

NUTRIENT CONSTRAINTS ON PLANT COMMUNITY PRODUCTION AND
ORGANIC MATTER ACCUMULATION OF SUBTROPICAL FLOATING
MARSHES

A Dissertation

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

in

The Department of Oceanography and Coastal Sciences

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December 2006

ACKNOWLEDGEMENTS

During my years of graduate school, I learned scientists are human, and science is not exclusive of personality despite what the purists say. I have been fortunate to know how some successful scientists think, make a living, and work toward understanding. My committee has helped me see these things in unique ways. My full gratitude goes to Dr. Charles E. Sasser. Not just for his guidance as professor, but he showed me a model for living that I thoroughly respect. Charles is a mentor who teaches by example and encourages individual thinking. I am fortunate for the opportunity of working and knowing such a remarkable naturalist, scientist, and above all, genuine person. I count him among my lifelong friends.

My other committee members played unique roles in my development, mostly through their tacit wisdoms. Dr. Irving A. Mendelsohn made time to answer questions about wetland plant biology, greenhouse plant cultivation, and nutrient solution preparation. By example, Irv showed me the importance of objectivity and the disarming value of admitting the limits of your knowledge. Another member of my committee, Dr. Dubravko Justic, has a passion for big questions, and although a discussion may begin with science, it always comes to rest with something personal. Dubravko sees the questions of science and people as inseparable. I admire his ability to see how it all fits together. Dr. Jaye E. Cable is among the brightest and most energetic faculty in our department—a positive role model for new students who want to find success in science. She gave me a glimpse into how a young investigator can balance her family life and still have an extraordinary research program. My dean's representative, Dr. Kurt Svoboda,

made my job simple: he was approachable and supportive. Looking back, my committee could not have been more professional and refreshingly devoid of ego issues.

Mike Francis made it possible for me to get my fieldwork done in comfort by offering his camp, Maison Misere—thank you Mike. I appreciate Roger Vincent for giving me access to Miami Corporation land. I am grateful to Elaine Evers (GIS expertise) and Erick Swenson (gage guru) for making my work easier. Charlie Milan and Tom Oswald helped me with water and soil chemistry. Dr. James Gosselink always showed interest in my development and helped in practical ways.

Fieldwork was made more enjoyable by the hard work of my friends Jay Gore and Lee Stanton. The sanity keepers included: Brian Perez (chef extraordinaire) and Saturday college ball (you too, Angie); the Piazza's and 'ienda' (where true stories, half-truths, and damned lies are perpetuated, alongside good food and malt). Hilary Collis always gave me a laugh, smile, or hug at the right times. At a young age, my mom gave me comfort, showed me nature, and released me. My sister is my best friend (save the Wet-Willie's), and I could not imagine life without her. Today, most dearly, I think of my father. Pop showed me that life must be lived with great humor, for how else can we bear life's tragedies? I will always adore our memories together among the woods and waters.

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ABSTRACT

In the cycle of delta growth and decay, peat-forming wetlands span a time and space continuum. Later in the delta cycle, freshwater floating marshes become increasingly removed from external sediment subsidy and internal nutrient cycling controls plant productivity and organic matter accumulation. An interesting question is whether increased external nutrient loading can affect the basic processes that lead to peat formation—plant production and organic matter decomposition. I conducted several field studies to understand whether belowground organic matter accumulation and decomposition were affected with increased nutrient exposure; in addition, the plant community was monitored over three years. A laboratory soil respiration experiment was run to determine potential limiting nutrients to microbial activity. After two years, there was a reduction of total belowground organic matter accumulation with increased nutrients; this partially resulted from reduced belowground root deposition coupled with accelerated root decomposition. This reduction in belowground accumulation, however, may be related also to the disappearance of a common plant of the community following fertilization, and not necessarily from a phenotypic shift in the allocation pattern by the dominant plant species. Fertilization accounted for an approximate doubling in aboveground biomass, accompanied by decreased stem density, and decreased species richness. Compared to other species, the grass, maidencane (*Panicum hemitomon*) responded most positively to increased nutrient availability at both sites, while at one site goldenrod (*Solidago sempervirens*) eventually captured a significant proportion of biomass. Nutrient resorption efficiency of nitrogen (N) and phosphorus (P) were both decreased with increased fertility. The degree of N- or P-limitation observed across

coastal populations of *P. hemitomom* reflect the composite influences of site geology, water source, fire frequency, and the more conservative cycling of P compared to N. Plant community nutrient limitation may not be a reliable predictor of the type of nutrient limitation to soil microbes. Floating marshes have developed and are sustained under nutrient restricted conditions compared to other coastal marshes. Although floating marshes may function as nutrient sinks, a change in community and plant allocation pattern can be predicted with increased nutrient enrichment of these wetland types.

CHAPTER 1
WETLAND ORGANIC MATTER ACCUMULATION AND FLOATING MARSHES
OF LOUISIANA

INTRODUCTION

In the Mississippi River Delta Plain, rapid geologic subsidence coupled with sea level rise, has resulted in extensive wetland loss (Boesch et al. 1994). The current working model of emergent marsh stability proposes that healthy plants drive soil organic matter production, which ultimately determines soil elevation (Nyman et al. 1990, Turner et al. 2004, DeLaune and Pezeshki 2003). The importance of mineral sediments in stimulating plant growth and organic matter accretion is also acknowledged (Bricker-Urso et al. 1989).

In the abandoned delta regions, peat production controls soil accretion (Kosters et al. 1987), and this is especially true of floating marshes that have developed extensively across the deltaic landscape (Swarzenski 1991, Sasser et al. 1996). These subtropical wetlands have relatively high rates of peat accretion ($>0.75 \text{ cm yr}^{-1}$; DeLaune et al. 1986; Nyman et al. 2006). Since mineral sedimentation is poor, the maintenance of high primary productivity is largely sustained by internal nutrient cycling (Sasser et al. 1991). An interesting question is how increased external loading of nutrients to floating marshes may affect rates of organic matter production and decomposition, in addition to plant community responses.

This introduction provides a brief background on the topics addressed in the research chapters: nutrient enrichment of wetland ecosystems, plant competition for resources, soil organic matter formation, and the context of the research problem in the

floating marshes of Louisiana. At the end of the introduction, the specific questions researched for the chapters are presented.

WETLAND NUTRIENT ENRICHMENT

Wetlands are increasingly valued for their ability to remove water-borne constituents—sediments, metals, and nutrients—and improve the condition of our natural waters. Increased population growth has led to nutrient enrichment of aquatic ecosystems (Verhoeven et al. 2006). Although wetlands are known for their capacity to transform or bury nutrients, there is concern that shifts in plant communities associated with increased nutrient loading may compromise wetland function and affect ecosystem resilience (Scheffer et al. 2001). Increased nutrient loading may favor the dominance of a few aggressive species at the expense of a diverse community. Community change may be perceived as undesirable, especially if it leads to the loss of habitat for ‘valuable’ plant and animal species. The Florida Everglades provides an example of how nutrient pollution from agriculture, in part, has resulted in the loss of a plant community tolerant of low phosphorus conditions (Davis 1991, Chiang et al. 2000). Nitrogen and sulfate pollution also has been linked to wetland landscape changes of European fens (Lamers et al. 2001) and riverine wetlands of the Danube River delta (Pringle et al. 1993). In the realm of ecosystem management, efforts to restore ecosystems to an original desirable state can be expensive and success is uncertain.

PLANT COMPETITION

In the absence of severe or frequent abiotic stress, nutrient enrichment may mediate community composition change by inter- and intraspecific plant competition. The processes of resource capture and utilization underlie these competitive interactions.

At the individual level, a plant may operate within a ‘functional equilibrium’, such that allocation to aboveground growth is increased in response to a light limitation, or root growth is increased with water or nutrient limitation (Brouwer 1962). When nutrient limitations are released, a relatively high allocation to aboveground biomass may be predicted with or without changes to belowground allocation (Craine et al. 2002). When nutrients are scarce, a species may gain dominance if it is capable of allocating more biomass to root production, thereby acquiring nutrients and reducing the pool of nutrients available to competitors (Gleeson and Tilman 1990, Craine et al. 2005).

Successful acquisition or conservation of limiting resources requires that a species possess certain advantageous physiological and structural traits (Chapin et al. 1986). The community, then, is an expression of multiple suites of life history traits that are either reinforced or become obsolete with changing conditions, or disturbances. Communities with high diversity may arise with intense inter- and intraspecific competition in habitats experiencing low or intermediate disturbance regimes (Goodman 1975). A complex debate has evolved among plant ecologists that have attempted to unify different theoretical models that can describe general community responses to competition and disturbance (Grace 1991, Craine 2005).

WETLAND ORGANIC MATTER FORMATION

Belowground production and subsequent organic matter decomposition are fundamental processes governing peat accretion (Hackney and de la Cruz 1980, Hogg and Wein 1987, Scheffer and Aerts 2000, Middleton and McKee 2001). Unlike high latitude wetlands, peat-formation in the lower latitudes is controlled by root production, more so than litter deposition (Chen and Twilley 1999, Chimner and Ewel 2005).

Following root deposition, decomposition of these structures may be slow despite relatively high temperatures (Chimner and Ewel 2005). Low quality organic matter may limit the rate of peat decomposition in southern wetlands (Bridgham and Richardson 1992), and highly anaerobic conditions can override any effect of litter quality (Conn and Day 1997). The control of organic matter decomposition by endogenous and exogenous nutrients is unclear and reflects the complexity of feedbacks that occur in the soil environment (Bridgham and Richardson 2003).

Shaver and Billings (1975) interpret high root:shoot ratios of wetland plants as adaptive mechanisms for stressful (low nutrient) soil conditions, which requires a greater root surface area for sustaining aboveground growth. With infertile soil conditions, root mortality may be lessened given the high cost of new growth (Eissenstat and Yanai 1997, Eissenstat et al. 2000). Given the difficulty of measuring root growth and the use of different methods, developing general relationships regarding fertility and root allocation patterns requires further research (Hendricks et al. 2006). Reduction in fine root biomass with nutrient enriched conditions has been demonstrated, but this reduction can arise with increased root turnover, in which case organic carbon allocation belowground can be unaffected or possibly increased (Hendricks et al. 2006). With increased sea level rise, soil organic matter accretion of coastal marshes is important to wetland plant survival (Turner et al. 2004).

FLOATING MARSHES IN LOUISIANA

In coastal Louisiana, peat-forming freshwater marshes have developed in habitats where the active influence of the river is diminished (Kosters et al. 1987). The subsidence of old river deposits resulted in the extensive development of marshes that are fully

floating or seasonally buoyant (Sasser et al. 1996). It is estimated that more than 140,000 ha of these marshes occur just within Barataria and Terrebonne basins (Evers et al. 1996). The relatively high primary production of these marshes is sustained largely by internal nutrient cycling. Approximately one-half of the yearly nitrogen requirement of the plant community is obtained through the pathway of soil N-fixation ($6 \text{ g N m}^{-2} \text{ y}^{-1}$; DeLaune et al. 1986). Although some floating marsh communities are species rich, the greatest contributor to production is the grass, *Panicum hemitomon* (maidencane) (Sasser et al. 1995).

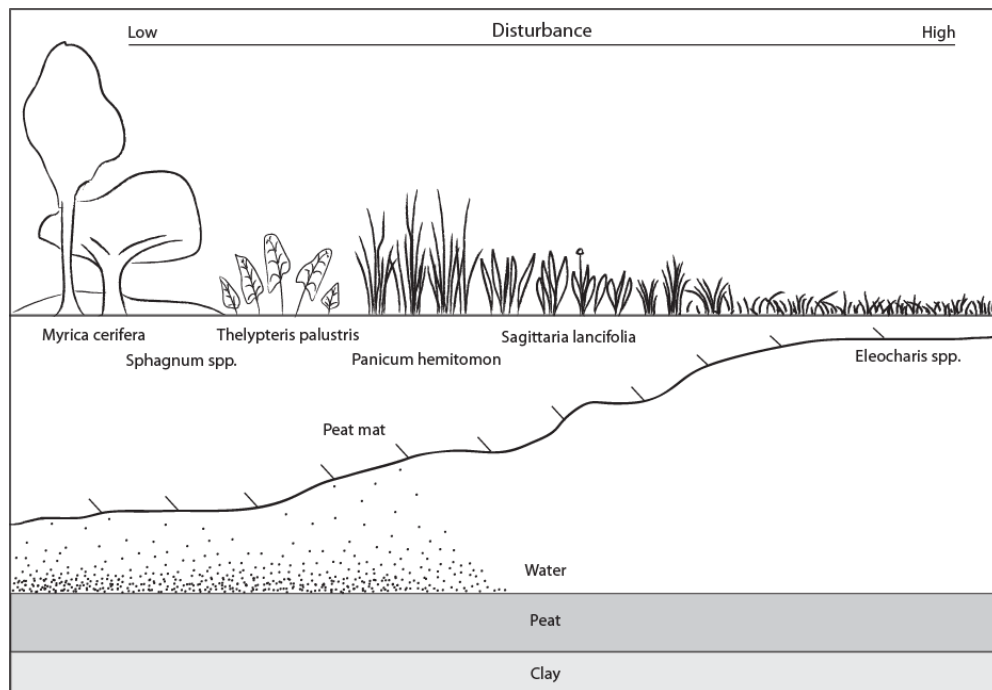


Figure 1.1. A general depiction of the dominant floating marsh types along a disturbance gradient. With low disturbance—primarily the absence of fire—forests of *Myrica*, *Ilex*, and *Acer* may develop, with a dense ground cover of bryophytes (*Sphagnum* spp. and liverworts) or shade tolerant herbaceous vegetation. Over time, these woody copses will deteriorate as the excessive weight causes mat submergence and lethal flood stress to the trees. Where fire suppresses woody competition, prairies develop with the grass, *Panicum hemitomon*, and the fern, *Thelypteris palustris*. The *Panicum*-dominated community typically exhibits high productivity, which contributes to a thick accumulation of peat. Increasing stress from salt water may cause a community shift to *Sagittaria lancifolia*. The highly disturbed *Eleocharis* spp. thin-mat may result from prolonged vertebrate herbivory.

Some areas of floating marsh have changed from the productive community type dominated by *Panicum hemitomon* to the low productivity sedge community dominated by *Eleocharis baldwinii* (Visser et al. 1999), and the causes are unclear. However, the relative stability of floating marsh communities may be generally related to the intensity and type of disturbance regime (Fig. 1.1) A shift in plant community may result in a loss of peat accumulation (Fig. 1.2).

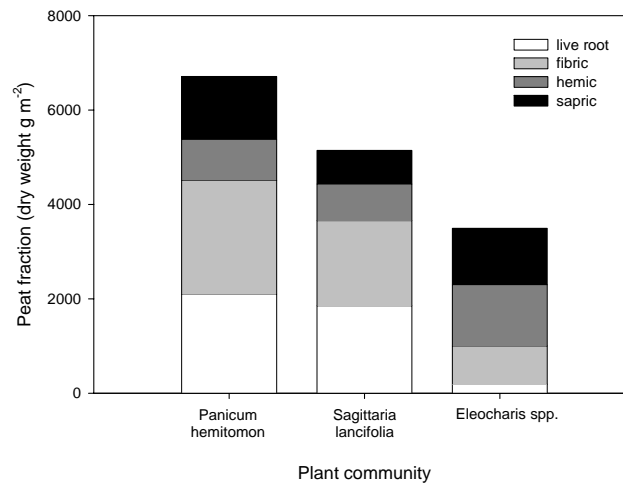


Figure 1.2. The effect of plant community on peat accumulation. The fibric and sapric peat fractions represent the least and most decomposed states, respectively. Total peat mass of the *Panicum* community is twice that of the *Eleocharis*, based on the same soil volume (0-16 cm of soil). The differences between these communities may suggest different rates of belowground production, but also the ability to retain both fine and coarse material, which can be regulated by root architecture (Holm and Sasser 2000).

The replacement of high productivity, mat-building species such as *Panicum* with a low productivity *Eleocharis* community results not only in a decline in peat accumulation, but also the reduced capacity for nutrient immobilization (Fig. 1.3).

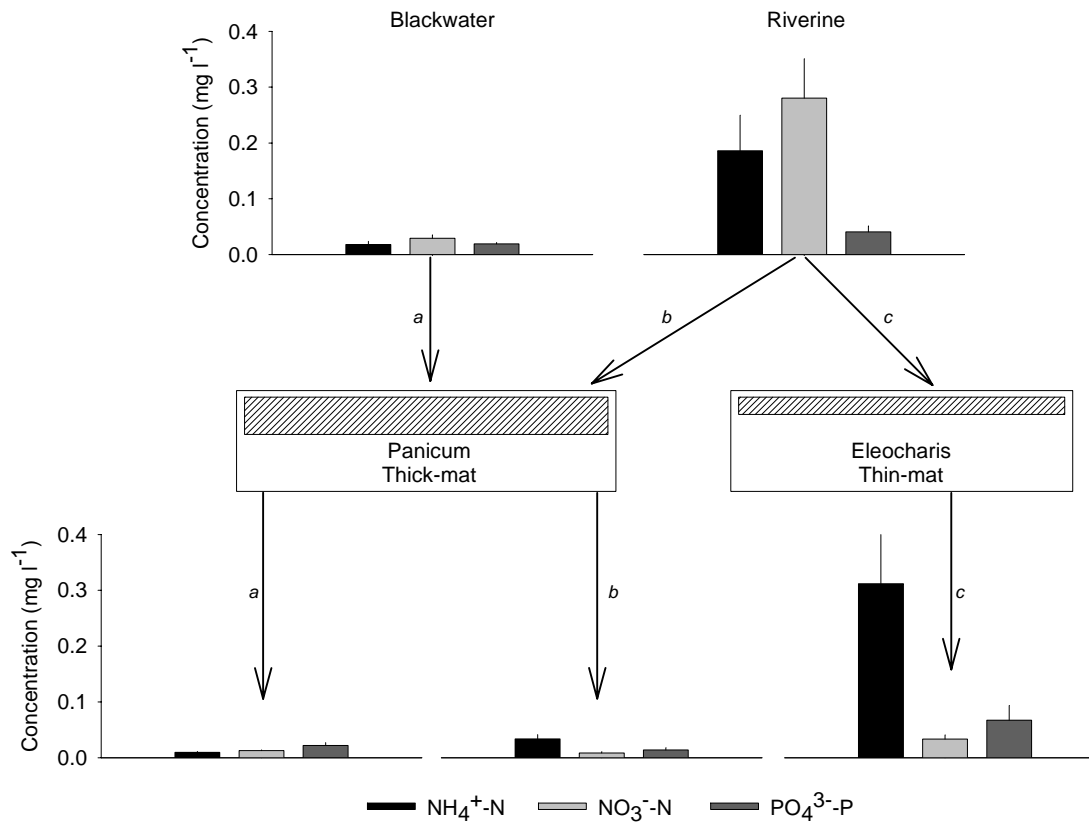


Figure 1.3. Available nutrient concentrations characteristic of blackwater and riverine source waters (upper graphs) and marsh pore-water (lower graphs) in Louisiana. The thick-mat *Panicum* marsh type is capable of reducing elevated loads of N and P from the riverine source (b) to low levels observed in blackwater systems (a). Although the concentration of NO₃⁻ is reduced in the thin-mat marsh, high levels of NH₄⁺ and PO₄³⁻ are persistent (after Sasser et al. 2000).

RESEARCH OBJECTIVES

The objectives here are to provide a better understanding of processes controlling organic matter accumulation in peat-forming floating marshes. Chapter two presents a review of the ecology and management of the grass, *Panicum hemitomon*, a plant that is common to southeastern wetlands and floating marshes of the Louisiana delta plain. The research questions that follow are addressed in field and laboratory experiments (chapters 3, 4, and 5).

- 1) What are natural rates of belowground organic matter accumulation and decomposition; and, to what degree are these processes controlled by nutrient availability?
- 2) What are the effects of increased fertility on aboveground biomass, species richness, and nutrient use efficiency? Among coastal freshwater habitats, which nutrient(s) are most limiting to community production?
- 3) How does soil microbial respiration respond with exposure to nitrogen, phosphorus, and sulfate?

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CHAPTER 2
THE ECOLOGY AND MANAGEMENT OF THE WETLAND GRASS, *PANICUM*
HEMITOMON OR MAIDENCANE

INTRODUCTION

Panicum hemitomon J.A. Schultes (maidencane, paille fine) is a warm season, perennial grass that is native to freshwater wetlands throughout the southeastern United States. It reproduces vegetatively, and its seed is seldom viable. Once established, it competes with other plants across a wide range of flooding depth and frequency and burning facilitates its dominance. Although maidencane can form dense monotypic stands, it also is associated with diverse communities of other grasses, sedges, ferns, and bryophytes. It commonly occurs on peat-based, nutrient poor sites; however, it has proven useful for removing nutrients in various wastewaters. It can be used to revegetate sediments after coal or phosphate mining and oil spills. The objective of this paper is to provide a comprehensive review of current and historical ecological information on *Panicum hemitomon* for wetland creation, restoration, and management.

DESCRIPTION AND GENERAL CHARACTERISTICS

Panicum hemitomon is in the tribe Paniceae, subfamily Panicoideae, and family Poaceae. Worldwide there are about 500 species of *Panicum*, which are mostly tropical, but they frequently extend into the temperate zones of both hemispheres (Webster 1988). In the contiguous United States, the genus *Panicum* comprises more than 30 species (most are concentrated in the southeastern U.S.), of which twenty-five are native and seven are considered established introductions (Freckmann and LeLong 2006).

P. hemitomon typically grows erect (<1.0 m tall), but its culms also will creep into open water. Adventitious rooting is common at culm nodes that are inundated (Lessmann

et al. 1997, Clark and Reddy 1998, Dowty 1998, Pahl 2002, Willis and Hester 2004). The net aerial primary productivity of *P. hemitomon* in natural communities ranges from less than 150 g m⁻² y⁻¹ (Schalles and Shure 1989) to more than 1,350 g m⁻² y⁻¹ (Sasser and Gosselink 1984). The standing crops of other dominant freshwater plants, such as *Typha domingensis* (1,480 g m⁻²) and *Schoenoplectus validus* (1,380 g m⁻²), may be greater than *P. hemitomon* (1,075 g m⁻²) (Polisini and Boyd 1972). In its subtropical range, it grows about 280 days per year (Sasser and Gosselink 1984).

The identification of *P. hemitomon* can be mistaken with other species in the genus, such as *P. repens* (torpedograss), and other grasses: cup- or bagscale grass (*Sacciolepis striata*), blue maidencane (*Amphicarpum muhlenbergianum*) and para grass (*Urochloa mutica*). Characteristics of roots, nodes, and internodes of the genus *Panicum* are variable and considered of little diagnostic use (Webster 1988). Line drawings and photographs for comparison of these species are available through the Center for Aquatic and Invasive Plants, Institute of Food and Agricultural Sciences, University of Florida (Fig. 2.1). Radford et al. (1964) give the following detailed description for *P. hemitomon*:

Culms 6-8 dm tall, nodes and internodes glabrous. Leaves cauline; blades to 3 dm long and 15 mm wide, glabrous or sparsely papillose-pilose on both surfaces, margins smoothish; sheaths glabrous to sparsely papillose-pilose or hirsute; ligules membranous and ciliate or lacerate, 0.5-1 mm long. Panicle constricted, 15-25 cm long, 3-16 mm broad; branches ascending, scaberulous. Spikelets 2.4-2.7 mm long; pedicels scaberulous, 0.5-6 mm long. First glume 3-nerved, glabrous, margins scarios, acute to cuspidate, 1.2-2 mm long, 2nd glume 5-nerved, glabrous, margins scarios, acute, 2.2-2.5 mm long, sterile lemma 3-nerved, glabrous, margins scarios, acute, 2.2-2.5 mm long, sterile palea scarios, 2 mm long; fertile lemma and palea faintly nerved, lustrous, yellowish, acute, 2.2 mm long.

Brown (1948) reported a chromosome number of $2n=36$ from cells collected in root tips. *P. hemitomon* is a C₃ plant based on its carbon isotope fractionation ($\delta^{13}\text{C} = -25.2$;

Smith and Brown 1973). In comparison of epidermal palea characteristics of *Dicanthelium*, *Panicum*, and *Echinochloa*, *P. hemitomon* exhibited unusual epidermal features—no papillae were present but there were spicules and numerous four-lobed silica cells (Clark and Gould 1975).

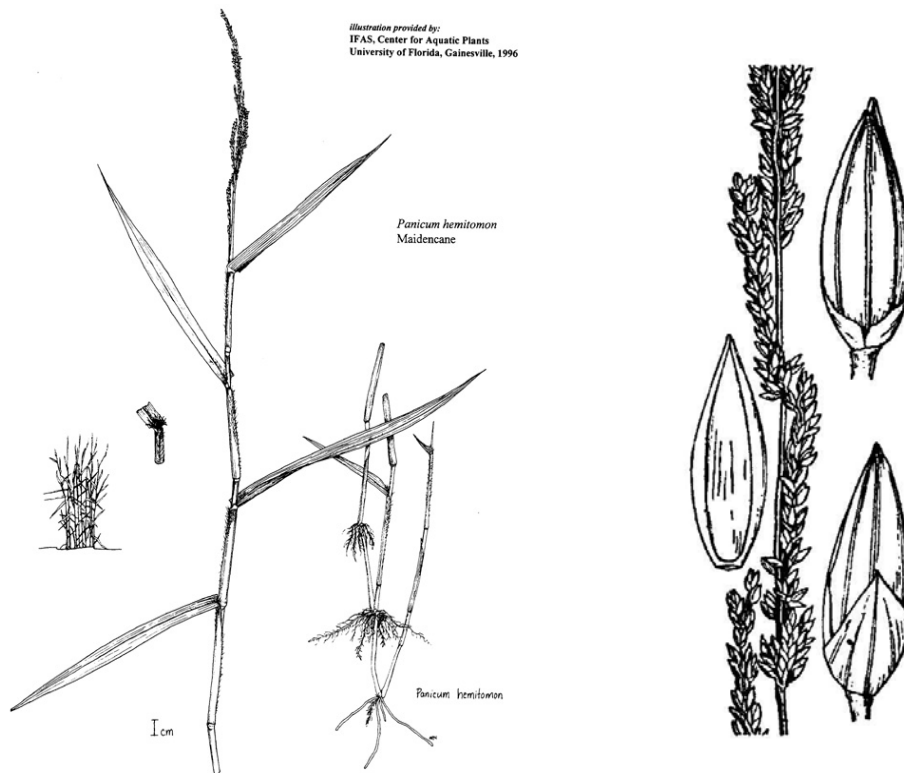


Figure 2.1. *Panicum hemitomon*: its growth habit, inflorescence, and spikelets. Line drawings courtesy of IFAS Center for Aquatic Plants, Univ. of Florida, Gainesville; and Texas Agriculture and Mechanical University, College Station Texas.

