that plants will translocate effort into regrowth of above-ground structures when preyed upon, thus limiting root biomass production. Root biomass production overall was significantly different between treatments in June (p=0.0362) and August 1994 (p=0.0529, Fig. 3.9), but not for any given increments, with the exception of the 5-10 cm increment in June 1994 (p=0.0231, Table 3.5). If herbivores are increasing losses due to a greater effort by the plants in the growth of above-ground structures versus below-ground structures, then this can contribute to either less root and rhizome biomass addition to the root zone. Reduction of root volume in the root zone can result in a reduction in the volume of the soil below-ground, which seems more important to the structure than biomass. This, unfortunately, was not measured.

The change in thickness of the root zone was different between grazed and ungrazed plots (Fig. 3.10). Between March and June 1994, the grazed plots decreased an average of 5 mm, while ungrazed plots increased in thickness an average of 10 mm (Fig. 3.10). This difference indicates that losses were still taking place in areas of intense herbivory while the protected plots had already begun to build new biomass. Plants in ungrazed plots have not had to use below-ground resources in the regrowth of above-ground structures lost to herbivores. Roots and rhizomes had not been preyed
upon and the soils had not been dug up, exposing buried tissues to the atmosphere. This results in no below-ground removal of structures, decreased root and rhizome growth or increased decomposition and degradation of plant materials in the soil.

Volume of the root zone changed over time (Fig. 3.11). This followed a similar pattern to that of the soil elevation changes for the grazed plots. Though surface accretion also followed a similar pattern, these data were subtracted from the calculation of root zone thickness and therefore, would seem not to be contributing to this layer (Fig. 3.11). It is important to note that overall increase in soil elevation from June to December 1994 was less than the change in root zone thickness. This indicates that the root zone was likely expanding both upwards and downwards during this time. Soils are fairly loose beneath the root zone. It is possible that the root zone is pushing down on these soils, which are still in a fairly rapid rate of subsidence, thus increasing compaction locally. If surface accretion was roughly 30 mm (Fig. 3.11C) and root zone expansion was roughly 30 mm (Fig. 3.11B) and soil elevation only increased by approximately 16 mm during the same time period, then subsidence was at a greater rate than indicated by the difference between the marker horizon and soil elevation measurements made with the SET.

In general, it appears that the thickness of the root zone increased over the growing season (Fig. 3.11B). It also decreased from March to June 1994 and from December to March 1995. During this time, few plants were still green. Virtually no new growth had occurred since the close of the previous growing season, in late November or early December. Animals continued to prey upon surface structures,
mostly of *Spartina patens*, which had a thick root system. It is possible that the root zone was growing slower in areas of intense herbivory as plants translocate resources to regrow above-ground structures lost to herbivory (McNaughton and Georgiadis 1986). Also, roots and rhizomes, primarily of *Sagittaria lancifolia* were preyed upon by nutria and wild boar. This action could serve to disrupt the root zone, possibly increasing decomposition of roots, rhizomes and buried above-ground structures. Also, water depths were higher from April to October, with water often above the soil surface to as much as 30 cm deep. From November to March, water levels dropped, typically below the soil surface. Soils may respond like a sponge, increasing in volume during periods of higher water, and then decreasing like a sponge as it dries out, during periods of lower water, when soils are exposed to the air (Kearny and Ward 1986). During these periods of low water, decomposition of plant tissues in the soil may increase as oxygen become more available to decomposers, resulting in a reduction of the volume of the root zone.

In conclusion, mammalian herbivores dramatically impacted the vegetation in the brackish marsh of the Pearl River. Vertical soil accretion increased more in grazed plots than in ungrazed, but this seemed to be a result of enhanced subsidence. Overall, soil elevation increased in both grazed and ungrazed plots, with the greatest increase in the protected plots. Still, soil elevation increases in grazed plots were greater than eustatic sea level rise. However, as long as adequate sedimentation occurs, areas with heavy herbivory can increase the soil elevation at a sufficient rate to keep pace with rising eustatic sea level. The effects of deep subsidence were not examined in this study.
and are likely are contributing to the overall subsidence. Expansion and contraction of the root zone seems to be contributing to these effects, though their exact contribution has not yet been determined.
INTRODUCTION