DISTRIBUTION, HABITATS, AND ASSEMBLAGES

P. hemitomon ranges from New Jersey south to Florida then west to Texas, and it is found in Arkansas and Tennessee (Freckmann and LeLong 2006). *P. hemitomon* is common to the wetland landscapes of the Florida Everglades (Loveless 1959, Kushlan 1990, Daoust and Childers 1999), the Okefenokee swamp (Cypert 1972, Duever 1982), and Carolina bays or depressional wetlands (Kirkman and Sharitz 1993, Miller and Bever

1999, De Steven and Toner 2004, Mulhouse 2005). In Louisiana, it is the dominant plant of most freshwater marshes in both the delta (O'Neil 1949, Sasser et al. 1995a) and chenier plains (Williams 1951, Evers et al. 1998, Holm et al. 2003a), but it is not commonly found in newly forming deltaic sediments (Chabreck and Palmisano 1973, Shaffer et al. 1992).

In Florida's lakes, floodplains, and the Everglades, *P. hemitomon* is associated with a 'wet prairie' community type (Loveless 1959), which comprises species such as spike rushes (*Eleocharis* spp.), nympheids (*Nymphaea*, *Nymphoides*), grasses (*Paspalidium*), beak rushes (*Rhynchospora* spp.), arrowheads (*Sagittaria* spp.), pickerelweeds (*Pontederia* spp.), lilies (*Crinum*, *Hymenocallis*) and bladderworts (*Utricularia* spp.) (Wade et al. 1980, Lowe 1986, Wood and Tanner 1990). In coastal plain depression wetlands and Carolina Bays, it is associated with the perennial graminoids, *Carex striata* and *Leersia hexandra*, in addition to *Sphagnum* spp., *Cephalanthus occidentalis*, *Nyssa biflora*, *Eleocharis* spp., *Rhexia* spp., and nympheids (*Nymphaea odorata* and *Brasenia schreberi*) (Schalles and Shure 1989, DeSteven and Toner 2004, Mulhouse et al. 2005).

In Louisiana's chenier plain, it creates dense nearly monotypic stands on sites with extended hydroperiods (Evers et al. 1998, Holm et al. 2003a); however, on the floating marshes of the delta plain it grows in diverse assemblages with up to 55 different species, including orchids (*Calapogon*, *Habenaria*), wildflowers (*Asclepias* and *Lobelia*), and bryophytes (liverworts and sphagnum mosses) (Sasser et al. 1995b, Visser et al. 1998). One-quarter of 116 floating islands (tussocks) on Florida's Orange Lake contained maidencane. On their 'grass-type' floating islands, Mallison et al. (2001) found these co-

occurring genera in order of their abundance: *Hydrocotyle*, *Panicum*, *Typha*, *Polygonum*, *Bidens*, *Sacciolepis*, *Schoenoplectus*, *Limnobiium*, *Pontederia*, and *Ludwigia*.

In a 6,400 ha rain-fed waterfowl impoundment (Lacassine NWR, Louisiana), *P. hemitomon* is the dominant emergent plant of higher elevations and extends into a lower ‘wet prairie’ community with *Eleocharis equisetoides* and several nymphaeids (*Brasenia*, *Nelumbo*, *Nuphar*, *Nymphaea*) (Fruge 1974, Holm et al. 2003a, Bass 2003, Howard 2005). Although it prefers full sunlight, *P. hemitomon* can be found at the margins or form the understory of *Taxodium* spp. bayheads and domes (Monk and Brown 1965, Ewel 1984, Gunderson 1984).

REPRODUCTION

Panicum hemitomon relies almost exclusively on rhizomatous growth for reproduction, and it can spread vegetatively 60-75 cm per growing season (Goude-lock 1974). Kirkman and Sharitz (1994) found that its persistence following burning or tilling was due to vegetative reproduction rather than seed germination. Seed viability is considered practically nonexistent (Pfaff and Maura 2000); however, it was found as a “seed bank species” in a Carolina Bay (Poiani and Dixon 1995). Inundation promotes seed production (Loveless 1959, Kirkman and Sharitz 1993). Patton (1988) described the phenology of a natural stand of *P. hemitomon* in Alachua County, FL, where flowering occurred from early to mid-June and fruit dispersal occurred thereafter into July. In Louisiana, flowering occurs from late April throughout May (pers. obs.). I am unaware of any studies that have tested different treatments (i.e. hormones, physical) to improve germination or of reports of ecotypic variation in seed production or viability.

GROWTH FACTORS

Sediment Type and Nutrient Chemistry

Panicum hemitomon will grow on either organic or mineral substrates (Williams 1951, Shiflet 1963, Monk and Brown 1965, Dowty et al. 2001, Willis and Hester 2004). Greenhouse manipulations of soil type with *P. hemitomon* have shown that aboveground growth is greater in mineral (silt and clay) than highly organic soils (Dowty et al. 2001, Willis and Hester 2004). But, in natural stands this species is most frequently found on peat-based soils (Wade 1980, Lowe 1986, Kirkman and Sharitz 1994) and floating peat masses (Metzen 1977 in Newsom et al. 1987, Sasser et al. 1996), indicating that plant competition may preclude its dominance on clay- or silt-based soils. Dense stands grow on sandy, acidic (pH 5.8) soils of moist pastures in Florida (Kalmbacher and Martin 1988). Birkenholtz (1963) reported *P. hemitomon* growing on entirely sandy soils in Florida's Paynes Prairie. Maidencane litter production contributed to higher soil carbon to nutrient ratios in semi-native compared to improved pasture wetlands (Gathumbi et al. 2005).

Acidic soil conditions (mean pH=4.6±0.3, range=3.9-5.2) are associated with *P. hemitomon* at several Carolina Bays (Miller 2000). At these sites, total soil carbon and nitrogen was 4.2 and 0.35%, respectively. Carolina Bays are considered nutrient poor, so the symbiosis of arbuscular mycorrhizal fungi with *P. hemitomon* roots likely improve, primarily, its phosphorus nutrition (Miller and Bever 1999; also see Miller 2000, Miller and Sharitz 2000). In the Everglades, maidencane tissue nutrient concentrations (molar N:P = 50) indicated that available phosphorus may limit its abundance (Daoust and Childers 1999).

Sasser et al. (1991) conducted a seasonal and spatial nutrient study of a maidencane-dominated floating marsh in Louisiana that formed the transition between a swamp and lake. They found that N and P concentrations in the marsh peat and water beneath the mat were consistently higher than those of the surrounding lake and swamp. They hypothesized that the marsh served as both a sink and source of nutrients to the lake and swamp depending on the seasonal evapotranspiration and precipitation.

Fire

Walsh (1994) presents a comprehensive literature review on fire and *P. hemitomom*. It is common to wetlands that experience frequent fires; its architecture—erect culms with numerous leaves, which persist on the culms throughout the dormant season—facilitates flammability (Cypert 1972, Vogl 1973, Wade et al. 1980, Lowe 1986, Kirkman and Sharitz 1994). In addition to the leaves, culms are also combustible with a slow or high intensity fire and low water levels (Fig. 2.2). Fire in the winter or early spring promotes rapid re-sprouting of tillers within a few days (Loveless 1959) and a more productive stand (Vogl 1973). The increase in sunlight, available nutrients from ash deposition, and soil insolation may explain the higher productivity in burned compared to unburned stands (Wilbur and Christensen 1983).

In a study in northeast Florida, Lowe (1986) hypothesized that although hydrology is important in controlling the landscape distribution of *P. hemitomom* and *C. jamaicense* at some sites, fire alters competitive interactions between the two species through the following mechanism: “maidencane, and its associated species, rapidly colonize areas where dense stands of sawgrass [are] destroyed by intense fire and then

inhibit the establishment of sawgrass seedlings. Sawgrass reclaims these areas through vegetative reproduction as a slowly moving front which monopolizes space and light.”



Figure 2.2. Maidencane facilitates fire (top left). Depending on the intensity of fire, remaining culms provide ventilation to newly emerging tillers (top right). Plant death occurs if the stubble is completely removed and the stand flooded for a lengthy period. Although maidencane can form dense monotypic stands on long hydroperiod sites, it also coexists with bryophytes, sedges, ferns, and other grasses on floating marshes or peat batteries (*Sphagnum* spp. bed, lower left). On continually wet sites, maidencane forms dense peat that contributes to soil elevation increase (lower right).

Since rhizome growth is the primary mode of regeneration for *P. hemitomon*, deep peat burns conceivably may reduce its reestablishment (Sipple 1979, in Walsh 1994). Fire exclusion results in woody plant invasion and subsequent decreased herbaceous plant dominance (Huffman and Blanchard 1991). Fire exclusion on floating marshes in Louisiana results in increased dominance of wax myrtle (*Myrica cerifera*) (Williamson et al. 1984). I am unaware of studies that have tested the effects of burning season on maidencane survival and regrowth.

Flooding

Maidencane tolerates a broad range of flooding, from deep, continual inundation to relatively dry conditions (Schalles and Shure 1989, Kirkman and Sharitz 1994, Miller 2000), and there is some ecotypic differentiation to flood stress (Lessmann et al. 1997). David (1999) reported the expansion of *P. hemitomon* coverage at Dupuis Reserve in Florida following increased inundation; its optimum flood depth was 30-60 cm but it also occurred in depths up to 80 cm. Loveless (1959) noted that it can grow in 1.0 m water depth for up to nine months. In the Okefenokee Swamp, sites containing *P. hemitomon* had a range of water level fluctuation of 40 cm above the soil surface (Duever 1982). During drought conditions, *P. hemitomon* can expand into previously open water sites in Carolina Bays (Mulhouse 2005).

Flooding under greenhouse conditions stimulates aboveground biomass production of *P. hemitomon* (Kirkman and Sharitz 1993, Lessmann et al. 1997, Willis and Hester 2004). Under field conditions in Florida, it produces a maximum biomass with an inundation frequency of 85-90% (Lowe 1986). A 30-40 cm flooding depth was optimum for biomass production in a Carolina Bay (Schalles and Shure 1989). Increased biomass production with flooding may be explained by stem elongation traits of maidencane. For example, Kirkman and Sharitz (1993) found that culm length was positively correlated ($r^2=0.78$) to water depth above the soil with approximately a 1:1 cm relationship; the range of water depth exceeded 1.0 m. Stem emergence, however, is significantly decreased when flooding occurs after culm removal (Kirkman and Sharitz 1993); apparently the erect, dead culms of maidencane are critical for maintaining ventilation to roots and emerging tillers. *P. hemitomon* produces adventitious roots at

culm nodes with inundation, and these roots may be important for nutrient uptake (Clark and Reddy 1998, Dowty 1998, Pahl 2002, Willis and Hester 2004) and improved flood tolerance (Lessmann et al. 1997).

Grazing

Maidencane is an important range grass in Florida (Kalmbacher and Martin 1988) and Louisiana (Williams 1951) and produces a high yield and forage quality (Kalmbacher 1983, Long et al. 1986). Pure stands of maidencane on cattle range in Florida produce between 4,000 and 6,000 kg ha⁻¹ of dry aboveground matter (Kalmbacher and Martin 1988, Kalmbacher 1990). In a defoliation and fertilization study, it was tolerant of simulated grazing intervals greater than 6 weeks, and fertilization improved yield. But frequent defoliation (three week intervals) was especially detrimental to yield and tiller density (Kalmbacher and Martin 1988). With frequent grazing of pasture wetlands in Florida (near Lake Okeechobee), palatable species such as maidencane were replaced with less palatable species such as *Juncus effusus*.

Under greenhouse conditions, aboveground biomass production is optimal at a clipping interval of 6-8 weeks (Holm and Sasser 2006). The combined effects of culm removal followed by flooding may result in reduced tiller and culm production (Kirkman and Sharitz 1993) or plant death (Middleton 1990). Transplants of *P. hemitomon* must be protected when nutria (*Myocastor coypus*) grazing is moderate to severe (Sasser et al. 2004).

Salt Tolerance

Willis and Hester (2004) conducted a greenhouse study to test the growth response of *P. hemitomon* to low level salinity (0, 1.5 and 3.0 mg l⁻¹), flooding (0, 10, 20

cm), and soil type (high or low organic). Both salinity treatments significantly reduced production over the eight-week study. Several other studies have found that *P. hemitomon* exhibits poor tolerance (Howard and Mendelsohn 1999a,b, LaPeyre 2001) and recovery following salt exposure (Flynn et al. 1995). However, some genotypic variation in salt tolerance has been identified in greenhouse trials (Hester et al. 1998). Other studies have elucidated the relative importance of salt and sulfide, singly and combined, in affecting the growth and physiology of *P. hemitomon* (Pezeshki et al. 1987, Koch and Mendelsohn 1989, Koch et al. 1990, Pezeshki et al. 1991, Pahl 2002). Apparently, it lacks the anatomical and physiological characteristics to tolerate elevated or long-term salt exposure (McKee and Mendelsohn 1989). The field distribution of *P. hemitomon* in Louisiana is restricted to areas protected from frequent or intense exposure to saltwater (Penfound and Hathaway 1938, Shiflet 1963, Chabreck and Linscombe 1982).

USES FOR SOIL AND WATER REMEDIATION

Since it spreads rapidly below and above the waterline and creates a dense network of fine roots, maidencane has been recognized for its ability to control erosion along shorelines of lakes and ponds (Goude-lock 1974, Bown 1975, Whitten 1998, Sistani and Mays 2001). It is not suitable, however, for stabilizing gullies in Florida's panhandle (NRCS 2000).

Its response to nutrient enrichment under experimental settings (Schwartz and Boyd 1995, Hubbard et al. 1998) and short-term field experiments (Kalmbacher 1983; DeLaune 1986) is positive. Stem numbers doubled with an application of 5 g m⁻² of nitrogen in a greenhouse experiment (Sistani and Mays 2001). In a Louisiana freshwater

marsh, aboveground biomass was increased 40 % with the application of 10 g m⁻² of NH₄-N; but at the dosage of 3 g m⁻² NH₄-N, no appreciable differences were detected (DeLaune et al. 1986). Soils associated with natural stands of *P. hemitomon* in Louisiana were shown to remove large inputs of inorganic nitrogen through denitrification (Lindau et al. 1991).

P. hemitomon has been used in the treatment of different wastewater effluents. It was used in the treatment of catfish pond effluent: along an 80 m effluent gradient standing crops ranged from 4,780 to 1,870 g m⁻²; the shoot to root ratios decreased from 1:1 to 1:3.5, indicating that aboveground growth is stimulated with nutrient exposure (Schwartz and Boyd 1995). In trials of swine lagoon effluent, it was useful in removing nitrogen when planted as riparian buffer strips (Hubbard et al. 1995, Hubbard et al. 1998, Entry et al. 2000). In another experiment involving swine lagoon effluent, Hubbard et al. (2004) found that *P. hemitomon* could be grown on floating-mat structures to remove nutrients. While *Juncus effusus* died in this experiment, *Typha angustifolia* and *P. hemitomon* produced 16,500 and 9,700 g m⁻² of biomass, respectively.

P. hemitomon growth was tested on coal mine spoil deposits and compared to *Pontederia*, *Typha*, and *Schoenoplectus validus* (Sistani et al. 1998). *Pontederia* had the greatest expansion followed by *P. hemitomon*, and *S. validus*; *Typha* spread was irregular. In Florida, it has been used to remove nutrients from municipal effluents (spray fields) and to stabilize phosphate mine spoil deposits (pers. comm. Janet Grabowski; NRCS 2001).

After a crude-oil spill in a freshwater floating marsh in Louisiana, *P. hemitomon* was transplanted in relatively high concentrations of total petroleum hydrocarbons (80 g

kg⁻¹ soil). After five months, culm numbers increased by a factor of 3.2 (non-fertilized) and 4.8 (fertilized); *Sagittaria lancifolia* increased by a factor of 1.5 (Holm et al. 2003b; Fig. 2.3). Greenhouse studies have confirmed a similar positive growth response of maidencane with crude-oil exposure (Dowty et al 2001).

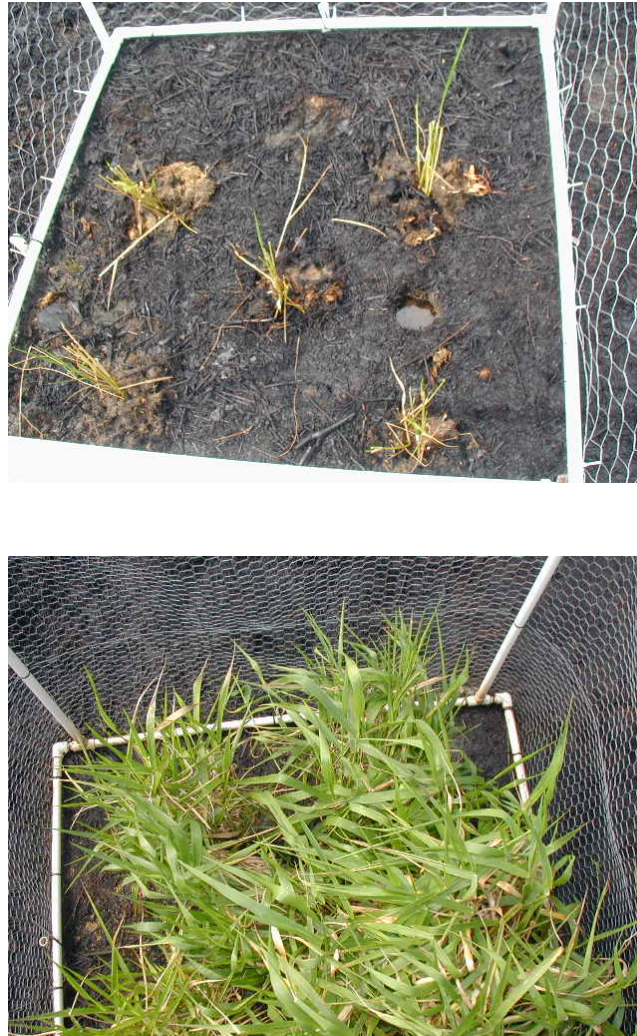


Figure 2.3. Maidencane may help accelerate the recovery process of contaminated soils. In this case, crude oil was trapped in the peat matrix and physical removal was not feasible. Clipped sods of maidencane from a donor marsh (upper) were transplanted into the heavily oiled peat. After five months of growth (lower), culm numbers multiplied by a factor of five with fertilization (Holm et al. 2003b).

WILDLIFE HABITAT USE AND VALUE

Vogl (1973) conducted a study on the wildlife use of maidencane habitats and the effects of burning. The usage of the burned compared to the unburned habitat was consistently greater for 'resident', 'transient', and 'occasional' bird species. Small mammals, reptiles, and amphibians also used both the burned and unburned areas, but alligators used the burned sites almost exclusively. Results of the study were not attributed to improved visibility in the burned areas; rather, burned areas became more densely vegetated upon regrowth.

Shallowly flooded maidencane, associated with spike rush (*Eleocharis cellulosa*), is important habitat for apple snails (*Pomacea paludosa*), which comprise the major food of the endangered Everglade Snail Kite (*Rostrhamus sociabilis*) (Bennetts et al. 2002). The endangered Florida Sandhill Crane prefers maidencane as a nest substrate in both the Okefenokee Swamp (Bennett 1989) and the Everglades (Thompson 1970). Another species of concern in Florida, the round-tailed muskrat (*Neofiber alleni*), uses *P. hemitomon* as nest material and food in shallowly flooded wet prairies (Birkenholtz 1963). Wood Storks (*Mycteria americana*) feed in wet prairie communities with maidencane (Kahl 1964). The Fulvous Whistling-Duck (*Dendrocygna bicolor*) may use maidencane marshes for nesting (Hohman and Lee 2001).

In the Okefenokee Swamp, batteries of floating peat dominated by *P. hemitomon* were selected as nesting habitat for the American Alligator (*Alligator mississippiensis*) (Metzen 1977 in Newsom et al. 1987). Maidencane-dominated floating marshes in Louisiana, support a high density (0.53 nests ha⁻¹; 14-yr mean; Visser et al. 1999) of alligator nests compared to a regional mean (0.02 nests ha⁻¹; McNease et al. 1994).

Depending on water level fluctuations, wet prairies are important refuges for invertebrates and small fish (Kushlan 1976, DuRant et al. 1979). Largemouth bass (*Micropterus salmoides*) use maidencane for nesting substrate in the absence of inorganic substrates (Bruno et al. 1990 in Walsh 1994). Maidencane may compete with food plants desirable to waterfowl (Lynch et al. 1947).

PLANTING AND MANAGEMENT

Ecotypes

USDA/NRCS Plant Materials Centers (PMC) have released two ecotypes or cultivars of *P. hemitomon*. ‘Halifax’ was released by the Coffeetown, MS PMC in 1974, and was selected based on its cold tolerance, rapid spread, and vigorous growth. None of the seed was found to be viable (Whitten 1998). The only other release was ‘Citrus Germplasm’ in 1998 from the Brooksville, FL PMC. The ‘Citrus’ was selected based on uniform spread and high productivity in a sub- to tropical climate (pers. comm. Janet Grabowski, NRCS Brooksville, FL). The ‘Citrus’ produces non-viable seed. Trials in Florida showed that the ‘Citrus’ out-produced the ‘Halifax’ ecotype (NRCS 2001).

Propagation and Field Establishment

Since seed viability is poor, vegetative propagation is required. Maidencane can be propagated from new tillers, mature culms, and inter-node pieces under warm conditions and full sunlight. Freshly clipped mature culms can be placed in shallow water and new culms and adventitious roots will sprout from the nodes. The plants are easily started in this manner, but extended hydroponic growth requires close attention to nutrient levels to avoid limitation. Milled peat is a good growth substrate combined with a timed-release fertilizer that ideally contains macro- and micronutrients; fertilizer should

be applied at 'low' rates given the sensitivity of *P. hemitomon* to salt. Pezeshki et al. 2000 grew maidencane in peat media and used water-soluble fertilizer (20-20-20, %N, P, K) at a concentration of 1.25 g l⁻¹. Different combinations of fertilizer N and P have not been tested for optimal growth response; however, shoot and root production of maidencane is increased with fertilization compared to peat alone (Pezeshki et al. 2000).

Bare-root plants or rhizomes are used to establish stands of maidencane in the field. For pond or water impoundment levees, rows of bare-root plants should begin about 30 cm above the normal water line and continue upslope with 30 cm spacing between the rows and individual plants. Rhizomes can be planted in furrows 2-6 inches deep (Whitten 1998, NRCS 2001). 'Citrus' maidencane was planted on phosphate mine spoil in Florida in early October with a Bermuda grass sprig-planter at a rate of 40 bushels of rhizomes per acre (NRCS 2001). At a different site in Florida, hand planting of rhizomes in July (25 bushels per ½ acre) resulted in a solid stand of 'Citrus' maidencane within six months (NRCS 2001).

In Louisiana, *P. hemitomon* was hand transplanted from a donor marsh into degraded peat-based floating marshes dominated by *Eleocharis baldwinii* (Sasser et al. 2004). The objective of the study was to test the feasibility of large-scale restoration of this heavily grazed (nutria) marsh type. Maidencane did not survive in unprotected plots; however, transplants in protected plots resulted in an almost complete coverage of 16 m² plots within three growing seasons. Although fertilization of protected maidencane improved coverage in the first growing season, at the end of three growing seasons, aboveground and belowground biomass was similar between the fertilized and non-fertilized treatments.

Methods of Control

In some settings, *P. hemitomon* may need to be controlled to prevent it from taking over other desirable submerged aquatic or emergent plants. Although physical removal of maidencane in the floating tussock form has been done (Mallison et al.2001), chemical control is most popular. Glyphosate (Rodeo[®] Monsanto Agricultural Co., St. Louis, MO) is a foliar herbicide recommended for emerged wetland plant control. Thayer et al. 1986 suggested use of Rodeo[®] for partial control of *P. hemitomon* in Florida ponds. Fosman (2000) found that 0.25 % Rodeo[®] resulted in 50% tissue damage to *P. hemitomon*; higher rates (1%) resulted in greater damage. The USACE Aquatic Plant Information System recommends 0.75 to 1.0% concentration of Rodeo[®] with a nonionic surfactant. The maximum allowable concentration of Rodeo[®] is 1.5%. Other glyphosate-based trade products are: Aquamaster[®], EraserAQ[®], Touchdown Pro[®], and AquaNeat[®].

SonarQ[®] (5% fluridone in a pelleted form, SePRO Corp. Carmel, IN) is an aquatic herbicide that does not control the growth of *P. hemitomon*, but it does partially control *P. repens*. Arsenal[®] (BASF, Research Triangle Park) controls *P. hemitomon* in pasture conditions but this form of 2,4D is not allowed in aquatic environments. Other formulations of 2,4D suitable for aquatic application will control *Typha spp.* and *Schoenoplectus spp.* but not *P. hemitomon* (USACE, Aquatic Plant Information Service).

SYNTHESIS

The persistence of *P. hemitomon* in southeastern freshwater wetlands can be explained by its tolerance of disturbance extremes such as drought, flooding, and fire. It has vigorous clonal growth and attains a moderate height and relatively high biomass production. So once it is established, it will out-compete most annuals and coexist with

other productive perennial species. However, for maidencane to remain dominant on drier sites, burning (once every 3-4 yrs) is required to prevent displacement by woody species. Under wet conditions, it contributes to rapid peat accumulation (0.75 cm yr^{-1} ; DeLaune et al. 1986). Attempts to control the abundance of maidencane by flooding alone will not be successful unless culms are removed (i.e. fire, grazing, or mowing) followed with deep flooding. Herbicides are a popular method of control.

For wetland restoration, maidencane is a good candidate for ameliorating sites that have been contaminated with crude oil, but not if brine is also present. It also grows well on coal and phosphate mining spoil deposits. It has been successfully used to remove nutrients from several types of wastewater. Given its prolific root growth and rapid spread, it has proven useful in protecting shorelines and levees from erosion. Maidencane multiplies quickly, which makes it easy to propagate under nursery conditions. On sites where herbivory is intense, field establishment may be complicated. Unique methods have not been developed for large-scale establishment in soils that have poor load-bearing capacity.

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CHAPTER 3
THE EFFECTS OF NUTRIENT-ENRICHMENT ON BELOWGROUND ORGANIC
MATTER ACCUMULATION OF SUBTROPICAL FLOATING MARSHES

INTRODUCTION

Nutrient enrichment is a pervasive disturbance to aquatic and wetland ecosystems that alters ecosystem structure and function (Svengsouk and Mitsch 2000, Verhoeven et al. 2006). In peat-producing wetlands, the rate of organic matter production exceeds decomposition, and the balance of these two processes can be influenced by nutrient availability, among other important biotic and abiotic forces (Webster and Benfield 1986, Neff et al. 2002). In contrast to north temperate and boreal *Sphagnum*-dominated communities, belowground production and subsequent organic matter decay largely determine rates of peat accretion in temperate marshes and tropical mangrove forests (Hackney and de la Cruz 1980, Hogg and Wein 1987, Scheffer and Aerts 2000, Middleton and McKee 2001, Turner et al. 2004). Even in tropical wetlands, slow root decay rates can control peat accumulation to compensate for low root productivity (Chimner and Ewel 2005).

Models of plant allocation to shoot or root growth have been described as a 'functional equilibrium' (Brouwer 1963) or optimal resource foraging (Tilman 1988). That is, an individual plant will respond to a light or CO₂ limitation with increased shoot growth; whereas, a water or nutrient limitation will result in greater allocation to root growth. It is also hypothesized that under restricted nutrient conditions a plant may increase root life-span to decrease nutrient loss and maximize nutrient acquisition (Ryser 1996, Eissenstat and Yanni 1997). Such phenotypic responses have been shown in controlled settings, but less evidence is available from wild communities to confirm the

hypothesis (Aerts and Chapin 2000). The majority of studies on root production in response to fertility gradients have been conducted in terrestrial grasslands and forests, with a focus on fine root dynamics. From this work it is accepted that a relative decrease in fine root biomass occurs with increasing soil fertility compared to aboveground biomass, but there are discrepancies as to the mechanisms responsible; that is, fertilization may actually increase root production with a concomitant reduction in root lifespan (increased root mortality; Hendricks 2006). Nonetheless, decreases in root biomass or macro-organic material with fertilization have been reported by some wetland studies (Valiela et al. 1976, Morris and Bradley 1999, Mack et al. 2004).

In addition to potential changes in plant allocation pattern and root life-span, decay of root-derived organic matter (OM) may be altered with increased nutrient availability. Compared to aboveground, information on belowground tissue decay is limited, much less so for tissue nutrient manipulations in wetland systems. The factors regulating aboveground decay may not exert the same order of importance belowground. For example, environmental and climate regulators were shown to be secondary to litter quality (nutrient and lignin tissue content) in controlling belowground root decay (Silver and Miya 2001). Belowground tissue decay in terrestrial habitats, from which most literature is available, is expected to be principally different from wetlands, based on the different biogeochemical transformations occurring in oxygen poor soils. For example, wetland sediment anoxia may minimize any effect of litter quality on OM decay rate (Conn and Day 1997).

The importance of OM nutrient quality and its influence on belowground decay remains an open question for different freshwater systems. Conflicting evidence exists

even within similar systems. For example, Qualls and Richardson (2000) reported an increased loss of *Cladium* tissue carbon with increased phosphate availability in a Florida marsh after one year. However, after three years Newman et al. (2001) found no effect of phosphate enrichment on *Cladium* litter decay. Accelerated short-term decomposition with fertilization is not necessarily sustained beyond the initial leaching phase (Valiela et al. 1976) when litter still contains a relatively high proportion of high quality carbon (Bridgham and Richardson 2003). Moreover, fertilization may stimulate the turnover of the low molecular weight soil organic matter fraction while stabilizing the heavier fraction (Neff et al. 2002).

The use of created and natural wetlands to control runoff of pollutants to aquatic systems has become a popular environmental management technique that has been used for the treatment of municipal wastewater and storm-water or agricultural runoff (Kadlec and Knight 1996). Although emergent wetlands are generally effective in reducing nutrients (especially N), how the process of plant production and organic matter decomposition are influenced with nutrient exposure is of increasing interest, especially as large scale restoration is planned for entire landscapes (e.g. Florida and Louisiana). Concerns that nutrient pollution can alter processes, stocks, and fluxes, and subsequently change emergent wetland composition and function are an impetus for this study. The objectives in this study were: 1) to determine natural rates of belowground organic matter accumulation and decomposition; 2) to determine whether increased N and P availability altered these rates; and 3) to estimate the rate of vertical accretion and nutrient accumulation.

MATERIALS AND METHODS

Study Sites

Two sites were located in the western (Francis Camp) and eastern (Lake Bouef) freshwater regions of the Louisiana coastal zone (Fig. 3.1).

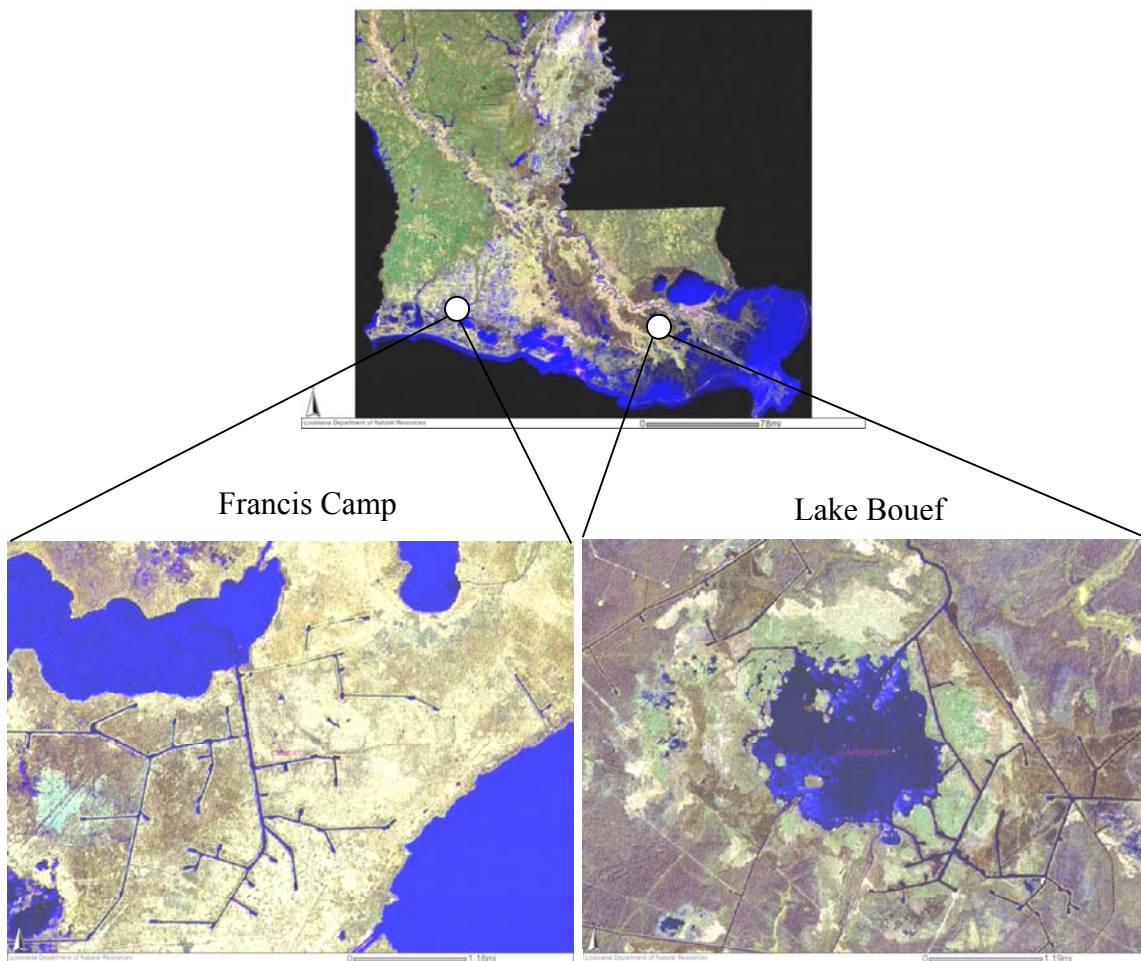


Figure 3.1. Locations of field sites in eastern (Lake Bouef) and western (Francis Camp) Louisiana.

The sites are geologically different with Francis Camp located in the low subsidence chenier plain and L. Bouef in the high subsidence delta plain. Despite these geological differences, both sites have floating peat-based mats. Lake Bouef is a long-term floating marsh research site (Sasser and Gosselink 1984, Sasser et al. 1995). At both sites the

cohesive floating mat is at least 30 cm thick, but the total peat thickness, including the free-floating mat and underlying peat deposit, is twice as thick (2 m) at L. Bouef than Francis Camp. Both sites were dominated by *Panicum hemitomon* (maidencane; comprising about 75% of the total biomass), and *Thelypteris palustris* (marsh fern) was an important species in terms of its density. Species richness was greater at L. Bouef (Sasser et al. 1995) than Francis Camp. Both sites can be described as organic-rich blackwater systems with minimal mineral sediment input.

Water and Soil Nutrients

Water from the marsh (pore) and from the closest source/receiving water body (open) was monitored for available nitrogen and phosphorus in the forms of NH_4^+ , $\text{NO}_3^- + \text{NO}_2^-$, and PO_4^{3-} . Samples were analyzed by the Coastal Ecology Institute Laboratory, Louisiana State University, with the following methods: alkaline phenol (NH_4^+), cadmium reduction ($\text{NO}_3^- + \text{NO}_2^-$), and ammonium molybdate/ascorbic acid (PO_4^{3-}). Pore-water was collected from the upper 5-8 cm of the mat and filtered through a 0.45 μm nylon filter, and aliquots of each sample were separated for N and P analysis. One pore-water sample was collected from each of five random plots in each treatment; open-water samples were collected from just below the water surface at three different stations. Samples were kept on ice in the field and frozen in the laboratory until analysis. For the duration of this study, there were eight sampling seasons that were common between the sites. The spring and summer of 2004 were not sampled at L. Bouef due to logistical problems. At each site and treatment, core samples ($n=9$; 680 cm^3) from the upper 15 cm of the peat mat were collected for soil nutrient analyses after one year of fertilization (spring 2003). After drying, the samples were homogenized in a Wiley mill (#40 mesh).

Soil samples were analyzed with a Perkin Elmer 2400 CHN analyzer by the Coastal Ecology Institute Laboratory, LSU. Soil nutrients for the radiometric dating core collected at L. Bouef were analyzed for total C, N, and P. These samples were analyzed by the Louisiana State University, AgCenter, Plant and Soil Analysis Lab (Baton Rouge). Total C and N were analyzed by combustion (Leco CHN analyzer), and total phosphorus was analyzed on an inductively coupled plasma spectrophotometer (ICP) following digestion with HNO₃ and H₂O₂. Nutrient concentrations were reported as % mass of dry weight.

Hydrologic Variables

Continuous water level, salinity, and temperature (YSI 6920, Yellow Springs, OH) was sampled at hourly intervals at both sites for 185 days (6Feb05-8Aug05) during the experimental ('enriched') decomposition experiment (see below).

Belowground Accumulation

Root and rhizome accumulation was measured with an ingrowth coring method. Since the interval of sampling was approximately one and two years, both production and decomposition occurred, resulting in an estimate of net organic matter accumulation. The time duration of ingrowth cores between their deployment (Apr 2002) and re-sampling (Apr-May 2003 and 2004) lasted 304 and 694 days for L. Bouef and 275 and 730 days for Francis Camp.

The ingrowth cores were deployed in the following manner. A 9.2 cm thin-walled aluminum core tube was used to excavate the peat to a depth of 20 cm and create a cylinder shaped hole. The bottom of the hole was naturally bound with cohesive peat, which extended another 20 cm deeper (total mat thickness~40cm). The hole was then

filled with milled sphagnum (no added nutrients; Jiffy, Batavia Illinois) and packed to a firm density that was level with the surrounding peat mat. A plastic marker flag was inserted in the center of the hole to enable re-coring. Re-coring was done with a smaller diameter (7.6 cm) aluminum tube, which was driven to a depth of 20 cm or more to capture the original peat bottom. The cored material was extruded in the field and the upper 15 cm was taken as the sample.

In the laboratory, the ingrown root and rhizome material was separated from the commercial peat by wet-sieving through a 1.0 mm mesh). The material was classified as either root (<2.0 mm) or rhizome (>2.0 mm). I could not distinguish with repeatable certainty, whether roots and rhizomes were live or dead, given their well preserved nature; thus, the material is considered total macro-organic matter. The material was dried to a constant weight and recorded to the nearest 0.01 g.

Belowground Decay

Two separate belowground decay experiments were conducted, referred to as ‘natural’ and ‘enriched’. The former was done to measure natural rates of root and rhizome decay over 17 months; whereas, the ‘enriched’ decay was done to determine whether nutrient availability (external) and tissue quality (internal) affected decay rates over 8.6 months. For the ‘natural’ decay experiment, roots and rhizomes were collected by coring at each site during spring 2002. The material was air dried in the laboratory, and roots and rhizomes that appeared ‘fresh’ were separated from more decomposed material. Uniform root and rhizome material (most roots and rhizomes were from *P. hemitomon*) was selected, and large tubers of some species (e.g. *Sagittaria*, *Solidago*, *Vigna*) were excluded. Fiberglass mesh bags (1.0 mm openings) were filled with

approximately eight and two grams of rhizomes and roots, respectively. In the field, root and rhizome bags were paired and inserted to a depth of 10 cm below the peat mat surface. Replicate bags (n=6) of each tissue type by site combination were retrieved at 93, 286, and 533 days from L. Bouef. At Francis Camp, replicate bags (n=9) were retrieved after only two time intervals 294 and 519 days.

For the 'enriched' decay experiment, root and rhizome tissue was collected from each site by treatment combination during summer 2004, two years after fertilization began. The methods of separating material, the mass of each tissue type used, and field deployment techniques were conducted in the same manner as the first experiment, except that enriched (fertilized) and un-enriched (controls) roots and rhizomes were crossed between fertilized and unfertilized plots; this resulted in two treatment levels each for site (L. Bouef, Francis Camp), internal enrichment (control, fertilized), external enrichment (control, fertilized), and tissue type (root, rhizome). Replicate bags (n=10) of each tissue type by treatment combination were retrieved after 269 and 246 days from L. Bouef and Francis Camp.

Sediment ^{210}Pb and ^{137}Cs

From the L. Bouef site, one core (10 cm diameter, 40 cm depth) was collected (3Feb2005) to estimate rates of organic matter and nutrient accumulation. The core was frozen and then sectioned at 0.8 cm intervals with a band-saw. Three measurements of thickness were taken on each section to compute an average thickness. Oven-dried (60°C) samples were weighed prior to being ground in a Wiley mill (#40-mesh screen). Sample vials were packed with ~0.5 g of homogenized material, sealed with epoxy, and set aside for at least 25 days to allow ingrowth of ^{214}Pb and ^{214}Bi with secular equilibrium

with ^{226}Ra . The activities of ^{210}Pb , ^{226}Ra , and ^{137}Cs were analyzed with gamma spectroscopy on an intrinsic germanium well detector (Canberra Industries, Meriden, CT). Excess ^{210}Pb was calculated by subtracting ^{226}Ra from total ^{210}Pb and decay corrected for the time of collection. A constant activity model (Appleby and Oldfield 1992) was used to estimate soil accretion, which was calculated as: $s = \lambda/m$, where (s) is the sedimentation rate (cm y^{-1}), (λ) is the decay constant of ^{210}Pb (0.0311 y^{-1}), and (m) is the slope of the regression of the natural log of excess ^{210}Pb activity (y) against depth (x). An additional check for sediment accretion was the depth (cm) of the peak of ^{137}Cs activity, which is assumed to represent the 1964 peak in thermonuclear weapons testing (Ritchie and McHenry 1990). Depth specific C, N, and P content was weighted by the mass of each depth interval and then summed for the whole core (40 cm) for nutrient accumulation calculations.

Experimental Set-up and Fertilization

Ingrowth cores and decomposition bags were established along four random plot lines, where each line comprised nine 1.0 m^2 experimental plots ($n=36$ plots, for each site-treatment). The plot lines were segregated by treatment, given the uncertainty of fertilizer drift. Ingrowth cores and decomposition bags were retrieved randomly by time period. Each plot received 68, 18, and 28 $\text{g m}^{-2} \text{ yr}^{-1}$ of N, P, and K, respectively. Fertilizer was applied twice yearly in March and October. The controlled release fertilizer was 19-5-8 (%N, P, K) Osmocote (Scotts-Sierra Horticultural Products Co., Marysville, OH). The forms of nitrogen and their percentages were: ammoniacal (6.6%), nitrate (5.6%), and urea (6.8%). Phosphorus and potassium were in the form of P_2O_5 and K_2O , respectively. The relatively high application rate was designed to reduce competition for

nutrients between the plant and microbial community and compensate for lateral and vertical hydraulic losses that were expected in these highly permeable peat mats.

Data Analyses

Rates of organic matter accumulation ($\text{g m}^{-2} \text{d}^{-1}$) were calculated based on ingrowth deployments of 304 and 694 days for L. Bouef and 275 and 730 days for Francis Camp. Accumulation of organic matter (g m^{-2}) was computed for 365 and 730 days to make sites comparable for analysis. A two-way ANOVA (PROC GLM, SAS 2003) with the effect of site and treatment on dependent variables of accumulation (total, root, rhizome) was performed separately for each year. These data were natural logarithm transformed for normality of the residuals (Shapiro-Wilk test), and homogeneity of variance was tested with a Levene's test. Tukey-Kramer adjustments were used for testing significance among site and treatment pairwise comparisons. Significance was determined at $\alpha=0.05$. Regression analyses (PROC REG; SAS 2003) were performed on pore-water nutrients, water level, salinity, and temperature.

For the natural decomposition experiments, annual decay coefficients (k) were calculated with a single exponential decay model: $\ln(X_t/X_0)=-kt$, where X_t =final mass, X_0 =initial mass, and t =time (Olson 1963). A double exponential was also calculated: $\text{mass remaining}=ae^{-k_1t} + be^{-k_2t}$, where a =percent labile organic matter, and b =percent refractory organic matter, and k_1 and k_2 are instantaneous decay rates for each organic matter fraction (Wieder and Lang 1982). Data from both sites were combined to estimate mean natural decay rates for freshwater marshes. For the 'enriched' experiment, a daily rate of mass loss was computed and then the mass remaining was standardized to 258 days to account for different deployment durations between the sites. The mass remaining

after 258 days was used as the dependent variable in the ANOVA to detect treatment differences.

RESULTS

Water and Soil Nutrients

Available nutrients under control conditions were low in the pore-water at both sites and were similar to the adjacent open water bodies (Fig. 3.2). At the beginning of the experiment (spring 2002), prior to fertilization, similar levels of N and P were observed in control and fertilized treatments within each site (Fig. 3.3). Not until fall 2002 were N and P fertilization effects noticeable (Fig. 3.3). In general, fertilization produced available N and P concentrations that were at least an order of magnitude higher than controls (Fig. 3.2). No discernable seasonal trends were observed of interstitial nutrient availability in either fertilized or control plots within each site (Fig 1.3). From fall 2002 to spring 2003 $\text{NO}_2^- + \text{NO}_3^-$ remained elevated at Francis Camp compared to L. Bouef. During winter 2004, L. Bouef had extremely high PO_4^{3-} concentrations ($>3.0 \text{ mg l}^{-1}$) that were not observed at Francis Camp (Fig. 3.3). There was a strong positive relationship ($r^2=0.79$) of NH_4^+ concentration in control plots between the two sites and a slight positive relationship ($r^2=0.37$) of $\text{NO}_2^- + \text{NO}_3^-$ (Table 3.1).

Table 3.1. Linear regression results of treatment effects between Lake Bouef (x) and Francis Camp (y) on pore-water nutrient concentrations for n=8 sampling seasons.

Nutrient	Control	Fertilized
$\text{NO}_2^- + \text{NO}_3^-$	$y=0.442x + 0.002$ $r^2=0.37$	$y=2.780x + 0.056$ $r^2=0.21$
NH_4^+	$y=1.567x - 0.004$ $r^2=0.79$	$y=-0.239x + 0.406$ $r^2=0.03$
PO_4^{3-}	$y=-0.092x + 0.013$ $r^2=0.35$	$y=-0.040x + 0.207$ $r^2=0.04$

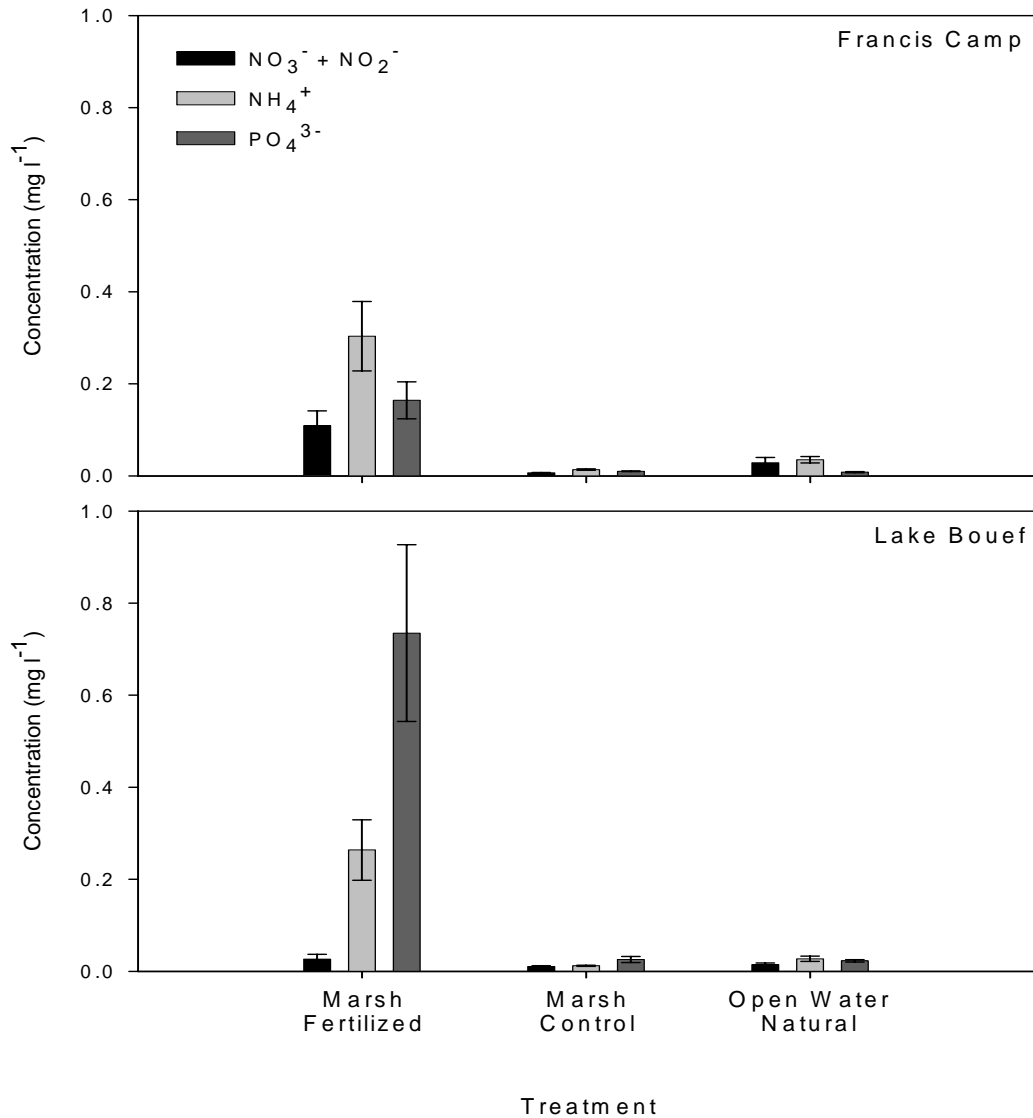


Figure 3.2. The mean effect of fertilization on pore-water nutrient concentrations compared to control conditions in the marsh plots at experimental sites. Nutrient concentrations of surface water from the adjacent bayous are included for comparison. High phosphate at the Lake Bouef fertilized plots was influenced by an immediate post-fire sampling during the winter of 2004 (see Fig. 3.3). Means ($\pm 1SE$) represent $n=10$ and $n=8$ sampling periods from Francis Camp and Lake Bouef, respectively, over three years.