Vertebrate herbivores play a central role in plant community dynamics (Crawley 1983) and have a range of profound effects on community structure and composition (Chapin et al. 1987). Hik et al. (1992) demonstrated that plant biomass increased in Manitoba salt marsh plots protected from herbivory by lesser snow geese. Gauthier et al. (1995) found, in grasslands of Canada's Northwest Territory, that though grazed grasses grew new foliage, net above-ground primary production (NAPP) remained roughly the same as ungrazed grasses. Grassland plots in New Zealand had an increase in cover when protected from grazing animals (Allen et al. 1995). Species diversity may also be affected by grazing. In an abandoned agricultural field at the University of Oxford's Wytham estate, Gibson et al. (1991) demonstrated that diversity decreased in ungrazed areas, after only a couple of years, while diversity increased in adjacent grazed areas. In the grasslands of northern Israel, plant species richness increased in areas grazed by cattle, versus those protected from grazing (Noy-Meir 1995).

In Gulf of Mexico coastal wetlands, vertebrate herbivores have been shown to have significant impacts on plant communities which depend on a number of factors. Marsh community type, for example, can be a factor in herbivore impacts. Above-ground biomass of *Panicum virgatum* L. was found to be significantly reduced in a fresh
community while significantly increased in an oligohaline community (Taylor and Grace, 1995). Studies conducted in the recently emerging islands of the Atchafalaya Delta in Louisiana have shown that high densities of nutria lead to significant changes in plant community composition (Fuller et al. 1985, Rejmanek et al. 1990, Shaffer et al. 1990, and Visser 1991). Linscombe et al. (1981) reported that as the density of nutria decreased in the brackish marsh of Vermillion Bay in Louisiana, Spartina patens (Aiton) Muhl cover decreased while Scirpus americanus Pers. (formerly Scirpus olneyi Gray), which is a preferred food of nutria, increased in cover. In the Atchafalaya Delta, cover of vegetation decreased while diversity increased in areas of intense herbivory that were also exposed to prolonged flooding (Shaffer et al. 1992). Ford (1996) reports that in three communities of the Pearl River that richness significantly increased overall, while cover was significantly reduced only for Vigna luteola, Panicum virgatum and Scirpus americanus. The objective of this study was to examine the effects of herbivory on plant biomass, frequency of occurrence of species, changes in plant species richness, and changes in diversity and community composition.

**Study Site**

The study site for this work was the Pearl River basin in Louisiana (Taylor and Grace 1995). The Pearl River drains about 2.3 million ha from south-central Mississippi into the extreme southeastern part of Louisiana. Study sites for this research were located near the mouth of the Pearl River, south of highway U.S. 90 in Louisiana, along the main channel of the river and a passage known as North Pass, which flows out of Little Lake. Marsh vegetation indicates a brackish community dominated by
Spartina patens and Scirpus americanus, with river salinities ranging from 0 to 14 ppt yearly. Muskrat (Ondatra zibethica), rabbit (Sylvilagus palustris) and raccoon (Procyon lotor) are all common in the marsh, but observations indicate that these species appear to have minor impacts on plants in the community. Exotic mammals such as nutria (Myocastor coypus) and wild boar (Sus scrofa) are present in large numbers and appear to be having an intense physical effect in the community.

METHODS

In order to document extreme impacts of nutria and wild boar herbivory on marsh soils and the plant community, ten eatout sites were selected in the brackish marsh during the spring of 1993. Fenced exclosures 4 m X 6 m were erected to establish the ungrazed treatment. Plastic coated 1.2 m wide garden fence with 2.5 cm² openings was buried in trenches 30 cm deep, with the intent of discouraging burrowing by animals. Boards 2.4 m long and 5 m X 10 cm thick were inserted into the soil to act as corner posts and to support the fences along the six meter sides. Gateways were cut in the middle of each fence to aid with entry into the exclosures and metal clips fashioned from bailing wire held the fence gates closed. Sampling started in June 1993, over a month after the sites were established, and was continued quarterly until June 1995.

Above-ground biomass of Scirpus americanus and Spartina patens was estimated non-destructively in permanent 1 m² plots using height-biomass regressions, derived from harvested samples outside the experimental plots (Grace et al. 1992). As measure of plant cover, changes in the abundance of the dominant species was measured
in permanent 1 m² plots, by counting the number of 1/16 m² subplots containing each species. The number and presence or absence of each species was recorded monthly (Diaz et al. 1992). Changes in the community were analyzed using detrended correspondence analysis (McCane and Metford 1995). A Wilcoxon Signed Ranks Test was conducted to determine significant differences between treatment plots for each species (Conover 1980). Plant litter, which included attached senescent structures, was collected from additional permanent 1 m² plots. Collections were made monthly from January through August and bi-weekly from September through December. This was to ensure that no material was lost during the fall senescence. Samples were dried for 48 hours at 80°C and weighed to the nearest tenth of a gram.