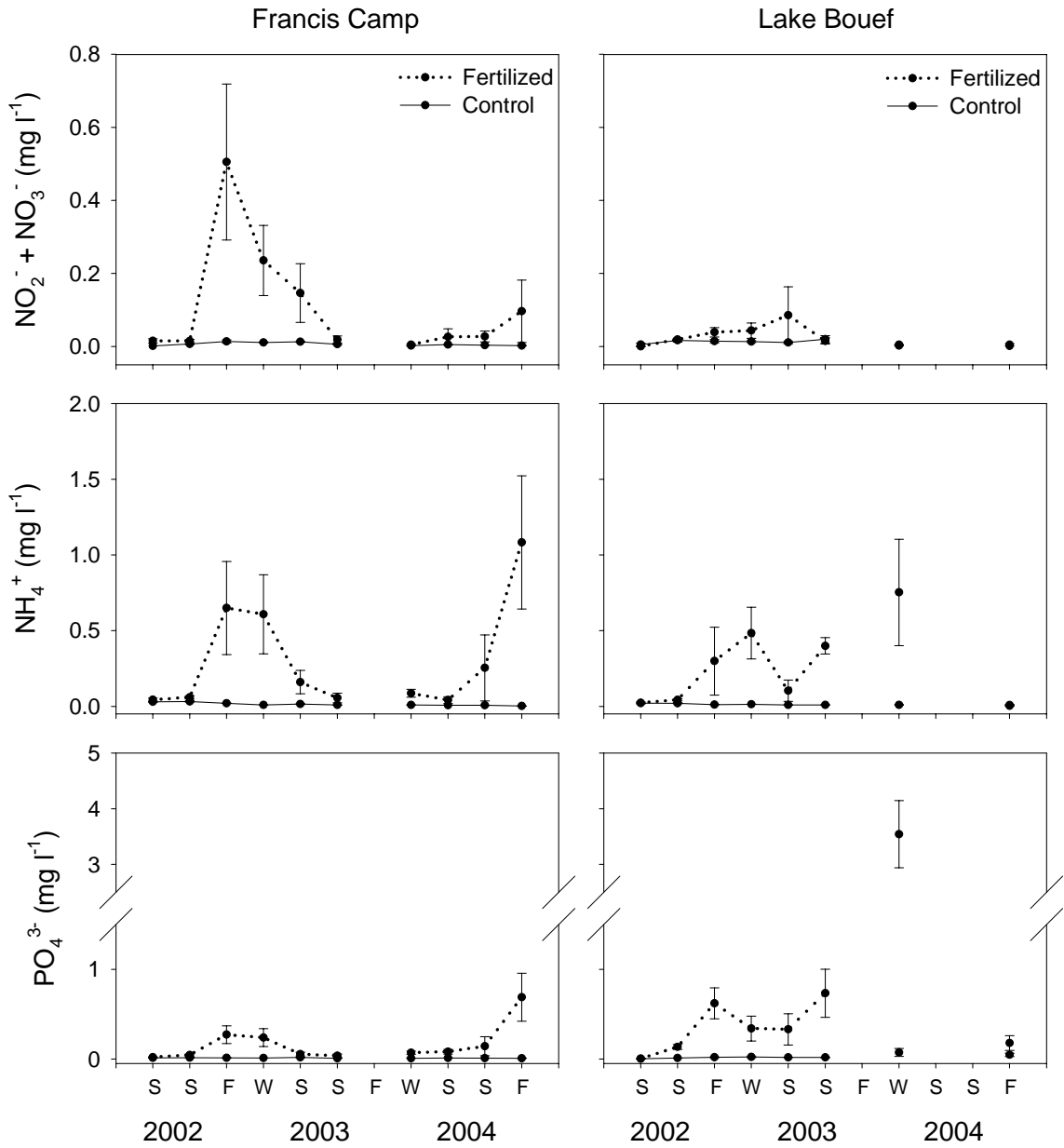


Figure 3.3. Comparison of seasonal changes of marsh pore-water nutrient concentrations at both sites in control and fertilized plots. The first samples (spring 2002) are prior to fertilizer treatment. During 2004, spring and summer samples are missing for Lake Bouef.

In contrast to available nitrogen, PO_4^{3-} was negatively related ($r^2=0.35$) between control plots at the sites (Table 3.1). Maximum concentrations of PO_4^{3-} in both control and fertilized plots were 3-fold greater at L. Bouef than those observed at Francis Camp. After one year of fertilization, C/N ratios decreased compared to control plots (Fig. 3.4).

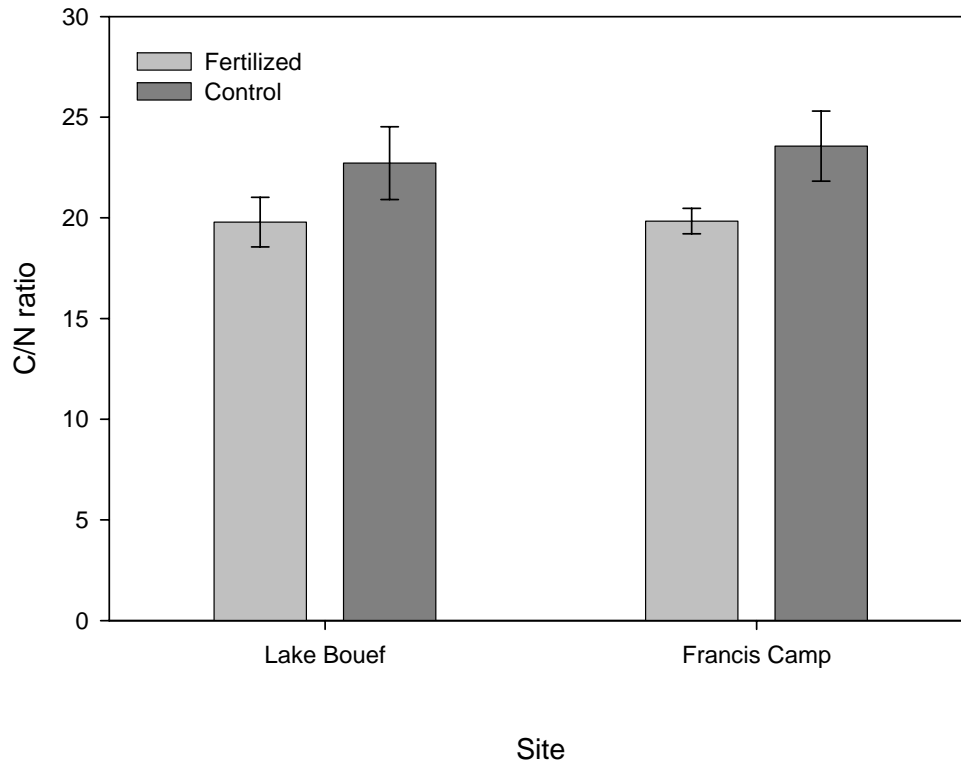


Figure 3.4. The effect of fertilization on the carbon:nitrogen ratio of the soils from each site after one year of treatment. Means ($\pm 1\text{SE}$) represent $n=9$ samples from each site and treatment.

Resulting C/N ratios were similar at 19.8 ± 1.2 and 19.8 ± 0.6 for L. Bouef and Francis Camp, respectively. Control C/N ratios were 22.7 ± 1.8 and 23.6 ± 1.7 for L. Bouef and Francis Camp, respectively.

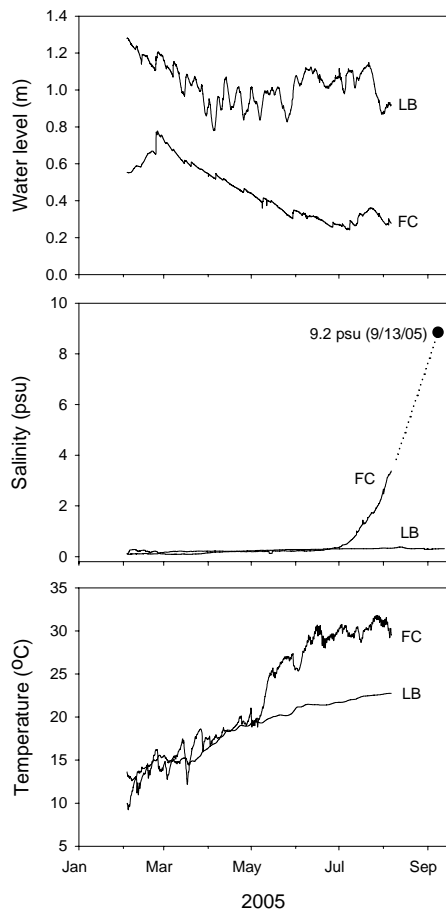


Figure 3.5. A comparison between sites (FC, Francis Camp; LB, Lake Bouef) of hourly water level (upper), salinity (middle), and temperature (lower) during a portion of the study period. Water levels are relative to an arbitrary datum. At Francis Camp, a locally severe drought began in June and lasted into early autumn. The gage at Francis Camp quit recording, but elevated salinity (>9.0 psu) was measured during gage retrieval on 9/13/2005.

Hydrologic Variables

From Feb-Aug 2005, both sites exhibited a similar total range (0.5 m) of water height fluctuation. But there was a marked difference in seasonal fluctuation with an incremental decrease in mean water level from spring to late summer at Francis Camp, while L. Bouef oscillated with frontal activity and stabilized in summer months (Fig. 3.5). A localized drought at Francis camp beginning Jun 2005 resulted in incrementally increasing salinity through 13 Sep 2005, when a measurement of >9.0 psu was recorded.

For the experimental period of 2002-2005, prior to this drought, Francis Camp remained entirely fresh (<0.5 psu). Coinciding with the 2005 summer drought, water temperature became elevated at Francis Camp compared to L. Bouef (Fig. 3.5). Based on daily means, water temperature was ~3.5 ° higher at Francis Camp than L. Bouef for this period of interest (Table 3.2). A 1.0°C change in water temperature at Francis Camp was related to a 0.45°C change at L. Bouef ($r^2=0.93$). Daily mean water levels were unrelated ($r^2=0.10$; Table 3.2).

Table 3.2. Means (1±SE) of the daily mean hydrologic variables and linear regression results between Lake Bouef (y) and Francis Camp (x) from 2Feb05-6Aug05. Depth of water level is above underlying clay pan.

Variable	Lake Bouef (y)	Francis Camp (x)	Regression
water level (m)	1.8±0.1	0.95±0.1	$y=0.233x + 0.926$ $r^2=0.10$
temperature (°C)	18.7±3.1	22.2±6.6	$y=0.449x + 8.739$ $r^2=0.93$
salinity (psu)	0.22±0.09	0.48±0.65	$y=0.066x + 0.185$ $r^2=0.26$

Belowground Accumulation

After one year, there was a significant treatment effect ($F_{1,44}=7.25$, $P=0.01$) on total accumulation, with greater accumulation in the fertilized than the control by 327 g m⁻² (Fig. 3.6 and Table 3.3). After two years, treatment significantly affected total accumulation ($F_{1,44}=6.18$, $P=0.02$); however, accumulation in the controls was 295 g m⁻² greater than fertilized. There was not a significant site or site-treatment interaction for total accumulation for either year (Table 3.3). The differences in total accumulation

between the first and second year (representing a gain or loss of organic matter with time) were influenced by treatment: the fertilized treatments at both sites showed a loss, while

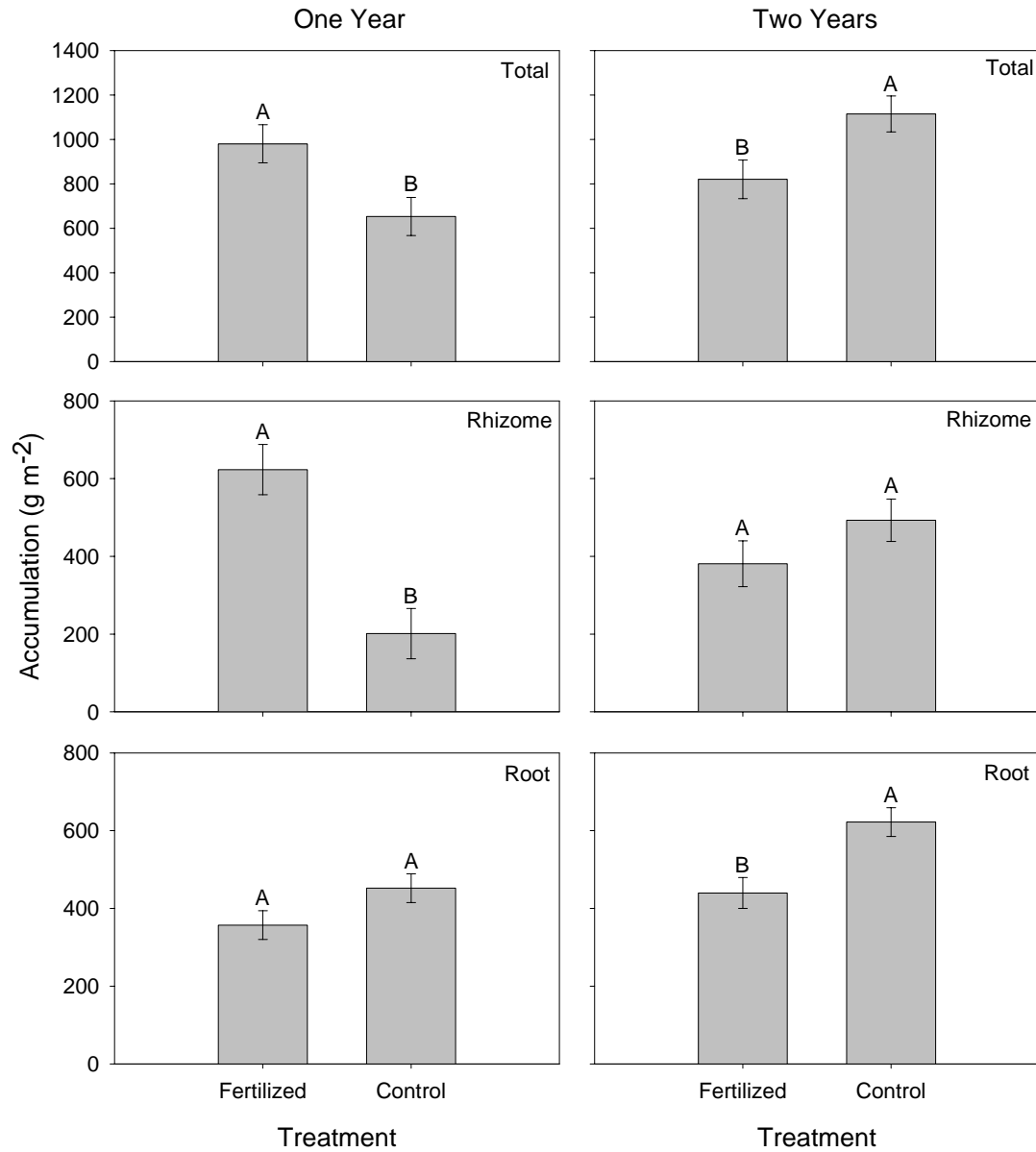


Figure 3.6. Cumulative belowground organic matter accumulation with treatment (mean of both sites) after one and two years. Year one means based on n=12 per treatment; year two means based on n=21 (fertilized) and n=27 (control). Significant differences ($p \leq 0.05$) of the means ($\pm 1SE$) are indicated by different letters.

the controls showed a gain in organic matter (Table 3.4). The between-year gain or loss of total organic matter was greater at L. Bouef than Francis Camp (Table 3.4).

Table 3.3. Statistical evaluation of root, rhizome, and total (root +rhizome) biomass accumulation using analysis of variance (ANOVA) for one and two years.

Year	Variable	Source of variability		
		Treatment	Site	Trmt* Site
One	Total	0.0100	0.4616	0.0807
	Root	0.0751	0.2044	<.0001
	Rhizome	<.0001	0.8027	0.7301
Two	Total	0.0168	0.2303	0.1777
	Root	0.0016	0.0020	0.6121
	Rhizome	0.1715	0.6802	0.1016

Table 3.4. Mean difference in the gain or loss (-) of belowground organic matter (g m^{-2}) between the ends the first year and the second year. Sites are Lake Bouef (LB) and Francis Camp (FC).

Site		Total		Rhizome		Root	
		LB	FC	LB	FC	LB	FC
Treatment	Fertilized	-232	-87	-299	-186	67	99
	Control	768	155	338	245	430	-91

The contribution of root or rhizome material to total accumulation was affected by site, treatment, and year (Table 3.3). Rhizome accumulation responded strongly to fertilization in the first year at both sites with an excess of 422 g m^{-2} in the fertilized compared to the control (Fig. 3.6). But by the second year rhizome accumulation was equal between treatments (Fig. 3.6).

Root accumulation in the first year exhibited a site-treatment interaction: at Francis Camp accumulation in the control exceeded the fertilized treatment ($P=0.0002$),

Table 3.5. Site-specific accumulation (g m^{-2}) of total, root, and rhizome tissue after one and two years. Different letters indicate significant differences ($P < 0.05$) within each row or tissue type.

	Lake Bouef				Francis Camp			
	Fertilized		Control		Fertilized		Control	
	yr 1	yr 2	yr 1	yr 2	yr 1	yr 2	yr 1	yr 2
total	1043.7 (112.6) ^a	811.4 (130.0) ^{ab}	499.7 (112.6) ^b	1267.8 (130.0) ^a	916.8 (121.3) ^a	829.5 (121.3) ^a	806.9 (121.3) ^a	961.6 (99.1) ^a
rhiz- ome	595.7 (76.2) ^a	296.8 (88.0) ^{ab}	205.5 (76.2) ^b	543.2 (88.0) ^a	650.5 (90.7) ^a	464.7 (90.7) ^{ab}	196.7 (90.7) ^b	442.0 (74.0) ^{ab}
root	448.0 (54.0) ^b	514.6 (62.4) ^{ab}	294.2 (54.0) ^b	724.6 (62.4) ^a	266.3 (50.5) ^c	364.8 (50.5) ^{bc}	610.2 (50.5) ^a	519.6 (41.2) ^{ab}

and at L. Bouef there was no difference between treatments ($P=0.1733$). By the second year, the main effects of site ($F_{1,44}=10.75$, $P=0.002$) and treatment ($F_{1,44}=11.36$, $P=0.002$) significantly affected root accumulation: L. Bouef was greater than Francis Camp by 177 g m^{-2} (Table 3.5), and the controls exceeded the fertilized by 182 g m^{-2} (Fig. 3.6). The gain or loss of root material from the first to second year was site dependent. At Francis Camp there was a non-significant loss of root mass in the controls, whereas there was a significant gain observed in the controls at L. Bouef (Table 3.4).

Belowground Decomposition

To estimate a general rate of belowground organic matter decay, the mass loss data was combined from both sites with respect to each tissue type. After about 530 days or 17 months, natural decomposition accounted for the loss of $34\pm 6\%$ and $40\pm 3\%$ of the original mass of roots and rhizomes, respectively. More than 90% of this loss occurred within the initial 270 days or nine months. Based on a single exponential model, loss rates (k , d^{-1}) were 0.0011 ± 0.0001 and 0.0013 ± 0.0002 of roots and rhizomes, respectively (Table 3.6). The decay rates were best described with a double exponential model, which captured the initial rapid rate of loss that affected $\frac{1}{4}$ of the organic matter and a slower rate of loss for the remaining $\frac{3}{4}$ of the organic matter (Table 3.6). Based on the double exponential model ($\text{MR}=26.0\% e^{0.0248\text{-d}*(3650\text{d})} + 74.0\% e^{0.00035\text{-d}*(3650\text{d})}$, $k =$ mean of root and rhizome), after 10 years, about 21% of the original material would remain, contrasted with about 1% if the of the single exponential model ($k=0.0012 \text{ d}^{-1}$) was used. The half-life and residence time of belowground organic matter in the single exponential model is estimated at 577 and 833 days, respectively.

Table 3.6. Natural decay rates ($-k$, day^{-1}) determined from single and double exponential decay models. A composite of data from both sites was used to estimate mean rates of decomposition after 17 months incubation.

Tissue type	$MR=100e^{-kt}$		$MR=ae^{-(k1)t} + be^{-(k2)t}$				
	$-k$	r^2	a	b	$-k1$	$-k2$	r^2
Rhizome	$0.0013 \pm$	0.59	26.7	73.3	$0.0251 \pm$	$0.0004 \pm$	0.77
	0.0002				0.0140	0.0001	
Root	$0.0011 \pm$	0.31	25.2	74.8	$0.0245 \pm$	$0.0003 \pm$	0.70
	0.0001				0.0142	0.0001	

Results from the ‘enriched’ decomposition experiment showed that internal ($F_{1,133}=3.13$, $P=0.08$) or external ($F_{1,133}=0.29$, $P=0.59$) treatments alone did not affect the combined mass loss of roots and rhizomes (Table 3.7). The cross of the main effects of internal and external enrichment resulted in no significant difference ($P=0.67$); such that, the mass loss of control tissue ($68.0\pm0.7\%$) and completely enriched (internal + external; $67.0\pm0.7\%$) was almost equal (Fig. 3.7).

Table 3.7. Statistical analysis of the internal vs external decomposition experiment. Tissue type refers to root or rhizome material. Site was used as a random variable.

Source of variability	DF	F Value	Pr > F
tiss_type	1	45.22	<.0001
int_trt	1	3.13	0.0793
tiss_type*int_trt	1	28.13	<.0001
ext_trt	1	0.29	0.5937
tiss_type*ext_trt	1	3.04	0.0836
int_trt*ext_trt	1	0.18	0.6709
tiss_type*int_trt*ext_trt	1	0.01	0.9384
site	1	41.13	<.0001
site*tiss_type	1	0.04	0.8454
site*int_trt	1	0	0.9605
site*tiss_type*int_trt	1	1.15	0.2861
site*ext_trt	1	0.82	0.3655
site*tiss_type*ext_trt	1	0.48	0.4908
site*int_trt*ext_trt	1	0.47	0.4923
site*tiss_type*int_trt*ext_trt	1	0.26	0.6079

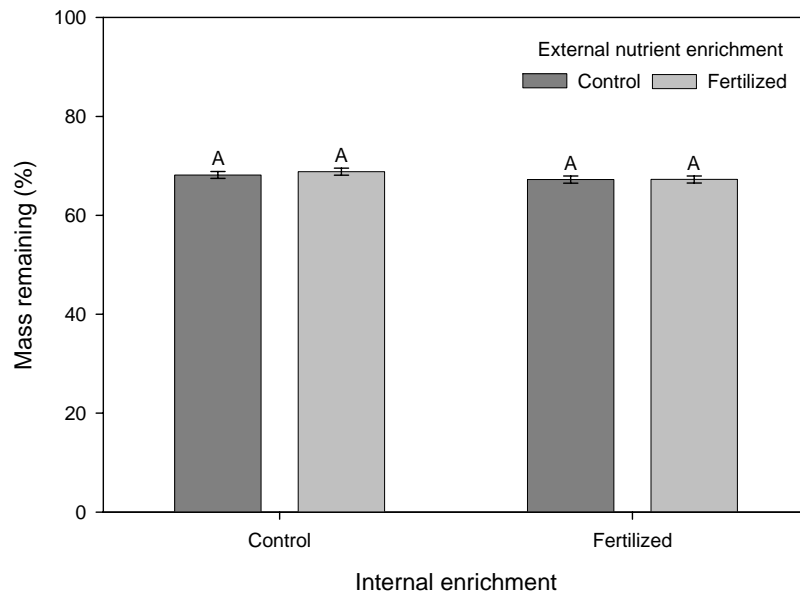


Figure 3.7. Means ($\pm 1SE$) of the mass remaining of roots and rhizomes combined after 258 days with internal and external nutrient enrichment.

The effect of tissue type-internal treatment was significant (<0.0001): although there was no difference in mass remaining between internally enriched vs control rhizomes, roots that were internally enriched decayed more than controls by 5% (Fig. 3.8).

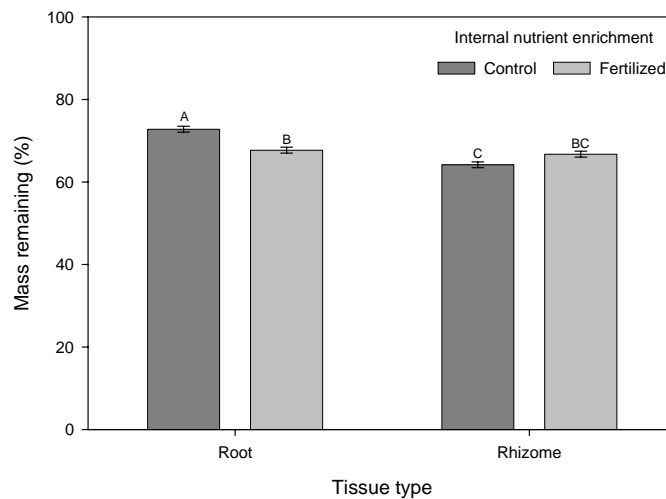


Figure 3.8. Root and rhizome mass remaining after 258 days by internal (tissue) nutrient enrichment treatment.

Pairwise comparisons of tissue type-internal treatment-external treatment showed that completely enriched roots lost significantly more mass (7%) than control roots, but this effect was not observed for rhizomes (Fig. 3.9).

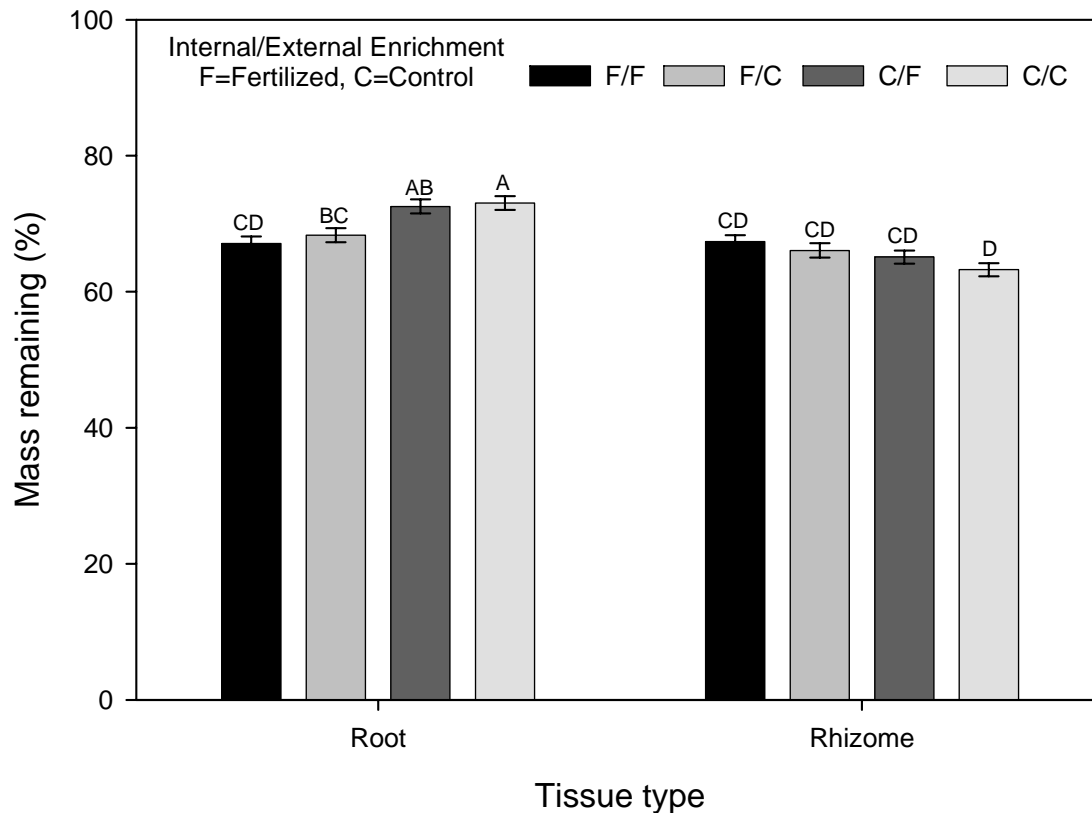


Figure 3.9. Root and rhizome mass remaining after 258 days by internal (tissue) and external (site) nutrient enrichment treatment.

There was a significant effect of tissue type, such that root mass loss was less than rhizomes ($70.1 \pm 0.7\%$ and 65.3% , respectively). The significant site effect ($P < 0.0001$; Table 3.7) was attributable to a 5% greater mass loss at Francis Camp than L. Bouef.

Sediment ^{210}Pb and ^{137}Cs

In general, excess ^{210}Pb activity decreased from the surface to a depth of 30 cm, below which, activity was highly variable and greater than 0 (Fig. 3.10). From 0-6 cm,

excess ^{210}Pb activity showed no variation with depth, which was interpreted as a zone of mixing (Fig. 3.10).

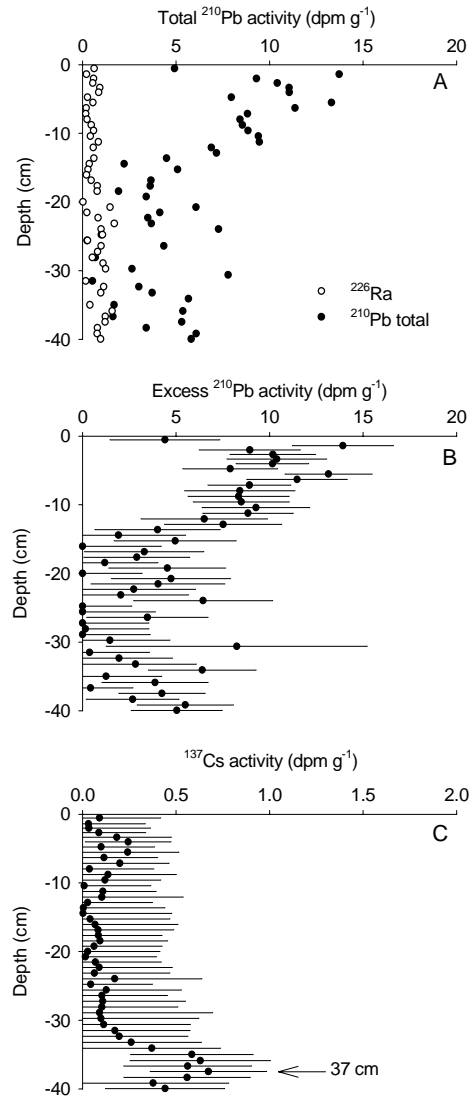


Figure 3.10. Total ^{210}Pb and ^{226}Ra (A), excess ^{210}Pb (B), and ^{137}Cs (C) activities with depth in a core from Lake Bouef. The two regions of the core used for ^{210}Pb dating were the 6-18 cm and 9-18 cm intervals, which yielded accretion rates of 0.21 cm yr^{-1} ($r^2=0.88$) and 0.28 cm yr^{-1} ($r^2=0.86$). A specious, low activity peak of ^{137}Cs was measured at 37 cm, which translates into an accretion estimate of 0.88 cm yr^{-1} (based on the 1964 fallout peak).

Table 3.8. Comparisons of sediment accretion rate and nutrient accumulation among different wetland types. All sediment accretion estimates are based on ²¹⁰Pb dating, or ¹³⁷Cs as indicated by (*).

Wetland Type	Accretion rate (cm yr ⁻¹)	Accumulation (g m ² yr ⁻¹)			
		Sediment	C	N	P
Everglades ¹ enriched	0.58-0.67	--	184-223	13.6-16.6	0.40-0.46
un-enriched	0.14-0.16	--	65-90	4.7-6.4	0.06
Depressional ²	0.14	948±257	70±18	5.3±1.3	0.25±0.08
Floodplain forest ²	0.19	1298±126	107±12	8.0±0.6	0.75±0.06
Brackish marsh ³	0.14-0.32	--	84±23	--	--
Salt marsh ⁴	0.26±0.04	--	--	--	--
Freshwater deltaic ⁵	0.75*	--	--	12	--
Freshwater deltaic ⁶	0.72-1.02*	621-1056	--	--	--
This study	0.21-0.28	120-160	50-67	2.1-2.8	0.10-0.13
	0.88*	503	210	8.8	0.41

¹Craft and Richardson 1998 (FL); ²Craft and Casey 2000 (GA), depressional included marsh, pine savannah, and tupelo-gum forest; ³Hussein et al. 2004 (MD), ⁴Roman et al. 1997 (RI), ⁵DeLaune et al. 1986 (LA); ⁶Nyman et al. 2006

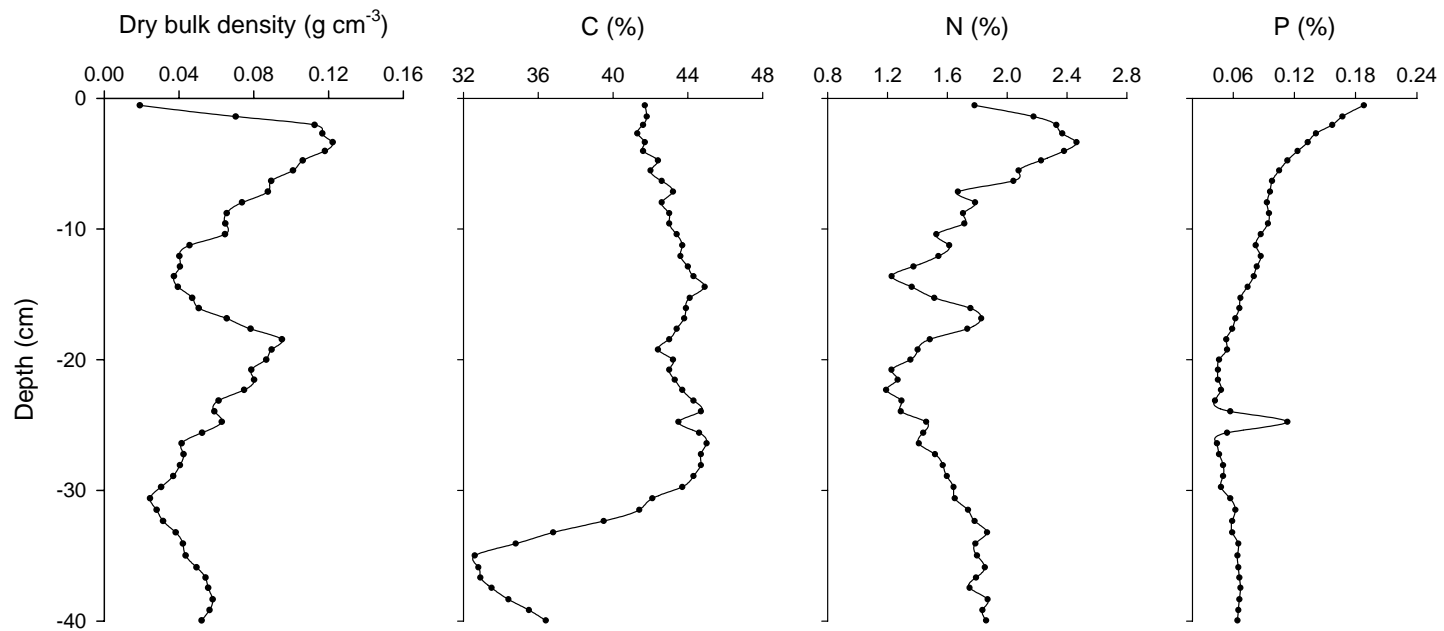


Figure 3.11. Depth distribution of soil nutrient content in a core from Lake Bouef used for estimates of carbon and nutrient accumulation. Multiply % by 10 to convert to mg g⁻¹.

The depth intervals of 6-18 cm and 9-18 cm showed accretion rates of 0.28 cm yr^{-1} ($r^2=0.86$) and 0.21 cm yr^{-1} ($r^2=0.88$), respectively. A low activity ^{137}Cs peak ($<1.0 \text{ dpm g}^{-1}$) was measured at 37 cm, which translated into an accretion rate of 0.88 cm yr^{-1} . Based on these estimates of accretion, a range of C, N, and P accumulation was calculated (Table 3.8). With depth, there was little variation of C, and there was an incremental decrease of P from the surface to the bottom of the soil column (Fig. 3.11). Nitrogen content was variable with depth, and there was a limited relationship with bulk density ($r^2=0.23$, Fig. 3.11).

DISCUSSION

An important finding of this study was that fertilization did not increase total belowground accumulation after two years. In fact, a reduction was observed, with a greater response at the L. Bouef site. In general, this reduction could be caused by either accelerated decomposition, reduced belowground allocation with fertilization, or a combination thereof. The combined results from both sites showed that fertilization resulted in a net loss of about 160 g m^{-2} of total organic matter between the end of the first and second years, while the controls gained 430 g m^{-2} . This difference was largely influenced by rhizome loss or gain; that is, rhizomes lost an estimated 240 g m^{-2} with fertilization and gained 290 g m^{-2} in controls between the first and second years. The loss of rhizome mass in fertilized plots between years is particularly interesting, since an accelerated decay of rhizomes was not observed, even with combined internal and external nutrient enrichment.

Although the loss of rhizome mass between the first and second year with fertilization is equivalent to the amount of decomposition that is estimated to occur over a

year (35% for rhizomes) regardless of treatment, this would imply that almost no new growth of rhizomes occurred during the second year with fertilization. This is conceivable only if new rhizome growth of the dominant plant (*Panicum hemitomon*) was not required to produce new culms during the second growing season—this is unlikely.

A summary of the community changes and aboveground biomass response (Chapter 2) is important at this point. In general, fertilization resulted in a doubling of aboveground biomass compared to the controls, with *P. hemitomon* representing almost all of the biomass increase. Individual culm biomass of *P. hemitomon* almost tripled with fertilization, while culm density remained similar between the treatments for both growing seasons. This large biomass increase of *P. hemitomon* with fertilization resulted in the disappearance of the rhizomatous fern, *Thelypteris palustris*. Though this fern was not highly productive in terms of aboveground biomass, it consistently ranked the highest in stem density (300-400 stems m⁻²) at both sites; most likely *T. palustris* contributes considerably to rhizome and root deposition. Thus, the decrease in belowground accumulation after two years of fertilization should include the potential lost contribution of an important species of the community rather than a simple decrease in belowground allocation (rhizome deposition) by the dominant species. Decreases in species richness typically occur as nutrient availability increases above a low or intermediate level (Pratt 1984, Tilman 1987, Theodose and Bowman 1997, Bedford et al. 1999).

During the first year, fertilization did not result in decreased root accumulation at both sites; by the second year, root biomass was greater in the control compared to fertilized plots by the same difference (29%) at both sites. Since decomposition of internally and externally enriched roots was enhanced by about 7% yr⁻¹ compared to

controls, any difference greater than 14% (two years of enhanced decomposition) should be attributed to reduced root deposition, which in this case amounts to about a 15% root biomass deficit. Reduction of fine root biomass with N fertilization has been attributed to increased root mortality (Aber et al. 1985), and root lifespan is predicted to be extended under infertile soil conditions, presumably due to the high metabolic investment into new growth (Eissenstat and Yanai 1997).

Wilson and Tilman (1993) propose that above- and belowground competition for a limiting resource (e.g. light or nutrients) is inversely related, such that increasing soil infertility may intensify belowground competition; or in contrast, increasing soil fertility may intensify aboveground competition. Rather than passively tolerating changing resources, plants are capable of adjusting their morphology and allocation pattern to optimally forage for nutrients, light, or water (Slade and Hutchings 1987, Tilman and Wedin 1991, Hendricks et al. 1993, Pregitzer et al. 1993, Gleeson and Good 2003). What remains uncertain here is, whether the reduced standing stock of root biomass relative to aboveground biomass that is commonly observed with increasing soil fertility is due to the mechanism of a simple reduction in allocation to root growth with constant mortality (differential allocation) or an increase in root mortality while root production remains constant or increases with increased fertility (constant allocation) (Hendricks et al. 2006). While there is strong evidence for a reduction in allocation to root biomass relative to shoot biomass or a reduction in root to shoot ratios with fertilization (Shaver and Billings 1975, Good et al. 1982, Aerts 1992, Gusewell et al. 2003, El-Kahloun et al. 2003), increased root production has also been observed with fertilization (Aber et al. 1985, Nadelhoffer et al. 1985, Tilman and Wedin 1991, Stevenson and Day 1996).

Although aboveground litter contributes to peat accretion, root deposition and slow decay rates are relatively more important (Hogg and Wein 1988, Kratz and DeWitt 1986, Chen and Twilley 1999, Middleton and McKee 2001, Chimner and Ewel 2005). In this study, both slow decomposition and moderately high production account for the deep peat accumulations that are typical of the freshwater deltaic wetlands of Louisiana (Kosters et al. 1987). Based on the double exponential model, about 20% of the original organic matter could remain after 10 years, which compares favorably with estimates of root decay in Micronesian mangrove forests (Chimner and Ewel 2005). The 35% loss of root mass after 17 months in this study is relatively low compared to the 55% loss of root mass after 18 months measured in a salt marsh by Benner et al. (1987). In a Louisiana oligohaline marsh, *Sagittaria lancifolia* roots lost approximately 75% of their original mass within 291 days (Laursen 2004). A comparison of the rate constants for initial leaching and decay phase (from the double exponential equation) show that *S. lancifolia* decay ($0.14 \pm 0.01 \text{ day}^{-1}$; Laursen 2004) is more rapid than *P. hemitomon* root decay ($0.025 \pm 0.01 \text{ day}^{-1}$) by an order of magnitude. Based on a global analysis of root turnover, annual fine root loss for wetlands is 55% (Gill and Jackson 2000). Rates of decay in this study, based on the single exponential calculation, are less than one-half of that reported by Silver and Miya (2001) in their global analysis of root decomposition studies from both terrestrial and wetland habitats.

An estimate of natural belowground root production can be calculated from accumulation measurements, since the ingrowth core estimates have compared favorably to other techniques, such as sequential coring and mini-rhizotron (Neill 1992, Symbula and Day 1988, Hendricks 2006). To obtain this estimate, root and rhizome accumulation

was adjusted for tissue specific decomposition, and then production was calculated (based on the one year and two years of biomass accumulation) for comparison. Production estimates based on one year ($983 \text{ g m}^{-2} \text{ yr}^{-1}$) and two years ($904 \text{ g m}^{-2} \text{ yr}^{-1}$) were quite similar. If there was stimulation of root or rhizome growth with ingrowth core disturbance, a greater inequality would be expected between these estimates. Thus, a conservative estimate of belowground production for this marsh type is at least $1,100 \text{ g m}^{-2} \text{ yr}^{-1}$, based on the assumption that the upper 15 cm accounts for 80% of root production. Belowground production estimated by the ingrowth technique for a Georgia salt marsh was $1,460 \text{ g m}^{-2} \text{ yr}^{-1}$ (Gallagher et al. 1984). Multiple techniques of root production are needed in floating marshes to refine these estimates, which are probably low.

Peat accretion as estimated by radiometric dating was inconclusive given the lack of corroboration between radionuclides (Table 3.8). The 'high' estimate of accretion (^{137}Cs , 0.88 cm yr^{-1}) is specious given the low activity of the peak and potential mobility of ^{137}Cs in mineral-poor sediments (Turetsky et al. 2004). Our ^{137}Cs estimate does, however, fall within the range of other freshwater deltaic sites ($0.72\text{-}1.02 \text{ cm yr}^{-1}$) as measured by DeLaune et al. (1986) and Nyman et al. (2006) (Table 3.8). Based on the ^{210}Pb estimate, a conservative range of accretion rate for the floating marsh is $0.21\text{-}0.28 \text{ cm yr}^{-1}$, which falls between the range of nutrient-enriched ($0.58\text{-}0.67 \text{ cm yr}^{-1}$) and un-enriched ($0.14\text{-}0.16 \text{ cm yr}^{-1}$) areas of the Florida Everglades (Craft and Richardson 1998; Table 3.8). Brackish marsh soil accretion rates at two Maryland sites ranged from $0.14\text{-}0.32 \text{ cm yr}^{-1}$ (Hussein et al. 2004), and salt marshes from Rhode Island ranged from $0.26\text{-}0.42 \text{ cm yr}^{-1}$ (Roman et al. 1997). Carbon accumulation for this floating marsh (67 g m^{-2}

yr⁻¹, based on the accretion rate of 0.28 cm yr⁻¹) is less than that of saltwater marshes (84 g m² yr⁻¹; Hussein et al. 2004) but similar to the freshwater Everglades (65-90 g m² yr⁻¹; Craft and Richardson 1998). The relatively low N accumulation of the floating marsh is related to low bulk density (<0.07 g cm⁻³) of the sediment, rather than low N content (>1.6 %).

CONCLUSIONS

Root and rhizome accumulation did not increase with fertilization after two years. Nutrient enrichment accelerated root but not rhizome decay. The degree to which fertilization potentially induced an active plant response of decreased allocation to root growth or increasing root turnover is uncertain. However, the disappearance of plant species from the community with fertilization could also contribute to the observed decrease in belowground accumulation. Further research is needed to determine whether C allocation belowground actually compensates (high root turnover) for the observed shift to increased aboveground biomass relative to belowground. Among other functions, root growth largely governs the physical attributes—volume and resistance—vital to maintaining wetland soil accretion and plant health in coastal areas that are susceptible to erosion, sea-level rise, and subsidence.

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CHAPTER 4
THE EFFECTS OF NUTRIENT-ENRICHMENT ON PRODUCTION,
COMPOSITION, AND NUTRIENT LIMITATION OF SUBTROPICAL FLOATING
MARSH COMMUNITIES

INTRODUCTION

Coastal and inland wetlands are increasingly subject to nutrient enrichment from agricultural runoff and municipal/industrial sources. Nutrient enrichment has been implicated as a contributing factor of landscape level changes to emergent wetland plant communities (Boorman and Fuller 1981, Boar 1989, Ostendorp 1989, Galatowitsch et al. 1991, Davis 1994, Verhoeven et al. 2006). With changes in nutrient availability, the plant community composition can shift, often resulting in the dominance of fewer highly productive species compared to the original community. The mechanisms responsible for plant community changes with increased resource availability are debated (Grace 1991, Craine 2005), but there is a consistent pattern of peak species richness that occurs at intermediate levels of productivity (Weiher 1999). This relationship, however, may have limited applicability to wetlands that are structured more by environmental stress rather than interspecific competition (Waide 1999). Reduced species richness may ultimately influence ecosystem stability or resilience (Romanuk et al. 2006). How wetland productivity and composition may change with increased nutrient availability is important for natural systems management and habitat restoration.

Peat-forming freshwater marshes are common to subtropical systems, and the Mississippi River delta is an area where these wetlands are floating or have seasonal buoyancy (Sasser et al. 1995). Just within Barataria and Terrebonne basins, buoyant marshes occupy more than 140,000 ha (Evers et al. 1996). These wetlands typically exist in quiescent areas of the river delta, where external nutrient loading can be low.

Consequently, internal nutrient cycling is important to maintaining a moderately high productivity (Sasser 1991). Plant communities of these marshes also can be diverse (>15 species 0.25 m⁻²; Sasser et al. 1984) since flood stress is minimal and water deficits are rare. Although organic matter accumulation and consequently nutrient burial may be high (DeLaune et al. 1986), there is limited knowledge of how these marsh types respond to elevated nutrients.

Concerning peat-based floating marsh communities, the objectives of this study were to: 1) understand how community production and composition change with increased nutrient availability; 2) understand the efficiency of nutrient use of the dominant, freshwater grass, *Panicum hemitomon*; and 3) determine the nature of nutrient limitation from different geographic habitats based on tissue nutrient signatures of *P. hemitomon*.

MATERIALS AND METHODS

Study Sites

For the fertilization experiments, two sites were located in the western (Francis Camp) and eastern (Lake Bouef) freshwater regions of the Louisiana coastal zone. The sites are geologically different with Francis Camp located in the low subsidence chenier plain and L. Bouef in the high subsidence delta plain. Despite these geological differences both sites have floating peat-based mats. L. Bouef is a long-term floating marsh research site (Sasser and Gosselink 1984, Sasser et al. 1995). At both sites the cohesive floating mat is at least 30 cm thick, but the total peat thickness, including the free-floating mat and underlying deposit, is more than twice as thick (2.0 m) at L. Bouef than Francis Camp (1.0 m). At both sites, *Panicum hemitomon* (maidencane) is the

dominant species in terms of biomass, and *Thelypteris palustris* (marsh fern) is an important species in terms of its density. Both sites can be described as organic-rich blackwater systems with low mineral sediment input. For comparison to the aforementioned experimental sites, tissue nutrient data was collected from other freshwater sites across the Louisiana coastal zone that contained *P. hemitomon* as the dominant species (Table 4.1).

Table 4.1. Site characteristics where indicators of N and P nutrition (live tissue) of *Panicum hemitomon* were measured.

Site name	n (yr)	Landscape ¹	Geology ²	Richness ³	Buoyancy ⁴
L. Bouef	3	L	deltaic	H	F
Francis Camp	3	L	chenier	M	F
Atchafalaya R.	3	R	deltaic	M	F
L. Salvador	1	L	deltaic	M	F
Pearl R.	1	R	deltaic	H	SF
Lacassine Pool	1	RF	chenier	L	NF

¹ L=lake, R=river, RF=rain-fed; ² peat thickness, deltaic=>2m, chenier=<1m; ³ plant richness(0.25m⁻²) H=>10, M=5-10, L=<5, ⁴ F=floating, SF=semi-floating NF=non-floating

Experimental Set-up and Fertilization

Aboveground biomass and tissue sampling was done along four random plot lines that comprised nine 1.0 m² plots (n=36 plots) at each site and treatment. The plot lines were segregated by treatment, given the uncertainty of fertilizer drift. Plots were randomly assigned for aboveground biomass sampling each year. Each plot received 68, 18, and 28 g m⁻² yr⁻¹ of N, P, and K, respectively. Fertilizer was applied twice yearly in March and October. The controlled release fertilizer contained 19-5-8% of N, P, K (Osmocote, Scotts-Sierra Horticultural Products Co., Marysville, OH). The forms of nitrogen and their percentages were: ammoniacal (6.6%), nitrate (5.6%), and urea (6.8%).

Phosphorus and potassium were in the form of P_2O_5 and K_2O , respectively. The relatively high application rate was designed to reduce competition for nutrients between the plant and microbial community and compensate for lateral and vertical hydraulic losses that were expected in these highly permeable peat mats.

Water Nutrients

Water from the marsh (pore) and from the closest source water body (open) was monitored for available nitrogen and phosphorus in the forms of NH_4^+ , $NO_3^- + NO_2^-$, and PO_4^{3-} . Samples were analyzed by the Coastal Ecology Institute Laboratory, Louisiana State University (Baton Rouge, LA) by the following methods: alkaline phenol (NH_4^+), cadmium reduction ($NO_3^- + NO_2^-$), and ammonium molybdate/ascorbic acid (PO_4^{3-}). Pore-water was collected from the upper 5-8 cm of the mat and filtered through a 0.45 μm nylon filter, and aliquots of each sample were separated for N and P analysis. One pore-water sample was collected from each of five random plots in each treatment; open-water samples were collected from just below the water surface at three different stations. Samples were kept on ice in the field and frozen in the laboratory until analysis. For the duration of this study, there were eight sampling seasons that were common between the sites. The spring and summer of 2004 were not sampled at L. Bouef due to logistical problems.

Aboveground Biomass

End-of-season aboveground live and dead standing crop was sampled each autumn for the years 2002, 2003, and 2004. Five replicate plots were harvested in the first two years; whereas in 2004, ten plots were harvested for each treatment and site. All the live and dead vegetation in 0.25 m^2 quadrats was clipped, and the surface litter was

collected. The standing vegetation was sorted by species, stem counts recorded, and dried (60° C) to a constant weight (0.01g).

Tissue Nutrients

Leaf tissue from *Panicum hemitomon* was collected from a total of six sites (Table 4.1) across the Louisiana coast to understand geographical variation and the nature of nutrient limitation. At three of the sites (L. Bouef, Francis Camp, and Atchafalaya R.) end-of-season live leaf tissue was collected for three years; the other sites were sampled only one season (L. Salvador, Lacassine Pool, Pearl R.; Table 4.1). Sampling at all sites was done at the end-of season on mature plants. To understand the nutrient resorption efficiency of *Panicum hemitomon* under natural and nutrient enriched conditions, the L. Bouef and Francis Camp sites were used. Live and senesced tissue from standing *Panicum hemitomon* plants was sampled during the autumn of 2002, 2003, and 2004. Five replicates (~5 g rep⁻¹) of each live and senesced leaf tissue were collected from each site and treatment. Fully exerted, mature, green leaves were collected from just below the apical portion of the culms, and senesced material was collected from the lower portions of the culms. N and P were analyzed at the Louisiana State University, AgCenter Plant and Soil Analysis Laboratory (Baton Rouge, LA). Total nitrogen was analyzed by combustion (Leco CHN analyzer), and total phosphorus was analyzed on an inductively coupled plasma spectrophotometer (ICP) following digestion with HNO₃ and H₂O₂. Nutrient concentrations were reported as % mass of dry weight. Resorption efficiency was calculated ($RE = [\%N \text{ or } P_{\text{live tissue}} - \%N \text{ or } P_{\text{dead tissue}}] / [\%N \text{ or } P_{\text{live tissue}}] \times 100$) on a nutrient mass-tissue mass basis, as opposed to a nutrient mass-leaf area basis, since the results are comparable (van Heerwaarden et al. 2003).