RESULTS

Herbivory significantly reduced biomass by the end of one year (p=0.0002). Roughly four times as much plant biomass grew inside the ungrazed plots (330.37 g/m²) as in the grazed (85.00 g/m²) for Spartina patens. Nearly six times as much biomass grew inside the ungrazed (172.40 g/m²) plots as in the grazed plots (27.32 g/m²) for Scirpus americanus (Fig. 4.1). In addition, differences between ambient light and light levels reaching the soil surface were dramatic between plots. Nearly 75% of ambient light reached the soils in the grazed plots while only 17% reached the soils in the ungrazed plots (Fig. 4.2).

Initial average richness in grazed plots was roughly 5 species compared to 6 species in ungrazed plots. By the end of sampling, August 1994, grazed plots had 6 species while ungrazed plots had been reduced to an average of 4 species (Figure 4.3).
Figure 4.1. Mean biomass for *Spartina patens* and *Scirpus americanus* for grazed and ungrazed treatments at the end of one year. Error bars represent ± 1 standard error.
Figure 4.2. Mean percent of ambient light reaching the soil surface for grazed and ungrazed treatments at the end of one year. Error bars represent ± 1 standard error.
Figure 4.3. Mean overall richness for two growing seasons for grazed and ungrazed plots. Error bars represent ±1 standard error.
Detrended correspondance analysis revealed little overall change in the community in the grazed plots (Fig. 4.4). Virtually all of the plots in August 1994 fell within the range of the grazed plots in August 1993 in a two-axis ordination. Only two plots differed greatly in composition and frequency of occurrence of species. In contrast, in the ungrazed plots, the community shifted in species composition and frequency of occurrence over time with four out of ten of the plots in August 1994 falling outside the range of the plots in August 1993 (Fig. 4.5).

Overall species means, without regard to date or treatment, were graphed on a log$_{10}$ scale to show abundance (Fig. 4.6). Species seemed to fall into five distinct groupings. The first contain *Spartina patens* (SPPA) and *Scirpus americanus* (SCAM) and were considered to be dominant species. The second group contains *Sagittaria lancifolia* (SALA) and *Spartina cynosuroides* and *S. alterniflora*. The two *Spartina* species were grouped together as *Spartina* sp. because they were difficult to distinguish as immatures and were called SPSP in this document. These species, including *Sagittaria lancifolia* are considered to be co-dominants. The next grouping contained *Eleocharis parvula* (ELPA) and *Scirpus validus* (SCVA) and are referred to as occasional co-dominants. The fourth group contained eight species and are called common sub-ordinants and the fifth group contained 10 species which only rarely appeared and were called occasionals (Fig.4.6)
Figure 4.4. Detrended correspondance analysis results for the grazed plots in August 1993 and 1994.
Figure 4.5. Detrended correspondance analysis results for the ungrazed plots in August 1993 and 1994.
Figure 4.6. Rank order abundances of overall means for all species on a log_{10} scale.
A signed rank test indicated that the frequency of occurrence in the 16 subplots of the permanent 1 m² vegetation plots differed between grazed and ungrazed plots for the two dominant species. Within five months of fence construction, *Spartina patens* was found in all 16 subplots in the ungrazed treatments (Fig. 4.7). However at that time *S. patens* occurred only in 12 of 16 subplots in the grazed treatment. In the fall of 1993, when other food species started to senesce, the occurrence of *S. patens* declined in the grazed plots until March of 1994. Then, at the start of the growing season, occurrence of *S. patens* increased until July 1994. The herbivory effect was significant (Table 4.1).

Herbivory effects on *Scirpus americanus* were significant (p<0.01) and dramatically different from effects on *S. patens* (Fig. 4.7, Table 4.1). Like *Spartina patens*, once fences were erected, *S. americanus* occurred in most subplots of the permanent plots. In the grazed treatment, however, it declined steadily from August of 1993 until January 1994. Presence in the subplots did not start to decline in the ungrazed treatment until November 1993, when *S. americanus* naturally senesces (Fig. 4.7). Unlike the grazed treatment, there was partial cover in the ungrazed treatment throughout the winter. There was growth in both treatments starting in February 1994, however by April *S. americanus* occurred in most subplots of the ungrazed treatment, but was very slow to recover in the grazed treatment, not catching up until July 1994 (Fig. 4.7).
Figure 4.7. Frequency of occurrence of 6 marsh species over time (SCAM, SPPA, SALA, SPSP, ELPA, SCVA). Error bars represent ± 1 standard error.