Data Analyses

A three-way ANOVA (PROC GLM, SAS 2003) with the effect of site (random; Francis Camp, L. Bouef), year (fixed; 2002, 2003, 2004) and treatment (fixed; fertilized, control) was performed on dependent variables of total, live, and dead biomass. Similar ANOVA's were run on individual species biomass, culm density and mass. Data were transformed with the natural logarithm to approach normality of the residuals. Tukey-Kramer adjustments were used for testing significance for treatment, year, and site pairwise comparisons.

RESULTS

Water Nutrients

At the beginning of the experiment (spring 2002), prior to fertilization, there were similar levels of N and P observed in control and fertilized treatments within each site (Fig. 4.1). In general, fertilization produced available N and P concentrations that were at least an order of magnitude higher than controls (Fig. 4.1). There were no discernable seasonal trends of interstitial nutrient availability in either fertilized or control plots within each site (Fig. 4.1). During winter 2004, L. Bouef had extremely high PO_4^{3-} concentrations ($>3.0 \text{ mg l}^{-1}$) that were not observed at Francis Camp (Fig. 4.1). There was a high positive correlation ($r^2=0.79$) of NH_4^+ concentration in control plots between the two sites and a slight positive correlation ($r^2=0.37$) of $\text{NO}_2^- + \text{NO}_3^-$. In contrast to available nitrogen, PO_4^{3-} was negatively correlated ($r^2=0.35$) between control plots at the sites. Maximum concentrations of PO_4^{3-} in both control and fertilized plots were 3-fold greater at L. Bouef than those observed at Francis Camp (Fig. 4.1).

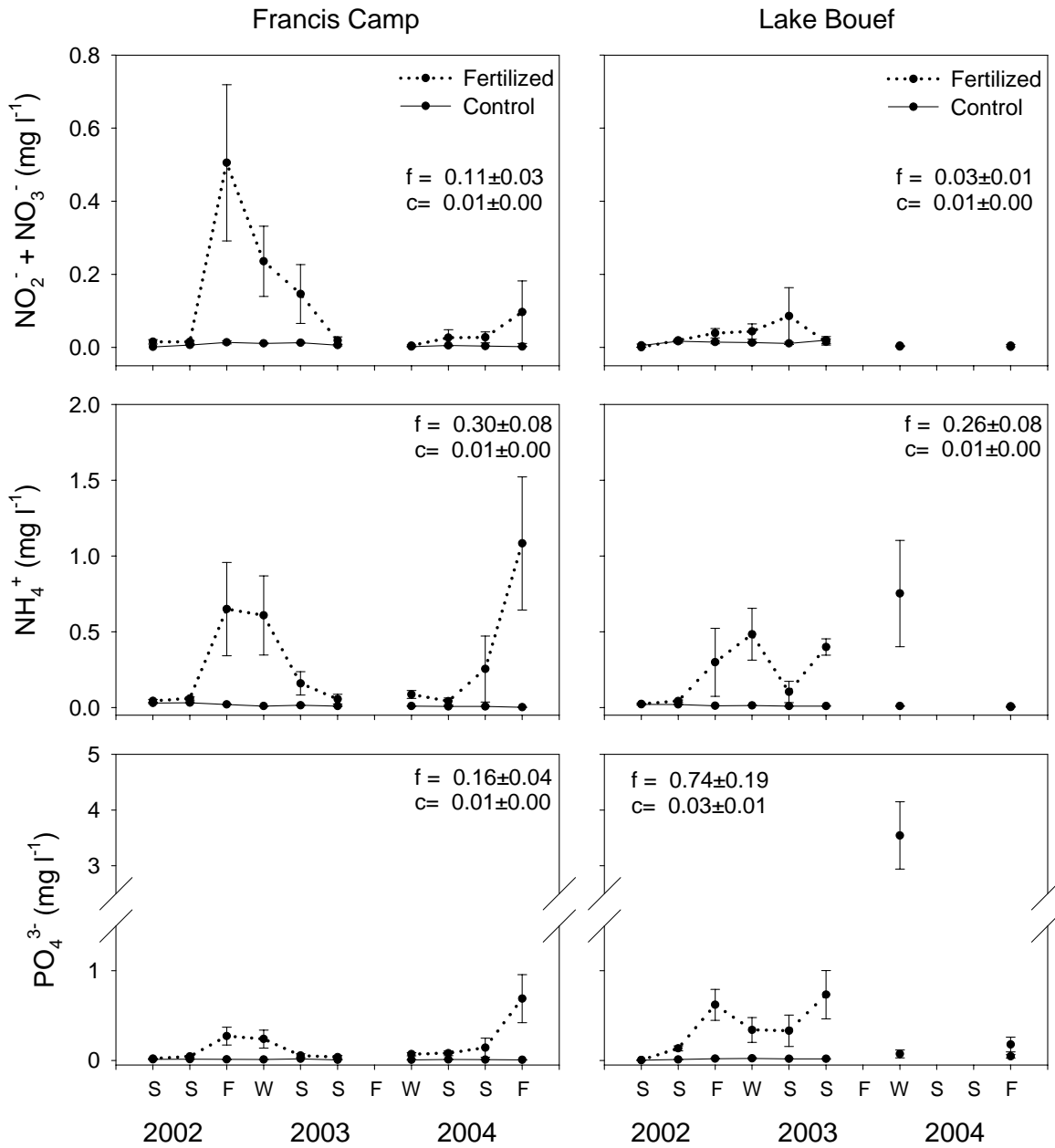


Figure 4.1. Comparison of seasonal changes in pore-water nutrient concentrations in control (c) and fertilized (f) treatments. Means ($1 \pm \text{SE}$) for each nutrient are shown inside the graph. The first point (spring 2002) is prior to fertilizer application. During 2004, spring and summer samples are missing for L. Bouef.

Aboveground Biomass

Based on the three year mean of both sites, fertilization resulted in significantly greater live aboveground biomass compared to controls, with 1,788 and 846 g m⁻² yr⁻¹, respectively ($P < 0.0001$, $F_{1,68} = 39.2$). The main effect of site was not significant for live aboveground biomass (Table 4.2).

Table 4.2. ANOVA results for aboveground biomass variables for year (2002, 2003, 2004), site (Francis Camp, Lake Bouef) and treatment (fertilized, control).

Source	df	Live		Dead		Total		Stem density	
		F	Pr>F	F	Pr>F	F	Pr>F	F	Pr>F
year (y)	2	16.5	<0.0001	21.2	<0.0001	22.5	<0.0001	12.3	<0.0001
site (s)	1	1.5	0.2301	13.6	0.0004	4.0	0.0501	12.7	0.0007
y*s	2	9.2	0.0003	15.9	<0.0001	13.4	<0.0001	4.4	0.0169
treatment (t)	1	39.2	<0.0001	15.5	0.0002	43.1	<0.0001	109.5	<0.0001
y*t	2	5.2	0.0082	3.7	0.0289	6.2	0.0033	42.5	<0.0001
s*t	1	0.1	0.7487	0.0	0.8927	0.1	0.8005	6.1	0.0163
y*s*t	2	6.8	0.0021	1.6	0.207	4.5	0.0142	2.7	0.0718

A year-site-treatment interaction was significant ($P < 0.002$, $F_{2,68} = 39.2$; Table 4.3): though both sites had consistently greater biomass each year with fertilization compared to controls (Table 4.3), only during the second year (2003) did Francis Camp have a statistically significant treatment difference, while L. Bouef exhibited significant treatment differences for each year (when years were analyzed separately). Fertilized live biomass was consistently at least twice as great as the controls at L. Bouef for each year (Table 4.3). The high standing crop ($>3,700$ g m⁻²) in the fertilized treatment during 2003 at Francis Camp also contributed to the significant year-site interaction. Controls at both sites followed a similar pattern of live standing crop that peaked in 2003 (Table 4.3).

Averaged over the three years, greater dead aboveground biomass accumulated with fertilization compared to controls, with 495 and 330 g m⁻² yr⁻¹, respectively ($P < 0.0002$, $F_{1,68} = 15.5$; Table 4.3). The significant site effect was due to greater dead accumulation at Francis Camp than L. Bouef (490 vs 336 g m⁻² yr⁻¹), respectively. Dead biomass accumulation was greater with fertilization at both sites for all years except for L. Bouef in the first year (2002; Table 4.3). A significant year-treatment interaction was the result of high dead biomass production in the second year with fertilization that was not observed in the other years. There was no significant year-site-treatment interaction for dead biomass.

Total aboveground biomass with fertilization (2,283 g m⁻² yr⁻¹) was significantly greater ($P < 0.0001$, $F_{1,68} = 43.1$; Table 4.3) than the controls (1,177 g m⁻² yr⁻¹). The proportion of fertilized:control total biomass was greater by a factor of 2.2 (L. Bouef) and 1.8 (Francis Camp) averaged over the three years. A year-treatment interaction showed that in 2003 and 2004 total biomass with fertilization significantly exceeded the controls, but this was not true for 2002, even though the difference between fertilized and control treatments was large (1,461 vs 836 g m⁻²).

The mean total stem density with fertilization (467 stems m⁻² yr⁻¹) was significantly different than the controls (791 stems m⁻² yr⁻¹) ($P < 0.0001$, $F_{1,68} = 109.5$; Fig. 2.2, Table 4.3). Stem density exhibited an overall decrease with fertilization compared to controls (Fig. 4.2). A significant year-treatment interaction was due to similar stem density between treatments in the first year, unlike the following two years. Sites responded differently in the first year, such that stem density was stimulated with

Table 4.3. Mean aboveground biomass (live, dead, and total) and stem density by site, treatment, and year. Different letters within a row indicate significant year-treatment differences ($P < 0.05$) based on Tukey's HSD. Unadjusted means (± 1 SE) are shown.

Site	Tissue	2002		2003		2004	
		Fertilized	Control	Fertilized	Control	Fertilized	Control
Francis Camp	Live	691(169) ^b	628(84) ^b	3738(523) ^a	1317(47) ^b	1137(174) ^b	939(57) ^b
	Dead	256(39) ^d	97(11) ^c	976(158) ^a	718(103) ^{ab}	494(49) ^{bc}	400(50) ^{cd}
	Total	947(187) ^{bcd}	725(82) ^d	4714(669) ^a	2035(128) ^{bc}	1631(207) ^b	1339(97) ^{cd}
	Stem	698(46) ^b	821(54) ^{ab}	434(72) ^c	864(27) ^{ab}	319(43) ^c	968(54) ^a
Lake Bouef	Live	1681(305) ^a	578(81) ^b	1826(342) ^a	948(124) ^{ab}	1657(388) ^a	666(56) ^b
	Dead	296(39) ^{bc}	370(32) ^c	576(90) ^a	170(22) ^{bc}	374(86) ^{ab}	231(21) ^{bc}
	Total	1977(325) ^{bcd}	948(105) ^d	2403(310) ^a	1117(105) ^{bc}	2031(409) ^b	897(72) ^{cd}
	Stem	774(55) ^a	530(88) ^{bc}	427(43) ^c	857(90) ^a	148(14) ^d	705(34) ^{ab}

fertilization compared to controls at L. Bouef, but this was not observed at Francis Camp (Table 4.3). In the final year, stem density was 233 vs 836 m⁻², for fertilized and controls, respectively.

Species Changes

In the first year (4.5 months after fertilization), there were no appreciable changes in species richness at either site (Fig. 4.3). However, there was a decline in species richness over time with fertilization compared to controls at both sites (Fig. 4.3). At Francis Camp, mean species richness for fertilized (4.4 species) and control (6.0 species) treatments was significantly different ($P < 0.0001$, $F_{1,34} = 27.4$). At L. Bouef, the same was true with 6.3 vs 9.5 species for fertilized and controls, respectively ($P < 0.0001$, $F_{1,34} = 30.0$). Between 2003 and 2004, there was a mean increase of three species in the control plots at L. Bouef (Fig. 4.3). In the final year, species richness of fertilized vs control for L. Bouef was 5.7 ± 0.3 vs 11.5 ± 0.9 , and at Francis Camp it was 3.7 ± 0.2 vs 6.5 ± 0.4 .

Across sites and years, the total live biomass comprised by *Panicum* in control and fertilized treatments was $74 \pm 10\%$ and $82 \pm 13\%$. This species was present in all replicate plots regardless of treatment, site, or year. *Panicum* biomass was significantly higher in the fertilized ($1,491 \text{ g m}^{-2} \text{ yr}^{-1}$) compared to control ($653 \text{ g m}^{-2} \text{ yr}^{-1}$) treatments (Fig. 4.4; $P < 0.0001$, $F_{1,68} = 68.7$). The second year (2003) of fertilization at Francis Camp resulted in peak *Panicum* biomass ($3,628 \text{ g m}^{-2}$); L. Bouef had a peak biomass ($1,443 \text{ g m}^{-2}$) within the first year of fertilization. By the final season, the treatment disparity in treatment biomass of *Panicum* was 476 vs 248 g m⁻² at L. Bouef and Francis Camp, respectively. There was not a significant effect of treatment on *Panicum* stem

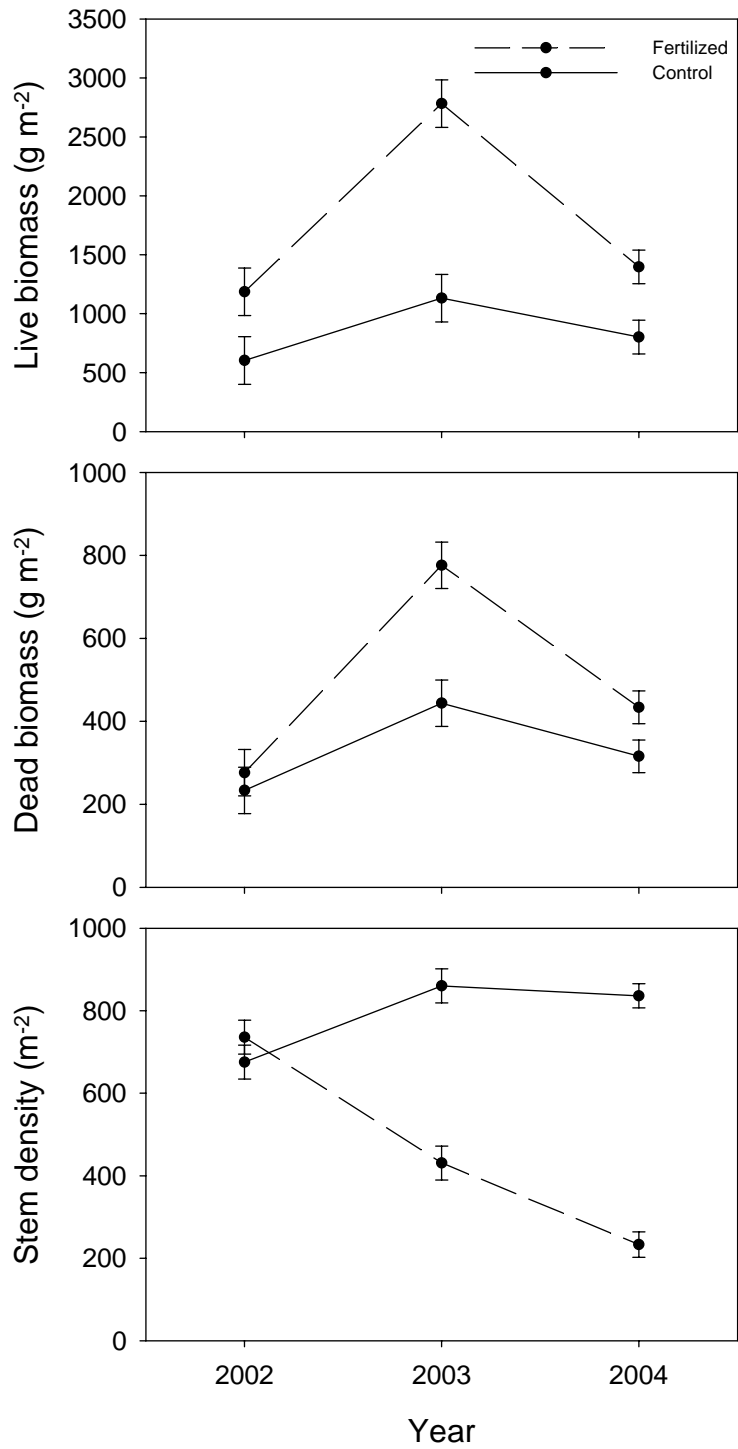


Figure 4.2. A comparison of control and fertilized treatments on yearly mean ($\pm 1SE$, sites combined) live and dead biomass and stem density (sites combined).

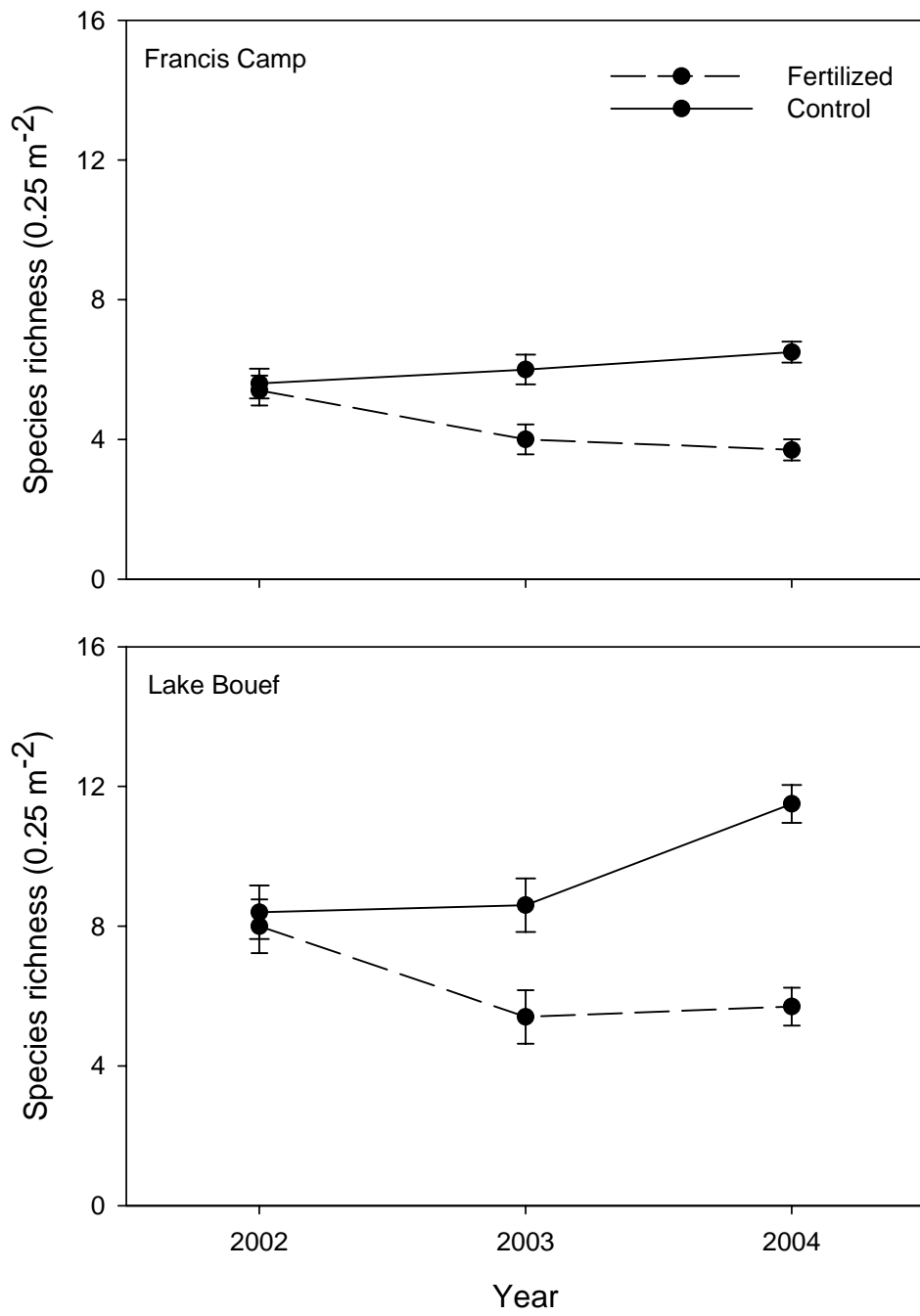


Figure 4.3. Site comparison of mean ($\pm 1SE$) species richness each year under fertilized and control conditions.

Panicum hemitomon

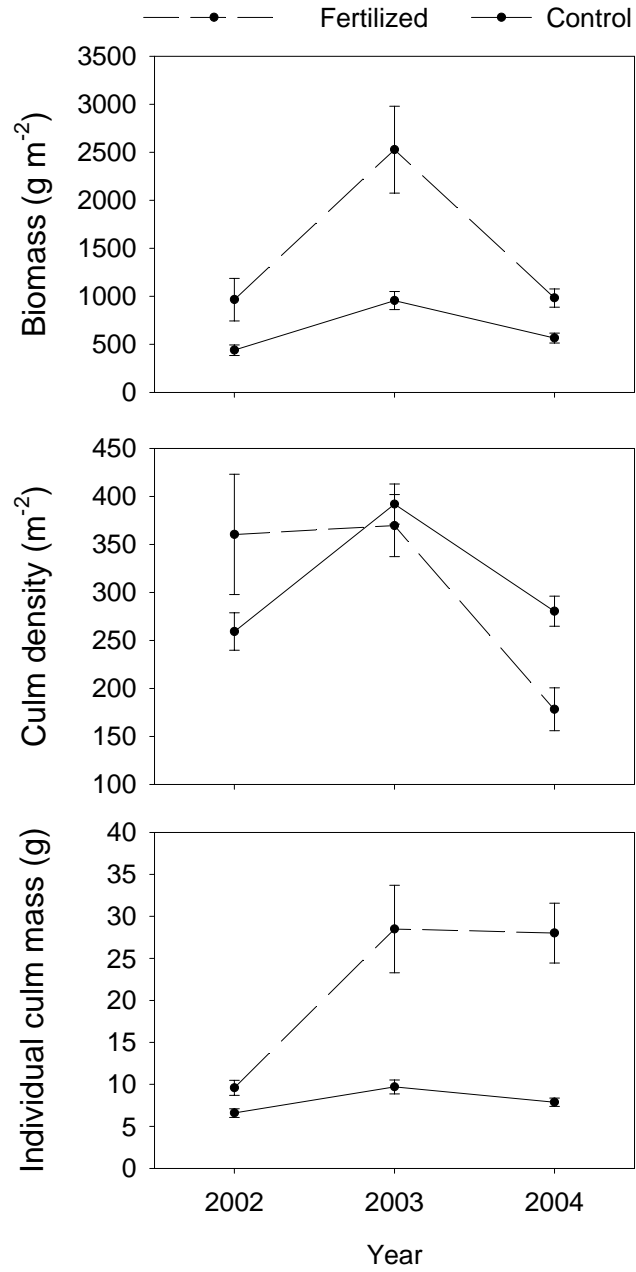


Figure 4.4. Combined site means ($\pm 1SE$) of live aboveground biomass, culm density, and individual culm mass for the grass, *Panicum hemitomon*.

density across years ($P= <0.6832$, $F_{1,68}=0.17$). In the first year, there was a different pattern with site, such that Francis Camp experienced a decrease in stem density with fertilization, but the opposite response was observed at L. Bouef. Nonetheless, by the final year, both sites had reduced stem densities of *Panicum* in fertilized compared to control treatments (Fig. 4.4). *Panicum* biomass was controlled more by increased individual culm mass than density by the end of the experiment.

Fertilization resulted in a significant decrease compared to controls of *Thelypteris* biomass (10 vs 83 g m⁻² yr⁻¹) and stem density (80 vs 339 stems) (Fig. 4.5). Biomass and stem density were greater at Francis Camp than L. Bouef. By the second year, both sites showed an almost complete loss of *Thelypteris* that was sustained into the final year (Fig. 4.5). At both sites, *Leersia* biomass and stem density were similar in the controls for the duration of the experiment (Fig. 4.6). At both sites in the first year, an increase in biomass and stem density was greater with fertilization than the controls; however, by the last year, fertilization resulted in the loss of *Leersia* at L. Bouef, and it returned to control levels at Francis Camp. *Solidago* was present only at the L. Bouef site. In the first year, fertilization resulted in a decrease in culm density of *Solidago* relative to the controls (Fig. 4.7). Although there was high variability, biomass of the fertilized vs control treatments was significantly different (396 vs 108 g m⁻² yr⁻¹; $P= <0.0001$, $F_{1,34}=29.3$). By the end of the experiment, the nature of the increased biomass of *Solidago* with fertilization was in the form of greater individual culm mass, not an increase in stem density (Fig. 4.7).

Thelypteris palustris

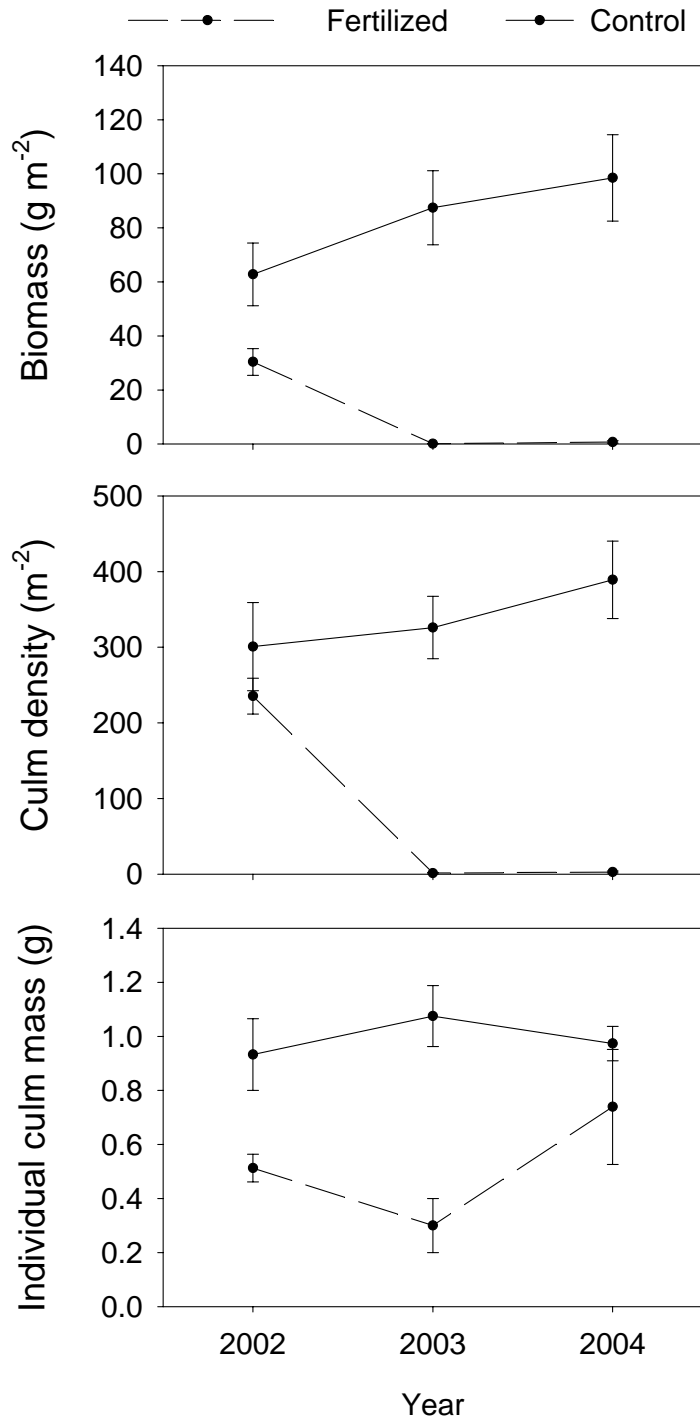


Figure 4.5. Combined site means ($\pm 1SE$) of live aboveground biomass, culm density, and individual culm mass for the fern, *Thelypteris palustris*.