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Table 4.1. Species life history, community status (dom=dominant, co-dom=co-dominant, subord=sub-ordinate, occ-dom=occasionally dominant, occas.=occasional), herbivory effect and significance (sig=significant, ns=not significant, NA=Does not apply). Asterisk (*) indicates significance. Prior difference means that the difference was present at the start of the study. Mixed indicates that several influences are affecting species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Code</th>
<th>Life History</th>
<th>Community Status</th>
<th>Herbivory Effect</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spartina patens (Ait.) Muhl.</td>
<td>SPPA</td>
<td>per</td>
<td>dom</td>
<td>reduced</td>
<td>*sig</td>
</tr>
<tr>
<td>Scirpus americanus Pers.</td>
<td>SCAM</td>
<td>per</td>
<td>dom</td>
<td>reduced</td>
<td>*sig</td>
</tr>
<tr>
<td>Sagittaria lancifolia L.</td>
<td>SALA</td>
<td>per</td>
<td>co-dom</td>
<td>reduced</td>
<td>*sig</td>
</tr>
<tr>
<td>Eleocharis cellulosa Torr.</td>
<td>ELCE</td>
<td>per</td>
<td>sub-ord</td>
<td>slight red.</td>
<td>ns</td>
</tr>
<tr>
<td>Echinochloa crusgalli (L.) Beauv.</td>
<td>ECCR</td>
<td>ann</td>
<td>occas.</td>
<td>reduced</td>
<td>ns</td>
</tr>
<tr>
<td>Eleocharis parvula (Roem &amp; J.A. Schults)</td>
<td>ELPA</td>
<td>per</td>
<td>occas.</td>
<td>stimulated</td>
<td>*sig</td>
</tr>
<tr>
<td>Lilaeopsis chinensis (L.) Kuntze</td>
<td>LICH</td>
<td>per</td>
<td>sub-ord</td>
<td>stimulated</td>
<td>*sig</td>
</tr>
<tr>
<td>Cyperus oderatus L.</td>
<td>CYOD</td>
<td>ann</td>
<td>sub-ord</td>
<td>stimulated</td>
<td>*sig</td>
</tr>
<tr>
<td>Pluchea purpurascens (Swartz) DC</td>
<td>PLPU</td>
<td>ann</td>
<td>sub-ord</td>
<td>stimulated</td>
<td>*sig</td>
</tr>
<tr>
<td>Ptilium sp.</td>
<td>PTSP</td>
<td>ann</td>
<td>occas.</td>
<td>stimulated</td>
<td>*sig</td>
</tr>
<tr>
<td>Phyllo nodiflora (L.) Greene</td>
<td>PHNO</td>
<td>per</td>
<td>occas.</td>
<td>eliminated</td>
<td>ns</td>
</tr>
<tr>
<td>Polygonum punctatum Elliot</td>
<td>POPU</td>
<td>ann</td>
<td>occas.</td>
<td>eliminated</td>
<td>ns</td>
</tr>
<tr>
<td>Lythrum lineare L.</td>
<td>LLYL</td>
<td>per</td>
<td>occas.</td>
<td>eliminated</td>
<td>ns</td>
</tr>
<tr>
<td>Scirpus robustus Pursh</td>
<td>SCRO</td>
<td>per</td>
<td>occas.</td>
<td>eliminated</td>
<td>ns</td>
</tr>
<tr>
<td>Cyperus polystachios var. texenis (Torrey) Fernald</td>
<td>CYPO</td>
<td>per</td>
<td>occas.</td>
<td>eliminated</td>
<td>ns</td>
</tr>
<tr>
<td>Panicum virgatum L.</td>
<td>PAVI</td>
<td>per</td>
<td>occas.</td>
<td>eliminated</td>
<td>ns</td>
</tr>
<tr>
<td>Spartina sp. (S.cynosuroides and S. alterniflora)</td>
<td>SPSP</td>
<td>per</td>
<td>co-dom</td>
<td>patchy</td>
<td>ns</td>
</tr>
<tr>
<td>Scirpus validus Vahl</td>
<td>SCVA</td>
<td>per</td>
<td>occ-dom</td>
<td>prior diff</td>
<td>NA</td>
</tr>
<tr>
<td>Juncus roemerianus Scheele</td>
<td>JURO</td>
<td>per</td>
<td>sub-ord</td>
<td>prior diff</td>
<td>NA</td>
</tr>
<tr>
<td>Vigna luteola (Jaacquim) Bentham</td>
<td>VILU</td>
<td>per</td>
<td>sub-ord</td>
<td>mixed</td>
<td>NA</td>
</tr>
<tr>
<td>Kosteletskya virginica (L.) Presl.</td>
<td>KOVI</td>
<td>per</td>
<td>occas.</td>
<td>prior diff</td>
<td>NA</td>
</tr>
<tr>
<td>Distichlis spicata (L.) Greene</td>
<td>DISP</td>
<td>per</td>
<td>occas.</td>
<td>mixed</td>
<td>NA</td>
</tr>
<tr>
<td>Aster tenuifolius L.</td>
<td>ASTE</td>
<td>per</td>
<td>sub-ord</td>
<td>mixed</td>
<td>NA</td>
</tr>
<tr>
<td>Aster subulatus Michx.</td>
<td>ASSU</td>
<td>ann</td>
<td>sub-ord</td>
<td>mixed</td>
<td>NA</td>
</tr>
</tbody>
</table>
Eleocharis parvula, on the other hand, was eventually lost in the ungrazed plots by May 1994. The Spartina species (SPSP) and Scirpus validus were not effected by herbivory (Fig. 4.7, Table 4.1).