Leersia oryzoides

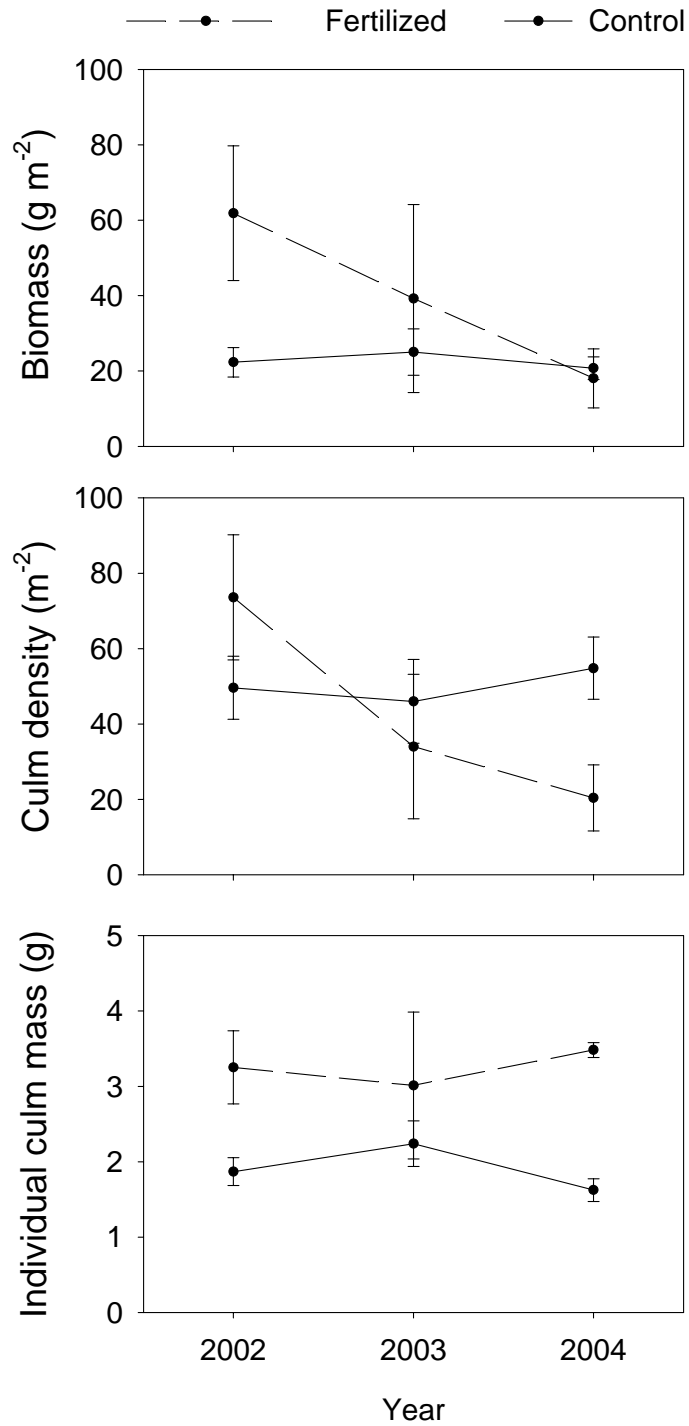


Figure 4.6. Combined site means ($\pm 1SE$) of live aboveground biomass, culm density, and individual culm mass for the grass, *Leersia oryzoides*.

Solidago sempervirens

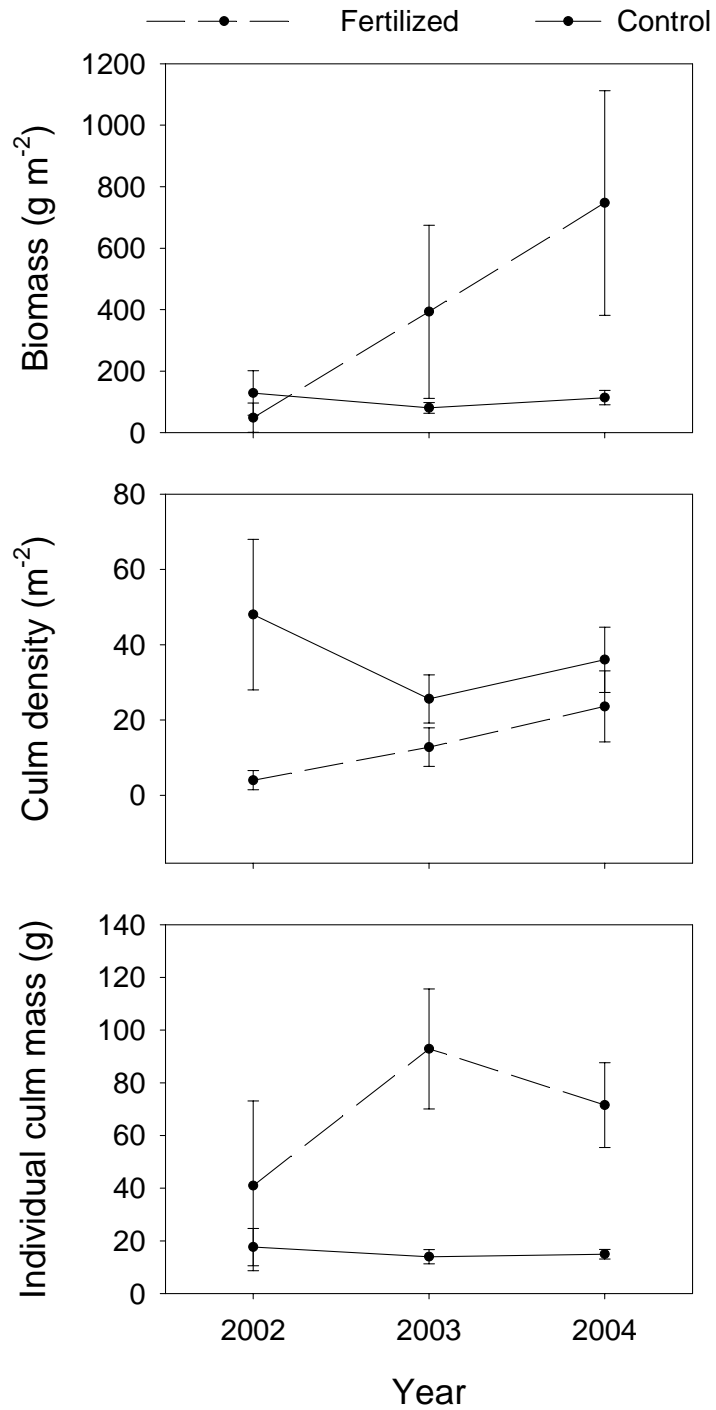


Figure 4.7. Combined site means ($\pm 1SE$) of live aboveground biomass, culm density, and individual culm mass for the composite, *Solidago sempervirens*.

Tissue Nutrients

Nitrogen and phosphorous concentrations in dead tissue were consistently lower than live tissue regardless of treatment (Table 4.4). Relative to controls, fertilization resulted in greater concentrations of N and P in live or dead tissues (Table 4.4). With fertilization, there was a decrease in the amount of N- or P-resorption compared to controls (Fig. 4.8). There was a significant treatment effect ($P=<0.0001$, $F_{1,56}=31.2$) on N-resorption, such that fertilized and control conditions were 57.1 and 67.2 %, respectively. A similar treatment effect ($P=<0.0001$, $F_{1,51}=53.4$) was observed for P, such that resorption in fertilized and control conditions were 72.8 and 87.8%. There was a significant site effect for P-resorption as Francis Camp (83.2%) was higher than L. Bouef (77.4%; Fig. 4.8). There was not a significant site effect for N-resorption, although L. Bouef was lower than Francis Camp (Fig. 4.8).

Between the two experimental sites, there was a different response of N:P ratios to fertilization (Fig. 4.9): L. Bouef consistently showed a decrease in nitrogen limitation

Table 4.4. Mean ($1\pm SE$) tissue nutrient concentrations of *P. hemitomom* over three years under fertilized and control conditions at two sites in Louisiana. All means based on (n=15), save Francis Camp, fertilized, dead (n=10).

Site	Treatment	Tissue*	N (%)		P (%)	
Francis Camp	Fertilized	D	1.213	(0.085)	0.045	(0.007)
		L	2.977	(0.141)	0.222	(0.009)
	Control	D	0.582	(0.014)	0.010	(0.001)
		L	1.858	(0.052)	0.133	(0.003)
Lake Bouef	Fertilized	D	1.523	(0.133)	0.084	(0.009)
		L	3.319	(0.134)	0.277	(0.013)
	Control	D	0.805	(0.014)	0.035	(0.003)
		L	2.382	(0.046)	0.233	(0.005)

* D=dead; L=live

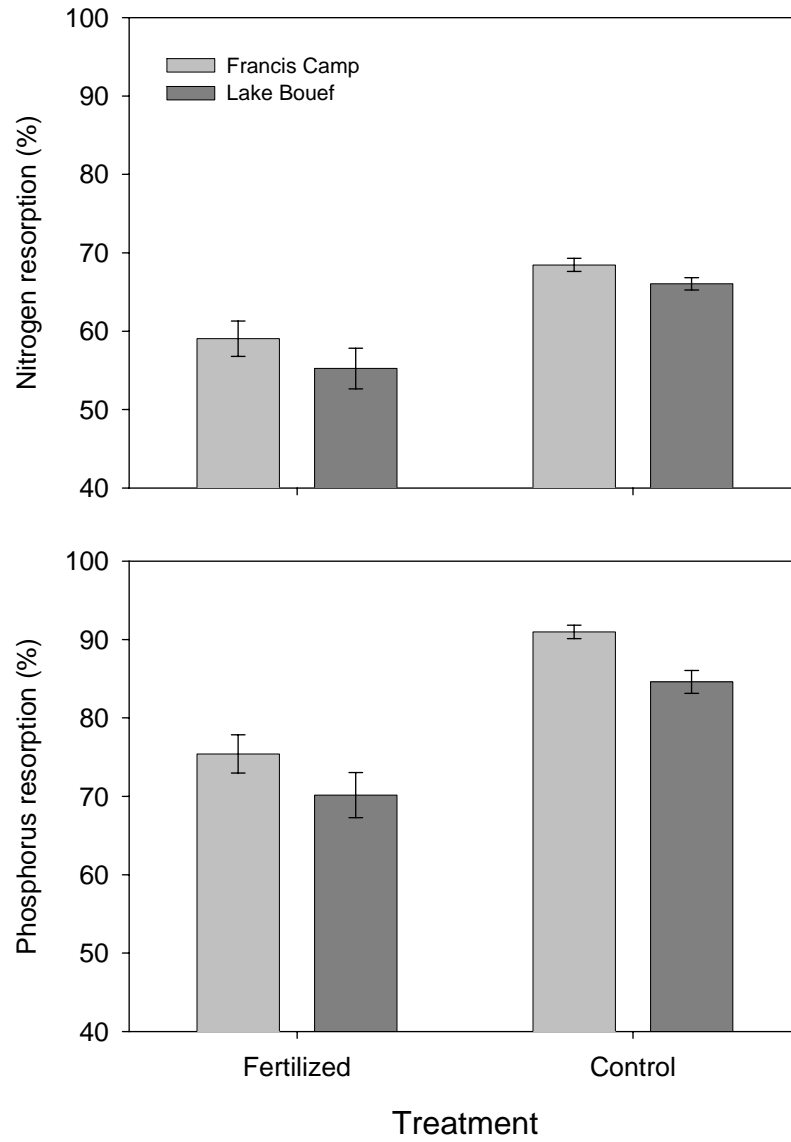


Figure 4.8. A comparison of site means (n=3 years) by fertilized and control treatments of N-and P-resorption efficiency of *Panicum hemitomom*. All means are based on n=15 samples, save P-resorption, fertilized, Francis Camp with n=10.

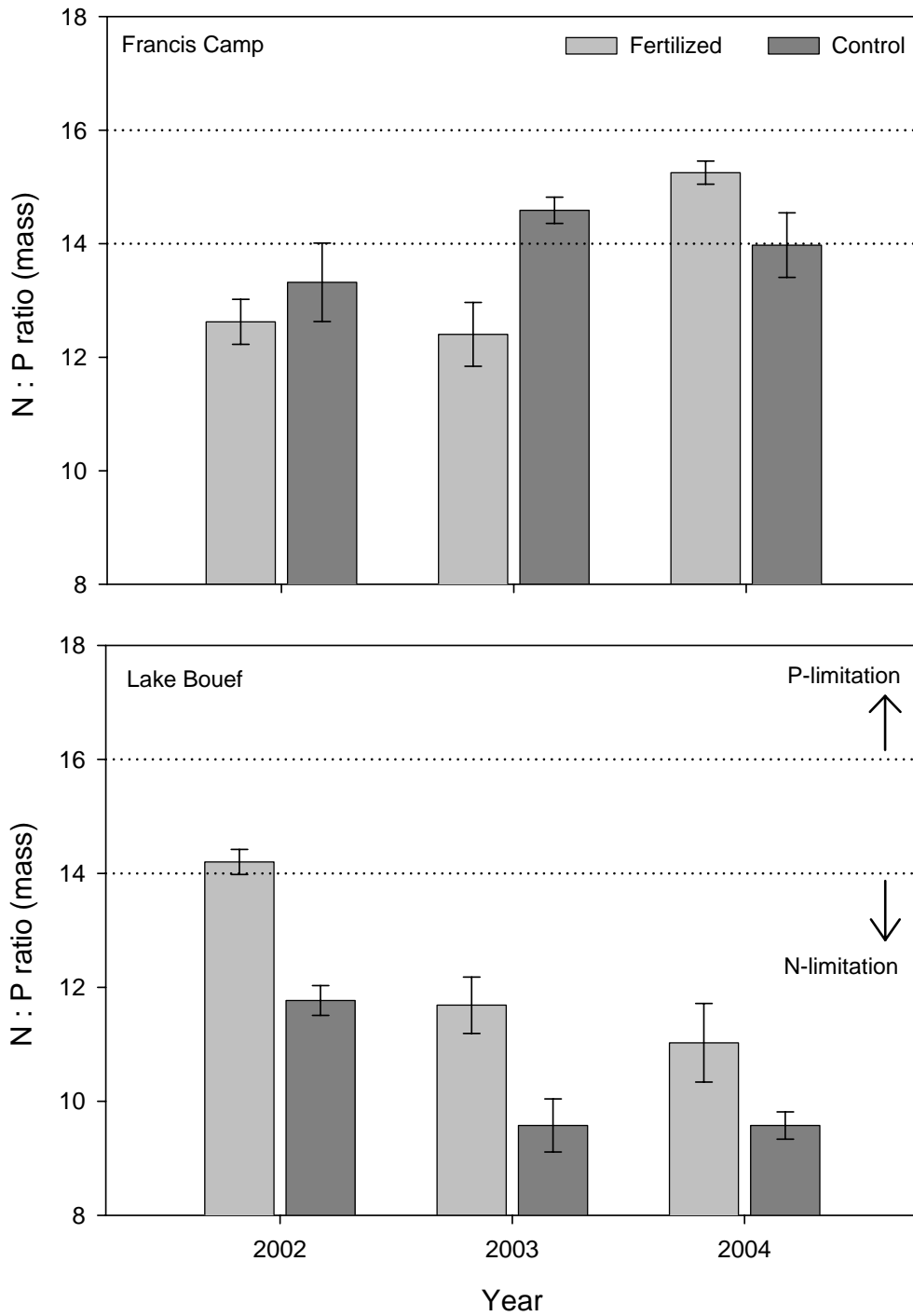


Figure 4.9. A site comparison of yearly mean ($\pm 1SE$) live tissue N:P ratios (*Panicum hemitomon*) by fertilized and control treatments. Upper and lower lines show the degree of N-, P-, or co-limitation of both N and P based on ranges identified by Koerselman and Meuleman (1996).

(higher N:P ratio) with fertilization; however, Francis Camp showed the opposite, save the final year. N:P ratios in the controls at Francis Camp (14.0 ± 0.3) and L. Bouef (10.3 ± 0.3) showed that the latter site was more nitrogen limited and the former was on the threshold of N and P co-limitation. At L. Bouef, fertilization relieved N-limitation only in the first year (Fig. 4.9). The comparison of sites along the coast showed a continuum of N to P limitation (Fig. 4.10). Two lacustrine sites in Barataria basin showed strong nitrogen limitation. Likewise, the Atchafalaya River site was considered N-limited. The Francis Camp site and the Pearl River exhibited N and P co-limitation. The rain-fed Mermentau site was P-limited.

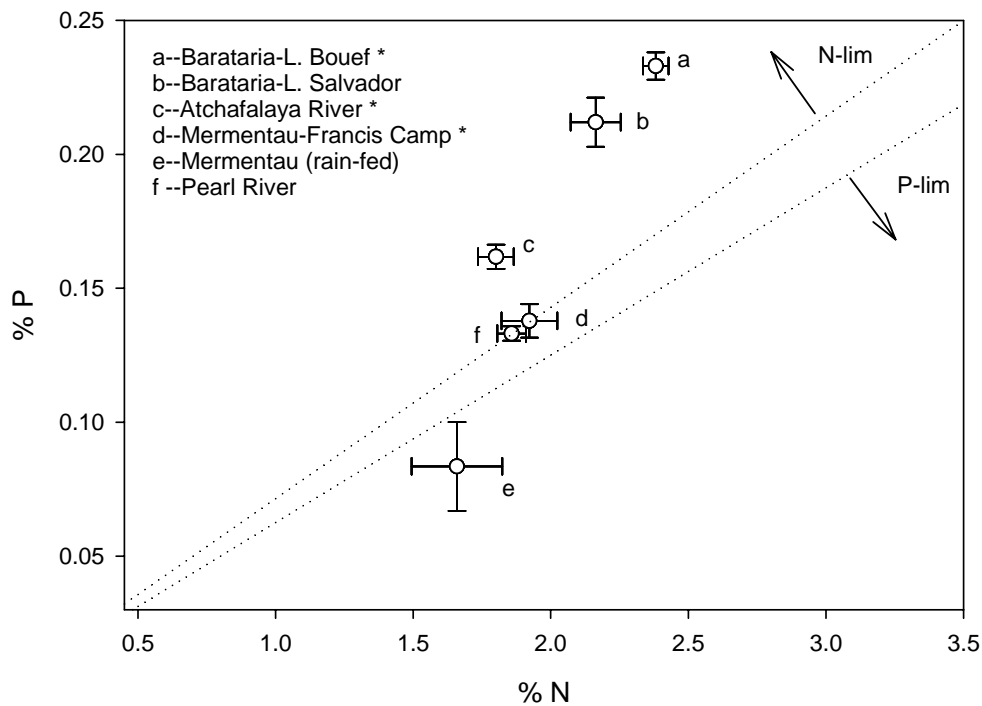


Figure 4.10. N:P mass ratios of leaf tissue of coastal populations of *Panicum hemitomon* sampled at the end-of-season. Asterisks denote the sites that were sampled for three years; other sites were sampled once.

DISCUSSION

A doubling of aboveground biomass with N and P fertilization was expected at the high rate of nutrient supply. The dominant grass, *Panicum hemitomon*, was the species that responded most positively to increased nutrients, and by the end of the experiment, this biomass increase was maintained at a lower stem density and greater individual culm mass compared to controls. Increased biomass of grasses compared to forbs in response to increased fertility has been observed in grasslands (Huenneke et al. 1990). With fertilization, a loss of vertical canopy structure was observed as *P. hemitomon* culms lodged and intensified shading of itself and subordinate species. The increase of live and dead plant biomass coupled with decreasing stem density suggests that there was a shift from nutrient to light limitation with increased fertility (Tilman 1987, Foster and Gross 1998).

Another notable change in the community was marked by loss of the fern, *Thelypteris palustris*, shortly after fertilization was begun. Based on its high density, this is an important plant that is common to the floating marsh community; the end-of-season estimates of its biomass probably underestimate its contribution to primary production and peat accumulation. Although their biomass was not measured, bryophytes (liverworts and *Sphagnum* spp.) disappeared within the first year after fertilization; the negative effects of N fertilization on moss cover have been noted in other studies (Gusewell et al. 2002, Chapin et al. 2004). Although *Solidago sempervirens* also increased in biomass with fertilization (only at L. Bouef), its abundance was patchy. Like other species in its genus, *S. sempervirens* appears to be competitive under nutrient enriched conditions (Bakelaar and Odum 1978, Pratt 1984).

The decrease in species richness under fertilization observed in this study has been also demonstrated in many terrestrial and wetland fertilization studies (Tilman 1987, Bedford et al. 1999, Day et al. 2004a). Species richness is expected to be highest at intermediate levels of fertility and decrease with higher plant production (Bowman et al. 1993). Based on the results of this study and others (Drexler and Bedford 2002), constraints on species richness can be expected with increased nutrient enrichment to freshwater, peat-based wetlands.

P. hemitomon occupies nutrient limited, peat-based wetlands of the southeastern United States, such as coastal plain pocosins and the Everglades, but apparently it has a broad ecological amplitude of competitive ability under elevated nutrient supply, based on this study and the results of Bayley et al. (1985). How *P. hemitomon* may compete under persistent nutrient enrichment cannot be predicted from this short-term study. With increased nutrient supply, community changes and invasibility can be time-dependent (Davis 1991, Gusewell et al. 2002, Woo and Zedler 2002).

Pore-water available nutrients in fertilized treatments, although an order of magnitude greater than controls, were not exceptionally high compared to that of municipal wastewater treatment effluents (Day et al. 2004) or river-borne N or P (Rabalais et al. 1996, Svengsouk and Mitsch 2001) or agricultural runoff (Koch and Reddy 1992). The consistently low availability of inorganic N and P observed in this study indicates that internal nutrient cycling within the floating peat mat, rather than external subsidy, is characteristic of these subtropical peat-forming marshes (Sasser et al. 1991).

In addition to a wide tolerance of environmental disturbance from fire and flooding, nutrient acquisition (Miller and Bever 1999) and conservation by *P. hemitomon*, in the form of nutrient re-translocation prior to senescence, may partially explain this species dominance of the relatively nutrient poor conditions found in floating marshes. The resorption efficiency of *P. hemitomon* for P (88%) was greater than that of species (*Cladium jamaicense*, *Rhizophora mangle*) found in P-limited environments (Feller et al. 1999, Richardson et al. 1999). The range of mean values of dead tissue N (0.58-0.81%) and P (0.01-0.04%) show that *P. hemitomon* is capable of 'complete' nutrient retranslocation according to nutrient proficiency thresholds ($N < 0.7\%$, $P < 0.05\%$; Killingbeck 1996). Why N resorption is considerably lower than P in this species is not entirely clear, but may be governed by differential solubility of N-based proteins/amino acids and P-based nucleic acids/phospholipids (Aerts 1996); however, N-resorption efficiency was found to be highly correlated to P-resorption efficiency in a review of deciduous and evergreen woody species (Killingbeck 1996). The consistent pattern (occurring over three years) of enhanced resorption of both N and P at Francis Camp compared to L. Bouef is interesting if there is a population or environmental explanation. The results of this study support the hypothesis that nutrient conservation decreases with increasing nutrient supply (Aerts 1996, van Heerwaarden et al. 2003). From a review of north temperate wetland studies, compared to bogs, fens, and swamps, marshes were largely nitrogen limited, as were vascular herbs as compared to shrubs and bryophytes (Bedford et al. 1999). The range of subtropical habitats surveyed, which vary in hydrology and geology, varied from N to P limitation. P-limitation was found in a rain-fed impoundment, which had species similar to those found in wet-prairie and slough

habitats of the Florida Everglades (Loveless 1959). The consistent pattern of N-limitation at the riverine site (Atchafalaya R.) was interesting since there is a relatively high supply of NO_3^- ($>0.4 \text{ mg l}^{-1}$; Sasser et al. 2004) to these marshes, but mineral sediments are also ubiquitous. It may be that the more conservative cycling of P relative to N (denitrification) may explain the N-limited nature of these habitats. The Francis Camp site showed N- and P-co-limitation. The lack of significant N-limitation at this site may be partially due to late summer decrease in water levels, late in the growing season, which could favor N-mineralization when the peat is not fully saturated. The persistence of N-limitation at the L. Bouef site may be partially due the frequency of fire, which was observed for four consecutive years during this study. Fire in peat-based systems can cause nitrogen volatilization and P mineralization (Smith et al. 2001). Moreover, the L. Bouef peat remains continuously saturated, which may favor denitrification.