Eleocharis cellulosa was significantly reduced by herbivory (Fig. 4.8, Table 4.1), though it existed in both grazed and ungrazed plots throughout the entire study. Cyperus oderatus and Lilaeopsis chinense were both significantly stimulated by herbivory (Fig. 4.8, Table 4.1). Juncus roemerianus and Aster tenuifolius exhibited no herbivory effects (Fig. 4.8, Table 4.1). Echinochloa crusgalli was reduced by herbivory, but the effect was not significant (Fig 4.9, Table 4.1). Ptilimnium sp. was significantly stimulated by herbivory (Fig. 4.9, Table 4.1). Vigna luteola, Aster subulatus, Distichlis spicata and Kosteletskya virginica were not affected by herbivory (Fig. 4.9, Table 4.1).

Phyla nodiflora (PHNO), Panicum virgatum (PAVI), Scirpus robustus (SCRO), Lythrum lineare (LYLI), Polygonum punctatum (POPU) and Cyperus polystachyos (CYPO) were all eliminated by herbivory (Fig. 4.10, Table 4.1). These species only appeared rarely. SCRO, PAVI and CYPO only appeared in the 1993 growing season (Fig. 4.10). PHNO, POPU and LYLl only appeared in the 1994 growing season (Fig. 4.10).

DISCUSSION

In the Pearl River mesohaline marsh, herbivores had dramatic effects on plant abundance. Biomass of Spartina patens was reduced by 75% and Scirpus americanus by 85% in grazed plots compared to ungrazed (Fig. 4.1). This reduction in biomass is greater than the 30% reduction in total biomass reported by Taylor and Grace (1995) for
Figure 4.8. Frequency of occurrence of 6 marsh species over time (ELCE, CYOD, ASTE, LICH, JURO, PLPU). Error bars represent ± 1 standard error.
Figure 4.9. Frequency of occurrence of 6 marsh species over time (ASSU, VILU, PTSP, ECCR, KOVI, DISP). Error bars represent ± 1 standard error.
Figure 4.10. Frequency of occurrence of 6 marsh species over time (SCRO, PHNO, PAVI, POPU, CYPO, LYLI). Error bars represent ± 1 standard error.
three marsh types in the same system during 1990-1991, and the 40% reduction reported by Chabreck (1959) for mesohaline marshes in coastal Louisiana. In the emerging islands of the Atchafalaya Delta, which have heavy nutria activity, biomass was 49% greater and 60% greater in exclosed plots in 1980 and 1981, respectively (Fuller et al. 1985). Gauthier et al. (1995) found reductions of biomass (88%), similar to this study, in grasslands grazed by snow geese at Bylot Island of Canada's Northwest Territory. In addition, only 17% of ambient light reached the soil surface in ungrazed plots, versus 75% which reached the soils in grazed plots (Fig. 4.2). This indicates that not only did biomass dramatically decrease in grazed plots, but also the amount of cover and number of individuals.

The major difference in herbivore effect on biomass between the studies in Louisiana might be, in part, because in this study eatout sites were specifically targeted in order to document the maximum effects of herbivore impacts and the potential for eatouts to lead to marsh submergence. Thus, these values do not represent average conditions across the marsh. Another potential cause of greater impact of herbivores found here compared to those reported by Taylor and Grace (1995) is change in herbivory over time. Due to a decrease in demand for fur worldwide, trapping in Louisiana has declined from 986,014 animals harvested in 1986-1987 to 171,470 in 1994-1995 (Louisiana Department of Wildlife and Fisheries). Field observations at the Pearl River during this time indicate that populations of nutria have increased substantially.
Species richness increased in grazed plots and decreased in ungrazed plots between the beginning of this study and sixteen months later, near the end of the second growing season (Fig. 4.3). As found in another study conducted at the Pearl River during the same time (Chapter 2), grazed plots increased from an average of 5 to 6 species between 1993 and 1994. During the same time, the ungrazed plots in this study decreased from an average of 6 species to only 4 species. Similar results have been reported elsewhere. In an abandoned agricultural field in England, Gibson et al. (1991) showed that after a couple of years, diversity increased in grazed plots and decreased in ungrazed plots. In a savanna of Uttar Pradesh, India, richness increased as grazing increased. This effect was greatest in moderately grazed areas (Pandey and Singh 1991). In Australian grasslands of New South Wales, severe grazing increased species richness (McIntyre and Lavorel 1994). Further, Ikeda and Okutomi (1992) discovered that some species of roadside herbs, in an experiment at the University of Tokyo, disappeared in protected plots.

The decline in richness with herbivore exclusion may involve several possible processes (Louda et al. 1990). Clearly one of the main factors that could be involved, however, is competitive exclusion associated with the greater biomass found in protected plots. While herbivory may not always reduce competitive dominance, grazing that has a major effect on the dominant perennial (such as found here) is likely to reduce competitive suppression of less abundant species. As an example of this process, in an experiment in a tall grass prairie in Kansas, when the dominants were removed, species richness increased (Glenn and Collins 1993). Based in part on data
from the Pearl River landscape, Grace and Pugesek (in press) have shown that peak richness is found in moderately disturbed sites and that as disturbance decreases below some intermediate level, competitive exclusion intensifies, resulting in a decreased richness. While the exact cause of the reduction in richness observed here is not known, enhanced competitive exclusion with herbivore exclusion is a likely explanation.

A detrended correspondence analysis revealed that the grazed plots were very similar in species composition at the end of the study compared to the beginning (Fig. 4.4). The ungrazed plots, in contrast, had shifted in frequency of occurrence and species richness and were somewhat different at the end of the study than at the beginning. Four out of ten of the ungrazed plots in August 1994 fell outside the range of the ungrazed plots in August 1993 (Fig. 4.5). Hik et al. (1992) found that community composition shifted in Canadian salt-marshes in plots protected from herbivory by snow geese. Dublin et al. (1990) found that when elephants were removed from an area of the Serengeti, the community did not revert back to its previous composition, but shifted into something different. This shift at the Pearl River seems to be related to the difference in frequency of occurrence of the dominant species and the particular species which became eliminated by herbivory in the grazed plots and excluded by the dominants in the ungrazed plots.

When the frequency of occurrence of each individual species was graphed on a log_{10} scale, the community seemed to fall into five rather distinct groups (Fig. 4.6). These were called dominant (dom) which occurred the most frequently, co-dominant (co-dom) for the species which occurred often, but not with the same frequency as the
dominants, occasional co-dominants (occ-dom), which were two species that were abundant in a few locations but not consistently abundant, common subordinants (subord) which occurred on a regular basis, but never with great frequency and occasionals (occas.), which showed up rarely (Fig. 4.6, Table 4.1).

Herbivory had the greatest impacts on the frequency of occurrence of the dominant and occasional species. Overall, 5 species (ELPA, LICH, CYOD, PLPU and PTSP) were stimulated by herbivory (Figs. 4.7, 4.8, 4.9, Table 4.1). *Eleocharis parvula* (ELPA) and *Lilaeopsis chinense* (LICH) are very short species that appear to be taking advantage of higher light levels. These species behave like mudflat specialists (personal observation), as they were recruited the most in areas of intense herbivory that were mostly exposed mud. These species also were eventually out-competed in the ungrazed plots by the dominants, which towered over them and allowed virtually no light to reach them at the soil surface. They were present in both treatments at the beginning of the study, but had been excluded in the ungrazed plots by the end of the study (Fig. 4.2, 4.7, 4.8). Data indicate that CYOD, PTSP and PLPU also seem to prefer high levels of light found in the grazed plots.