CONCLUSIONS

Fertilization resulted in decreased species richness with a concomitant increase in biomass. The doubling in biomass with fertilization signifies that the floating marsh community is nutrient limited. The loss of the fern, *Thelypteris palustris*, indicates this species cannot compete with *Panicum hemitomon* under nutrient rich conditions. While *P. hemitomon* responded most positively to fertilization at both sites, at one site, *Solidago sempervirens* captured a considerable amount of biomass by the end of the experiment. Nutrient resorption of N and P is apparently quite high for *P. hemitomon*, and its nutrient resorption efficiency decreased with increased fertility. High nutrient resorption efficiency may account for this species ability to compete under nutrient poor conditions observed elsewhere in its range. Tissue nutrient signatures of *P. hemitomon* largely

indicated community N-limitation across the range of coastal habitats that were surveyed; phosphorus limitation was found at a site that was rain-fed.

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CHAPTER 5 RESPIRATION OF LOUISIANA FRESHWATER PEAT SOILS AMENDED WITH AMMONIUM, PHOSPHATE, AND SULFATE

INTRODUCTION

For wetlands, the dominant controls on organic matter decomposition include temperature, sediment anoxia, availability of electron acceptors, and substrate quality (Clymo 1983, Morris and Lajtha 1986, Webster and Benfield 1986, Bridgham and Richardson 1992). Substrate quality, as defined by nutrient and lignin/cellulose content of organic matter, is a robust predictor of detritus decomposition among a range of photosynthetic organisms (Enríquez et al. 1993). In addition to substrate quality, exogenous nutrient supply can also influence organic matter decay (Brinson et al. 1981, DeBusk and Reddy 2005), with inorganic nitrogen and phosphorus comprising the main limiting nutrients (Thormann and Bayley 1997). However, sulfate pollution to organic-rich freshwater wetlands is of recent concern (Lamers et al. 2001, Castro et al. 2005). The role of exogenous nutrients can be complex, as the addition of limiting nutrients may accelerate the decomposition of low molecular weight organic fractions of soil organic matter, while simultaneously stabilizing the heavy fractions (Neff et al. 2002).

In the Mississippi River Delta Plain, rapid geologic subsidence coupled with sea level rise, has resulted in extensive wetland loss (Boesch et al. 1994). The current working model of emergent marsh stability proposes that healthy plants drive soil organic matter production, which ultimately determines soil elevation (Nyman et al. 1990, Turner et al. 2004, DeLaune and Pezeshki 2003). The importance of mineral sediments in stimulating plant growth and organic matter accretion is also acknowledged (Bricker-Urso et al. 1989).

In the abandoned delta regions, peat production controls soil accretion (Kosters et al. 1987), and this is especially true of floating marshes that have developed extensively across the deltaic landscape (Swarzenski 1991, Sasser et al. 1996). These subtropical wetlands have relatively high rates of peat accretion ($>0.75 \text{ cm yr}^{-1}$; DeLaune et al. 1986; Nyman et al. 2006). Since mineral sedimentation is poor, the maintenance of high primary productivity is largely sustained by internal nutrient cycling (Sasser et al. 1991). Given the reduced external loading of nutrients to these peat-based soils, how soil respiration may be influenced by exposure to elevated nutrients (N, P, N+P, and S) was examined.

MATERIALS AND METHODS

Soil samples were collected during Dec 2005 from a long-term freshwater floating marsh research site (Lake Bouef, Louisiana; Sasser and Gosselink 1984, Sasser et al. 1995). The floating portion of the mat (40-60 cm thick) consists of densely intertwined live roots, which contains peat in all stages of decomposition. Since the mat is buoyant all year (the surface 3 cm is moist but unsaturated), the soils are exposed to oxygen; therefore, no attempt was made to completely remove oxygen after collecting the soil. Eight cores (~10 cm deep) were taken with an aluminum core tube (7.6 diameter). Cores were put in plastic bags and excess air was expelled followed by storage on ice. In the laboratory, coarse live or dead roots and rhizomes ($>2 \text{ mm}$) were removed, and the peat matrix including the fibric, hemic, and sapric fractions was homogenized with a blender (Amador and Jones 1993). A composite batch of all material was created, from which 24 sub-samples (~3.5 g dry soil) were measured for wet-dry weight conversion and

bulk properties; five sub-samples were analyzed for total soil C, N, P concentrations (Table 5.1).

Table 5.1. Mean ($\pm 1SE$) pre-treatment soil characteristics after wet homogenization. Ratios are expressed based on %.

Parameter	Mean ($\pm 1SE$)
pH	5.6 (0.2)
water content (%)	93.4 (0.001)
dry bulk density ($g\ cm^{-3}$)	0.072 (0.001)
organic density ($g\ cm^{-3}$)	0.064(0.004)
mineral density ($g\ cm^{-3}$)	0.007(0.001)
specific gravity	1.4 (0.08)
C (%)	42.1 (0.3)
N (%)	2.08 (0.14)
P (%)	0.126 (0.015)
C:N	20.2 (1.1)
C:P	334 (15)
N:P	16.5 (0.9)

Thirty-six flasks (250ml I-CHEM Certified TM Septa-jars) were filled with 57.8 ± 0.6 g of homogenized soil organic matter at field moisture (water content= $93.4 \pm 0.001\%$) followed by the addition of 40 ml of de-ionized water. This resulted in about 190 ml of headspace. To be fairly representative of field conditions, a ‘low oxygen’ headspace environment was created with He-evacuation for four minutes for each flask. Flasks were stored in the dark under laboratory temperatures ($22-24^{\circ}C$) for 48 hours prior to treatment application. Following this 2-day acclimation period, treatments were applied to each flask and re-purged with He. Following treatment application, pH among the treatments was similar (5.5 ± 0.3) so no adjustments were made. Treatment application marked time zero. Samples were removed from the flasks and analyzed at day 0, 1, 2, 3, 4, 5, 6, 14 and 28 days.

Flasks were gently shaken for two minutes prior to headspace sampling. A 0.5 ml sample was withdrawn and injected into the gas chromatograph (Tremetrics 9001). The sample volume removed from the flask headspace was replenished with He. CO₂ and CH₄ were detected by flame ionization, and CO₂ was converted to CH₄ with a methanizer. Gas standards (Scott Specialty Gases, Plumsteadville, PA) were run in triplicate at four concentrations that spanned the range of sample concentrations. Peak analysis software (EZ Chrom, Scientific Software, Inc. San Ramon, CA) was used to compute gas concentrations. At the end of the experiment, headspace was estimated for each sample flask by addition of water.

Treatment concentrations for N and P represented control, ‘moderate’ and ‘high’ loading conditions (Table 5.2). The low (20 mg l⁻¹) and high (200 mg l⁻¹) SO₄⁻ treatments

Table 5.2. Nutrient amendment treatment combinations and target nutrient concentrations (mg l⁻¹, mM) of NH₄, PO₄³⁻, and SO₄²⁻. All treatments received a total of 100 mg l⁻¹ of salts. Controls received all NaCl, and the other treatments received ‘nutrient’ salts or the balance as NaCl.

Level	Treatment*			
	N	P	N + P	S
control	--	--	--	--
1	10, 0.714	0.5, 0.016	10 + 0.5	20, 0.2
2	100, 7.14	5.0, 0.16	100 + 5.0	200, 2.0

simulate the concentration in North American rivers (Schlesinger 1997) or that associated with a 3 ppt marine saltwater pulse. Target nutrient concentrations were determined with a dilution equation:

$$M_i V_i = M_f (V_f + \text{ml H}_2\text{O soil})$$

M_i = initial molarity of solute
V_i = volume of solute to be added

M_f = final molarity of solution
 V_f = final molarity of solution
 ml H₂O soil

To prevent any differential physical degassing or ‘salting-out’ of gases, all treatments received 100 mg l⁻¹ of salts; that is, controls received all NaCl, and the treatments received the appropriate portion of NaCl in addition to the N, P, and S nutrient salts (NH₄Cl, Na₂HPO₄, Na₂SO₄).

Prior to statistical analysis, gas concentrations were transformed (natural logarithm) to approach normality. Cumulative mean CO₂, CH₄, and CO₂+CH₄ concentration was analyzed with a repeated measures ANOVA (PROC MIXED, SAS version 9.0, Cary NC) with contrasts of each treatment to the control over the entire 28 days. A Toeplitz estimate of the covariance structure was used. Significant differences among all the means contrasts were adjusted (Dunnett) for protection at $\alpha=0.05$.

RESULTS

Only the sulfate treatments resulted in elevated pH by the end of the experiment, otherwise all other treatments remained similar to the controls (Table 5.3).

Table 5.3. Mean (± 1 SE) soil pH by treatment at the end of the 28 day respiration experiment.

Treatment	Ending pH
Control	5.68 (0.30)
N1	5.73 (0.30)
N2	5.56 (0.17)
P1	5.71 (0.05)
P2	5.75 (0.06)
N1P1	5.64 (0.08)
N2P2	5.52 (0.02)
S1	6.08 (0.10)
S2	6.80 (0.08)

Treatment mean concentrations of CO₂, CH₄, and CO₂ + CH₄ (total C) evolved were significant in the repeated measures model, as was time (Table 5.4). CO₂ evolution had a non-significant interaction of treatment-time (Table 5.4). The time course of total C, CO₂, and CH₄ are shown in Figs. 5.1, 5.2, and 5.3, respectively. All treatments produced enhanced CO₂ respiration compared to controls for most of the experiment until the last sampling (day 28), when a return to control levels was observed (Fig. 5.2). In the controls, CO₂ respiration reached its maximum after day six, and this was generally similar among treatments. In contrast, CH₄ concentrations were treatment and time dependent throughout the course of the experiment (Fig. 5.3). Appreciable CH₄ production did not occur until day three (Fig. 5.3).

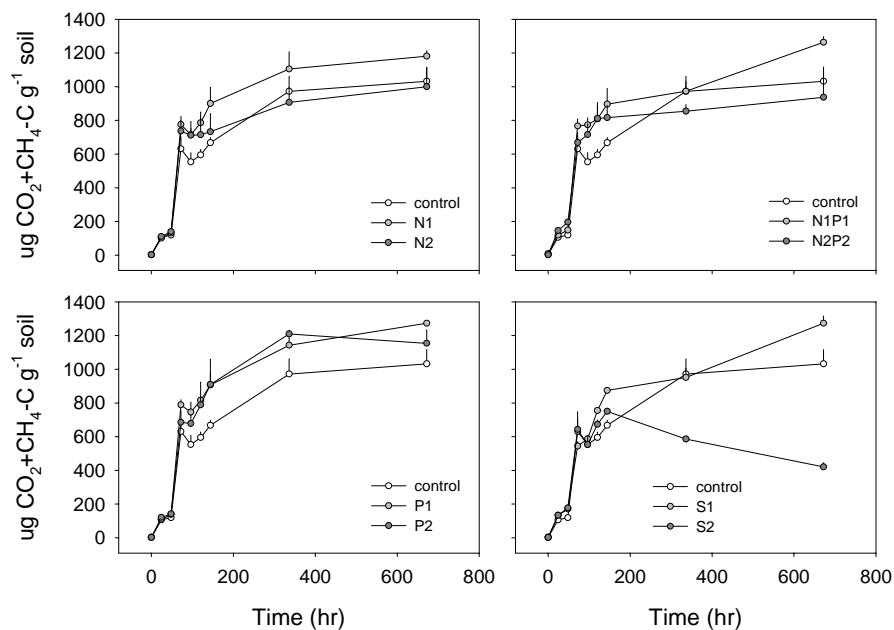


Figure 5.1. Mean (± 1 SE) cumulative CO₂+CH₄ concentration over the 28 day respiration experiment.

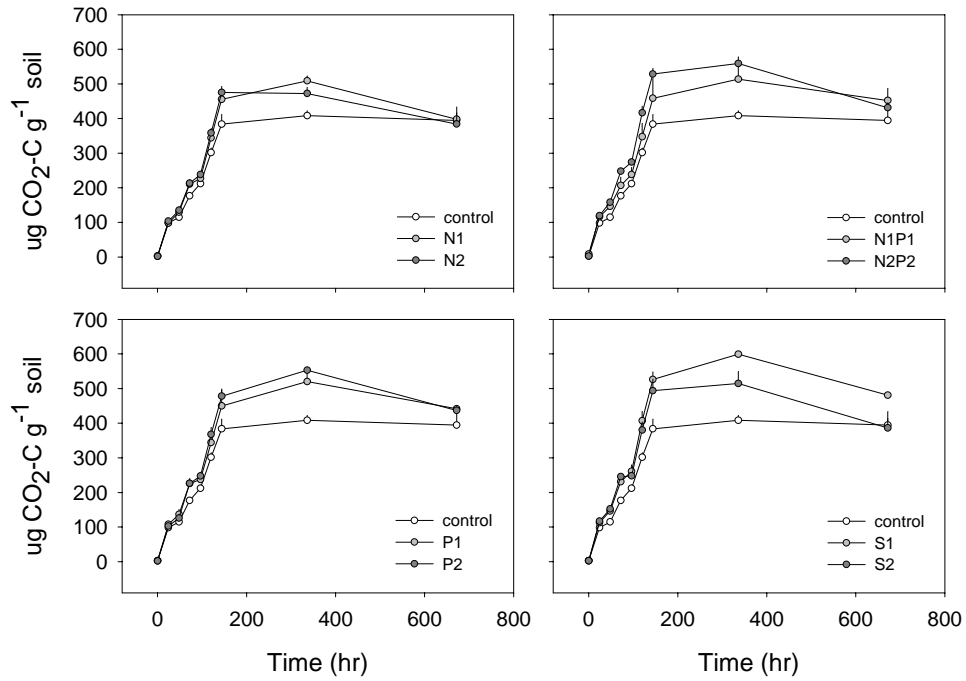


Figure 5.2. Mean (± 1 SE) cumulative CO₂ concentration over the 28 day respiration experiment.

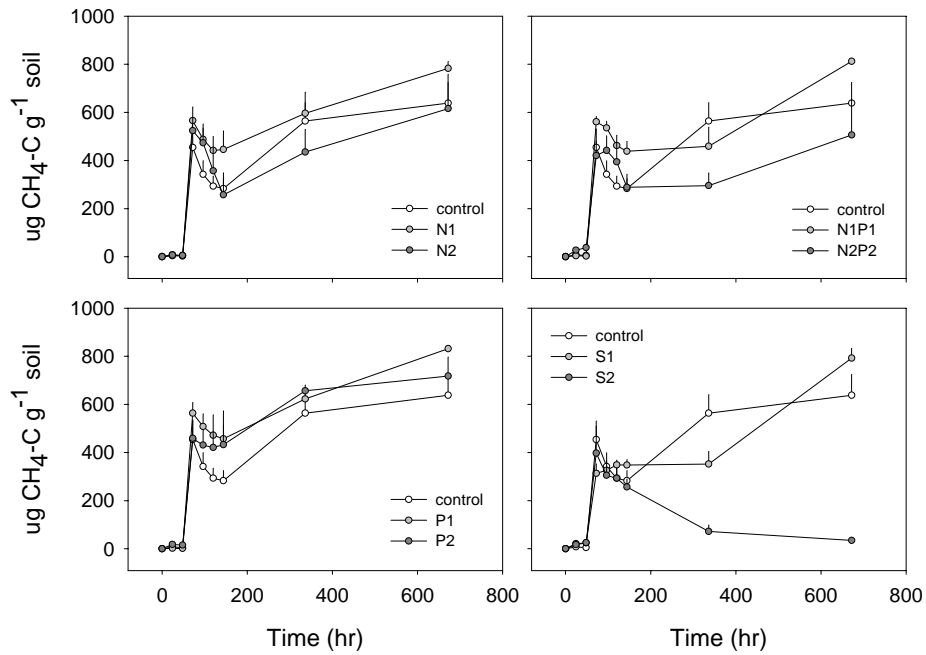


Figure 5.3. Mean (± 1 SE) cumulative CH₄ concentration over the 28 day respiration experiment.

The effect of the low ammonium (N1) addition on total C concentration was significantly greater than the control by $22\pm 5\%$, with a greater contribution from CH_4 than CO_2 (Table 5.5, Fig. 5.4). A similar relationship was observed at the low ammonium and low phosphorus (N1P1) treatment (Table 5.5, Fig. 5.4). At high levels of ammonium (N2), CO_2 production was significantly different from controls by $14\pm 4\%$ (Table 5.5, Fig. 5.4), but with time, N2 actually resulted in a decrease of CH_4 compared to controls (Fig. 5.3). Although N2P2 resulted in significantly higher CO_2 concentrations than controls ($31\pm 4\%$), it also decreased CH_4 concentrations with time (Fig. 5.3). At both N2 and N2P2, cumulative CH_4 concentration was not different than the controls.

Table 5.4. Repeated measures ANOVA probabilities of mean cumulative carbon respiration ($\mu\text{g C g}^{-1}$ soil) over the 28 day respiration experiment.

	Num df	Den df	$\text{CO}_2 + \text{CH}_4$	CO_2	CH_4
treatment	8	162	<.0001	<.0001	<.0001
time	8	162	<.0001	<.0001	<.0001
trt*time	64	162	<.0001	0.0955	<.0001

At both levels of phosphorus addition (P1, P2), total C concentrations were significantly higher than the controls. At the P1 level, CH_4 was stimulated more than at the P2 level, and the opposite was true for CO_2 (Fig. 5.4). The highest mean concentration of CO_2 was observed at the lowest sulfate level (S1) and this difference was significant, but CH_4 concentration with low sulfate was not different from controls (Fig. 5.4). Although the highest sulfate level (S2) produced significantly more CO_2 than controls, it also significantly decreased CH_4 concentrations by $46\pm 4\%$ compared to controls (Table 5.5, Fig. 5.4).

Table 5.5. Least squares means of cumulative carbon respiration, mean difference from control (MDC), and significance contrasts between treatment to control means based on a repeated measures ANOVA and Dunnett's adjusted probability.

Treatment	CO ₂ + CH ₄ (ug C g ⁻¹ soil)				CO ₂ (ug C g ⁻¹ soil)				CH ₄ (ug C g ⁻¹ soil)			
	Mean (SE=19)	MDC (SE=27)	% (SE=5)	Pr > t	Mean (SE=6)	MDC (SE=9)	% (SE=4)	Pr > t	Mean (SE=18)	MDC (SE=26)	% (SE=9)	Pr > t
Control	520				233				287			
N1	633	113	22	0.0003	264	31	13	0.0049	370	82	29	0.0116
N1P1	640	120	23	0.0001	276	44	19	<0.0001	364	76	27	0.0230
N2	562	42	8	0.5063	265	32	14	0.0034	297	10	3	0.9997
N2P2	572	52	10	0.2693	304	72	31	<0.0001	268	-20	-7	0.9711
P1	658	138	27	<0.0001	274	41	18	<0.0001	384	97	34	0.0017
P2	633	112	22	0.0004	282	50	21	<0.0001	350	63	22	0.0910
S1	588	68	13	0.0728	307	75	32	<0.0001	281	-7	-2	1.0000
S2	438	-82	-16	0.0179	282	50	21	<0.0001	156	-132	-46	<0.0001

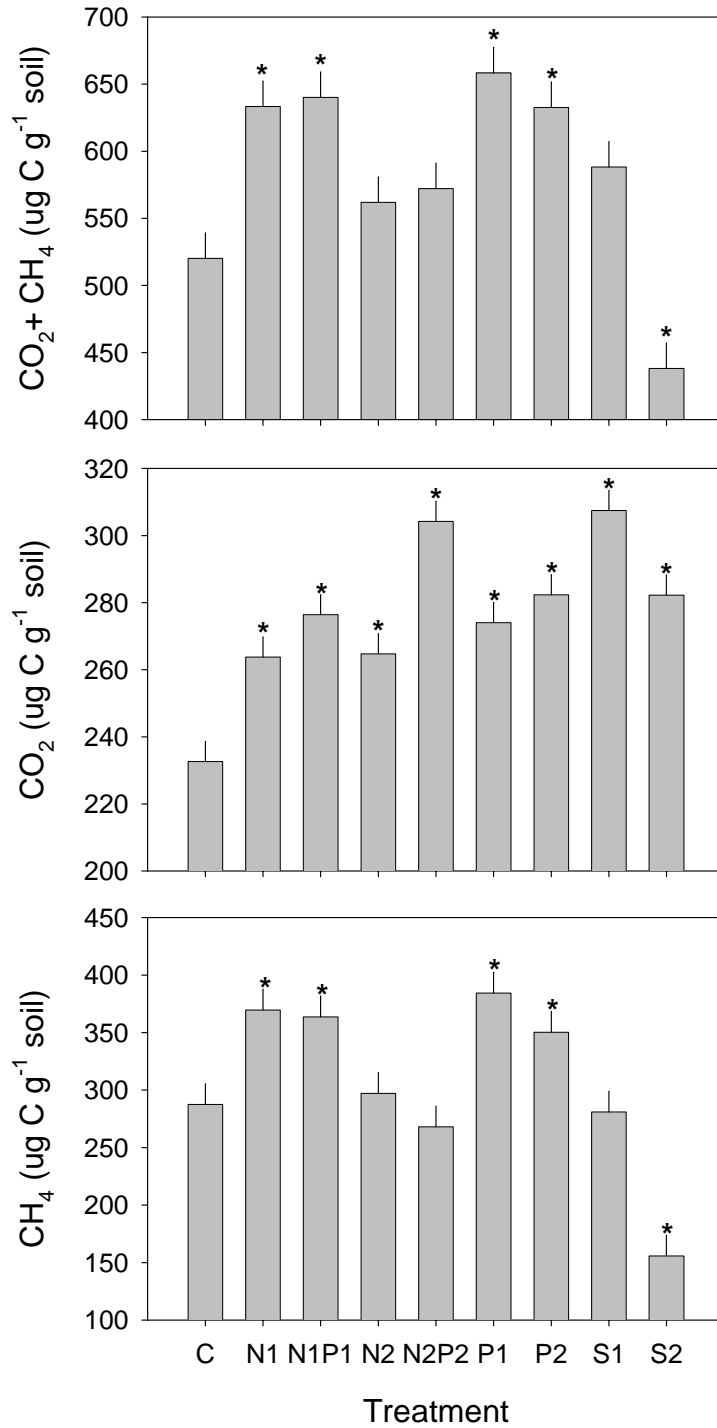


Figure 5.4. Statistical summary of the differences in mean cumulative CO₂+ CH₄, CO₂, and CH₄, evolved over the 28 day experiment by treatment. *Indicates significant differences at the $\alpha=0.05$ (Dunnett's adjusted P) compared to the control.

Total C respiration at the highest sulfate treatment resulted in a $16 \pm 5\%$ decrease compared to controls. The cumulative amount of CH₄ evolved relative to CO₂ was about equal for the controls (Table 5.6), and this relationship was similar for N1, N1P1, P1 and P2. A reduction of CH₄ relative to CO₂ (<1.00) evolution occurred in the N2, N2P2, S1, and S2 treatments.

Table 5.6. Ratio of mean (± 1 SE) cumulative CH₄:CO₂ (mass) by treatment over the 28 day respiration experiment.

Treatment	CH ₄ : CO ₂ (± 1 SE)
Control	1.02 (0.18)
N1	1.16 (0.19)
N1P1	1.13 (0.19)
N2	0.97 (0.18)
N2P2	0.78 (0.12)
P1	1.13 (0.18)
P2	1.01 (0.15)
S1	0.76 (0.11)
S2	0.53 (0.12)

DISCUSSION

An interesting finding of this experiment was that overall C production was enhanced with both N and P additions, but the combination of these two nutrients and their concentration altered the type of C respiration. The lowest level of N alone or in combination with the lowest level of P significantly increased total C respiration, and this was not true for high N alone or in combination with high P. Although there was a stimulatory effect on CO₂ respiration, CH₄ respiration was limited at any high N treatment. High ammonium levels are known to stimulate the growth and activity of methane oxidizing bacteria, but the presence of these bacteria have been associated with

the root zone of rice plants (Bodelier 2000). Updegraff et al. (2001) suggested that the stimulation of methanotrophs rather than the direct inhibition of methanogens by elevated ammonium may explain the negative relationship they observed between pore-water ammonium and methane production in temperate fens.

The increase in CO₂ respiration with P additions to P-deficient soils has been demonstrated for peat soils of the Florida Everglades (Amador and Jones 1993). The similar observation in this study is interesting because C:P concentrations of the Louisiana peat soil (355) is similar to that of P-polluted soils (236) in the Florida study, where the authors observed no increase in CO₂ evolution with increased P additions. The C:P of 'pristine' Everglades peat is over 2050 (Amador and Jones 1993). The N:P ratio of this floating marsh soil (16.5) was similar to that of the P-polluted Everglades soil (16.9). Further, tissue nutrient signatures of the dominant vegetation collected at the Louisiana site over three years consistently indicated N-limited productivity (Chapter 2). There is support, however, that wetland microbial communities can be limited by P even when the emergent plant community is N limited (Sundareshwar et al. 2003). P-limited decomposition of soils with C:P ratios >200 (Louisiana peat C:P=355) has also been demonstrated (Brinson 1977).

The enhanced CO₂ respiration associated with sulfate addition was expected given the greater energy yield to sulfate reducing bacteria (Lovely and Klug 1986). In contrast to the highest sulfate treatment, methane inhibition at the lowest treatment was not observed. Results from this study agree with other findings that methane oxidation in freshwater systems may occur at sulfate concentrations greater than 0.5 mM but not less than 0.2 mM (see Segers 1998). The low and high levels of sulfate exposure in this

experiment were equivalent to concentrations found in North American rivers (Schlesinger 1997) or a low level marine saltwater pulse (~3 ppt), respectively. In addition to increased CO₂ respiration, sulfate pollution to peat soils deficient in mineral sediments may mediate the release of phosphorus (Lamers et al. 2001) or stimulate the activity of microbial assemblages that are capable of complete organic matter oxidation (Castro et al. 2005).

CONCLUSIONS

Amendments of N, P, N+P, and S to Louisiana peat soils resulted in significant increases of CO₂ respiration for all treatments compared to the control. CH₄ respiration was co-limited by N and P, except at high levels of N. Methane oxidizing bacteria may be stimulated at high ammonium concentrations. High sulfate concentrations resulted in a significant decrease in CH₄ respiration, while enhancing CO₂ respiration. Peat soils may be subject to increased C loss with nutrient pollution. Although the plant community where these soils were collected indicated N-limitation, both N and P limited the activity of the microbes.

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