Five species (SPPA, SCAM, SALA, ELCE and ECCR) were all reduced by herbivory (Figs. 4.7, 4.8, 4.9, Table 4.1). *Scirpus americanus* (SCAM) is a preferred food, as noted above. *Sagittaria lancifolia* (SALA) did not appear to be grazed much when observed during sampling events, with the exception of the grubbing of rhizomes during the non-growing season months. Still, herbivore impacts were great enough to be significant (Table 4.1). Herbivory on ELCE and ECCR was not noted often during
sampling events, but the data indicate significant impacts. These likely were grazed as tender young shoots and, therefore, were not observed as larger damaged structures.

As the results of this study indicate, although *Spartina patens* is not the preferred food of nutria, they will consume it, especially when other species are not available. Stomach content analysis of nutria have shown that *S. patens* is a regular part of their diet (Chabreck, personal communication). Also, nutria will switch food preferences with seasons (Ehrlich and Jedynak 1962, Willner 1982). Abba (1988) reported that nutria in western France switched to feeding on grasses in the winter when other species were not available. *Spartina patens* occurrence in grazed plots increased throughout the growing season, but by July 1994, it still did not occur in all subplots (Fig. 4.7). It appears, therefore, that in the absence of intense herbivory pressure by nutria, that *S. patens* may out-compete other species in the brackish marsh. The lack of complete senescence and ability to overwinter likely gives this species an advantage at the start of each growing season, simply because it already occupies more space than other species (Silvertown *et al.* 1992).

Seasonal effects of grazing on *Scirpus americanus* were somewhat different from those reported for *Spartina patens*. As with *S. patens*, once fences were erected, *Scirpus americanus* occurred in most subplots of the permanent plots (Fig. 4.7). Likewise, occurrence steadily declined in the grazed treatment until January 1994 when all individuals had been consumed. Cover declined in the ungrazed treatment starting in November 1993 continuing through January 1994 due to senescence, though some subplots still contained individuals. By February 1994, *S. americanus* started to recover.
slowly in both treatments, in March however, almost all subplots of the ungrazed
treatment contained individuals, while the grazed treatment was slow to respond and
still had not caught up by July 1994 (Fig 4.7). Indications are that selective predation of
nutria on *S. americanus* severely limited its presence in April 1994. Thus, herbivores
were observed to have a strong effect on *S. americanus*. The conclusion that nutria are
contributing to the decrease in *S. americanus* is consistent with the observations by
Linscombe et al. (1981) who found that as nutria populations in Vermillion Bay,
Louisiana marshes declined, cover of *S. americanus* increased significantly. These data
are also consistent with the findings of Belsky (1992) who demonstrated that two
species increased in cover in protected plots at the end of one year in grassland
communities of the Syringed National Park, Tanzania. Belsky (1992) further showed
that tall perennial species tended to increase in cover when protected from grazing while
shorter perennial and annual species tended to decrease.

Six species (PHNO, POPU, LYLI, SCRO, CYPO and PAVI) were eliminated by
herbivory (Fig. 4.10, Table 4.1). Of these species, 3 (PAVI, CYPO and SCRO) showed
up the first growing season and the other 3 (PHNO, POPU and LYLI) only showed up
during the second growing season.

In conclusion, herbivores dramatically reduced biomass overall and of five
individual species. Six species experienced stimulation in frequency of occurrence in
the grazed plots, probably because of an increase in light levels at the soil surface. Six
species were eliminated in the grazed plots, due to herbivory and several species were
eliminated in the ungrazed plots due to competitive exclusion. Richness increased in
the grazed plots while decreasing in the ungrazed plots. These results indicate that the grazed community remained basically the same in terms of frequency of occurrence and richness, while the ungrazed plots changed between the beginning of the study and the end. Overall, herbivores are keeping the dominant species from eliminating some species and maintain the current community composition.
CHAPTER 5

SUMMARY AND CONCLUSIONS

As global temperatures and sea levels continue to rise, impacts on wetlands worldwide will have increasingly greater effects. As human travel increases, the introduction of exotic species continues to increase as well. Much of the Louisiana Gulf coast has already experienced severe negative impacts by humans through dredging of oil canals and the limiting of sediments into the marshes as a result of man made levees, which restrict seasonal flooding.

This dissertation examined the impacts of exotic herbivores in a coastal marsh of Louisiana. Though it may be widely believed that nutria are contributing to wetland loss based on negative impacts they effect in some places, this does not seem to be the case at the Pearl River. Overall, both fire and herbivory, common features of the Pearl River marshes, resulted in reduced biomass of all species. Mammalian herbivores dramatically impacted the vegetation in the brackish marsh of the Pearl River. Grazing clearly led to a preferential reduction in *Scirpus americanus* but had few additional effects on species composition. Burning, in contrast, had more widespread effects on species composition by tending to reduce the prevalence of *Spartina patens* in all communities, though not always to a great degree. These results, therefore, are consistent with the hypothesis that burning acts to reduce the dominance of *Spartina patens*, a species generally regarded as unpalatable to most wildlife (Lynch et al. 1947,
In addition to affecting biomass, burning (in the absence of grazing) led to a substantial increase in species richness when plants were protected from grazing. Similar to the findings by Taylor et al. (1994), in this study, burning neither caused a major increase in the effects of grazing, nor promoted eatouts, which are believed to contribute strongly to the acceleration of wetland loss in Louisiana.

Vertical soil accretion increased more in grazed plots than in ungrazed, but this seemed to be a result of enhanced subsidence. Overall, soil elevation increased in both grazed and ungrazed plots, with the greatest increase in the protected plots. Still, soil elevation increases in grazed plots were greater than eustatic sea level rise. However, as long as adequate sedimentation occurs, areas with heavy herbivory seem to be capable of increasing soil elevation at a sufficient rate to keep pace with rising eustatic sea level. The effects of deep subsidence were not examined in this study and are contributing to the overall subsidence. Expansion and contraction of the root zone seems to be contributing to these effects, though their exact contribution has not yet been determined.

Herbivore impacts on the plant community increased diversity and richness and seemed to keep the community structural changes to a minimum. Six species experienced stimulation in frequency of occurrence in the grazed plots, probably because of an increase in light levels at the soil surface. Six species were eliminated in the grazed plots, due to herbivory and several species were eliminated in the ungrazed plots due to competitive exclusion. Richness increased in the grazed plots while
decreasing in the ungrazed plots. These results indicate that the grazed community remained basically the same in terms of frequency of occurrence and richness, while the ungrazed plots changed between the beginning of the study and the end. Overall, herbivores are keeping the dominant species from eliminating some species and maintain the current community composition.

In the example of the Pearl River marsh, exotic species have not yet resulted in wetland loss. It is possible that such a loss may be taking place in rapidly deteriorating regions of the Mississippi River deltaic plain. Further study is needed to ascertain this possible loss. Overwhelmingly, exotics worldwide have strong negative effects on the communities into which they are introduced. This is one of many ecological problems we must continuously work on. Our wetlands are essential to our well being.
LITERATURE CITED


VITA

Mark Alan Ford was born in Lincoln Park, Michigan, on July 21, 1959. He attended John Glenn High School in Westland, Michigan, and received his diploma in 1977. Mark studied Biology-Ecosystems at Eastern Michigan University, in Ypsilanti, Michigan, and was awarded the Bachelor of Science Degree in 1986. While an undergraduate, Mark worked as a Biological Aid for the U.S. Fish and Wildlife Service at the National Fisheries Laboratory-Great Lakes in Ann Arbor, Michigan. Mark continued his studies in Biology-Ecosystems at Eastern Michigan University, earning his Master of Science Degree in 1990. In December 1990, Mark was awarded the Graduate Dean’s Award for Research Excellence for his thesis; Patterns of Wetland Plants Germinating from Seedbanks of a Southeastern Michigan Landscape. After completing his master of science degree, Mark worked as a Biological Technician for the National Oceanic and Atmospheric Administration at the Great Lakes Environmental Research Laboratory in Ann Arbor, Michigan, until entering his doctoral program in the Department of Plant Biology at Louisiana State University, Baton Rouge, in 1992. In June 1995, Mark won second place for best student paper; Herbivore Effects on Soil Accretion, Subsidence and Elevation Changes in Coastal Louisiana, at the Annual Society of Wetland Scientists Meeting in Boston. In June 1996, Mark won the Daisy and William Luke Graduate Assistant Excellence in Teaching Award from the Department of Plant Biology at Louisiana State University. He is currently a candidate for the doctor of philosophy degree.
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Mark Alan Ford

Major Field: Plant Biology

Title of Dissertation: Impacts of Fire and Vertebrate Herbivores on Plant Community Characteristics and Soil Processes in a Coastal Marsh of Eastern Louisiana, USA

Approved:

[Signatures]

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Date of Examination:

June 17, 1996